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with a monographic revision of North American taxa

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MORPHOLOGY, EVOLUTION, AND HOST ASSOCIATIONS OF BEE-ASSOCIATED MITES OF THE FAMILY CHAETODACTYLIDAE (ACARI: ASTIGMATA) WITH A MONOGRAPHIC REVISION OF NORTH AMERICAN TAXA

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CONTENTS

PAGE

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ABSTRACT

A detailed comparative analysis of the external morphological structures of feeding instars and heteromorphic deutonymphs of the mite family Chaetodactylidae was conducted. Several important diagnostic characters were identified for the gnathosoma (feeding instars), reproductive system (males, females), attachment organ (deutonymphs), coxisternal region, and legs, including ambulacra.

Chaetodactylids are probably unique in the presence of ventral trochanteral levators I-II. These muscles are attached to the proximal portions of posterior apodeme II and anterior apodeme III, respectively and operate as synergists of the dorsal trochanteral levators.

The ambulacra play an important role in mite locomotion and especially in the attachment to the host setae (deutonymphs). In the latter case, the tarsus-apotele joint is monocondylar and the ambulacra can probably accomplish movements in different planes. The ambulacra of chaetodactylids are characterized by the underdevelopment of the depressor/protractor muscle. It is hypothesized that the condylophores (adults) and the dorsal folds of the caruncle (deutonymphs) may accumulate and release recoil energy and, therefore, compensate for the loss. Models for claw-pretarsus movements are proposed for both adults and phoretic heteromorphic deutonymphs.

The postembryonic ontogeny of chaetodactylids is a complex mechanism combining developmental and adaptive features with evolutionary constraints. Deutonymphal dimorphism in *Chaetodactylus* and the presence of three developmental pathways (-protonymph-tritonymph-, -protonymph-phoretic heteromorphic deutonymph-tritonymph-, and -protonymph-inert heteromorphic deutonymph-tritonymph-) are conspicuous features of chaetodactylids, which are also known for a few other families of Astigmata. Male dimorphism is known only for *Roubikia*. Ontogenetic transformations of chaetodactylids superimposed on their phylogeny imply that structural reductions are an essential evolutionary mechanism within Chaetodactylidae. They are probably irreversible, thus capable of channeling further pathways of morphological evolution.

Biological adaptations of chaetodactylids to their bee hosts are discussed. In certain instances these adaptations are reciprocal. For the first time we describe metasomal acarinaria (special pouches for mite transfer) in some Neotropical *Ceratina* and *Tetrapedia*. We also report phoresy of *Sennertia* (*Spinosennertia*) in the genital acarinarium of females of *Xylocopa* (*Neoxylocopa*). In contrast to the majority of chaetodactylids that are phoretic as heteromorphic deutonymphs, species of the newly described *Sennertia vaga* group disperse as feeding instars on adult bees. The deutonymphal instar is presumably suppressed, and feeding and reproducing may occur while dispersing. The hysterosomal pouch in *Sennertia hipposideros* and *S. koptorthosomae* contains fungal spores and is probably a sporotheca.

Phylogenetic relationships among putative chaetodactylid genera and subgenera were reconstructed using Bayesian and maximum parsimony analyses. The results were used to analyze historical biogeography and host associations. Biogeographic analysis in DIVA supports the hypothesis of a post-Gondwanan origin of chaetodactylids, prior to the late Eocene. The most probable center of origin is the Neotropical region.

Historical associations of major lineages of chaetodactylid mites and long-tongued bees display a strong and significant departure from a random pattern. Early derivative mite taxa are associated with derived bee hosts and vice versa, suggesting the reverse interpretation of Fahrenholz's rule. In order to find the most optimal coevolutionary explanation in this system, we analyzed phylogenetically conserved association patterns through the exploration of cost space of four coevolutionary events (TreeFitter). The analysis revealed significant duplication-switching constraints. The results were compatible with other distance and topology-based coevolutionary methods (ParaFit, TreeMap2). We interpret this salient violation of Fahrenholz's rule in the light of dispersal ecology of mites and available biological data of their hosts. A logistic regression model fitted to several host characteristics affecting mite dispersal demonstrated that mass provisioning, solitary bees with nests built in wood and cells arranged in linear series are primarily involved in the associations. These features impact the ability of mites to disperse to new nests (by allowing brood cross-contamination) and constrain evolution and host shifts of

the mites.When applied to extant host and non-host bee lineages, the overall predictive power of the model was 82.1%, indicating that the host shifts have been influenced by the bee biology and nest architecture. Thus the strong negative correlation between phylogenies ('reverse codivergence') of chaetodactylids and long-tongues bees is probably caused by ecologically constrained sequential host shifts to distantly related hosts followed by colonization of related host groups.

Phylogenetic analyses of the genus *Chaetodactylus* showed recent multiple intercontinental dispersals and independent host shifts of speciose lineages distributed in temperate regions. In contrast, *Sennertia* probably has experienced only a limited number of intercontinental dispersals. Our preliminary phylogenetic analysis demonstates that New World clades originated within Old World lineages, probably tracing the ancient (34–34.6 Mya) dispersal of Old World *Xylocopa* to the New World (Leys *et al*., 2002). No other major intercontinental dispersal has occurred in this genus while host shifts were restricted to only two related genera, *Ceratina* and *Xylocopa*. We explain the two biogeographic patterns of *Sennertia* and *Chaetodactylus* by their host ranges and dispersing abilities of their hosts. Unlike *Chaetodactylus* from temperate regions, *Sennertia* and a few tropical lineages of *Chaetodactylus* are associated with bees that could not widely use northern intercontinental bridges for dispersal. The *Chaetodactylus ludwigi*-group is an exception. It has the broadest distribution among any group of chaetodactylids below the generic level: South America, Africa, India, Oceania, Australia, and the eastern Palaearctic (southern Japan). Close morphological similarities among its species suggest that this distribution is a consequence of transoceanic migrations as nests of their hosts may disperse in drifting wood.

Mutivariate analyses of cryptic species are conducted for 1) *Chaetodactylus* associated with *Osmia* (*Cephalosmia*); 2) *Chaetodactylus* associated with *Lithurgus* in North America, and 3) the *Sennertia frontalis* group associated with large carpenter bees, *Xylocopa* spp. in the New World. Computer assisted identification of these species based on the multivariate models is available at http://insects.ummz.lsa.umich.edu/beemites/Morphometrics.html.

The database containing interactive maps, pictures and host information on species of Chaetodactylidae and other tools are parts of a larger online project on bee-associated mites in North America available at http://insects.ummz.lsa.umich.edu/beemites.

The following descriptions of new taxa and taxonomic changes have resulted from this study: Eighteen new species are described: *Chaetodactylus antillarum* **sp. n.**; *Chaetodactylus furunculus* **sp. n.**; *Chaetodactylus kouboy* **sp. n.**; *Chaetodactylus azteca* **sp. n.**; *Chaetodactylus micheneri* **sp. n.**; *Chaetodactylus rozeni* **sp. n.**; *Chaetodactylus claudus* **sp. n.**; *Chaetodactylus hopliti* **sp. n.**; *Chaetodactylus zachvatkini* **sp. n.**; *Sennertia vaga* **sp. n.**; *Sennertia haustrifera* **sp. n.**; *Sennertia recondita* **sp. n.**; *Sennertia sodalis* **sp. n.**; *Sennertia hurdi* **sp. n.**; *Sennertia lucrosa* **sp. n.**; *Sennertia segnis* **sp. n.**; *Sennertia pirata* **sp. n.**; *Sennertia loricata* **sp. n.** *Afrosennertia* Fain, 1981 is considered senior synonym of *Asiosennertia* Fain, 1981, **syn. n**.; *Sennertia* Oudemans, 1905 is considered senior synonym of *Eosennertia* Kurosa, 2005. The following new combinations are proposed: *Achaetodactylus leleupi* (Fain, 1974), **comb. n**. (from *Chaetodactylus*), *Sennertia antarctica* (Trägårdh, 1907), **comb. n.** (from *Trichotarsus*). The following synonymies of species-group names are established: *Chaetodactylus birulai* Zachvatkin, 1941 (=*Chaetodactylus poetae* Samšiňák, 1973, **syn. n.**), *Chaetodactylus chrysidis* Fain and Baugnée, 1996 (=*Ch. chrysidis aurulenticola* Fain and Baugnée, 1996, **syn. n.**; *Sennertia delfinadoae* Fain, 1981 (=*Sennertia bakeri* Ramaraju and Mohanasundaram, 2001, **syn. n.**); *Sennertia robusta* Delfinado and Baker, 1976 (=*Sennertia carpenteri* Ramaraju, Mohanasundaram, 2001, **syn. n.**). Lectotypes are designated for the following species: *Chaetodactylus birulai* Zachvatkin, 1941; *Sennertia potanini* Zachvatkin, 1941; *Sennertia zhelochovtsevi* Zachvatkin, 1941.

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INTRODUCTION

The mite family Chaetodactylidae includes 5 genera more than 112 species distributed worldwide, except for Antarctica. This diverse group comprises obligate associates of long-tongued bees and has developed striking morphological, developmental, and biological adaptations to its hosts. The mites live in nests of bees as mutualists (feeding on nest waste), parasitoids (killing the bee egg or larvae), commensals or cleptoparasites (feeding on provisioned pollen) (Roubik, 1987; Krombein, 1962; Qu *et al*., 2002). Some parasitoids and cleptoparasites cause substantial damage to managed colonies of mason bees used as commercial pollinators (Bosch, 1992; Fain, 1966; Kurosa, 1987).

Chaetodactylids disperse as heteromorphic deutonymphs on the adult insects, and the life cycles of the mites and their hosts are usually synchronized. In the *Sennertia vaga* group (described herein), the deutonymph is probably lost and the mites disperse as feeding instars on adults of large carpenter bees. This group is unusual among astigmatid mites in that reproduction and feeding may occur during dispersal.

At least some species of the genus *Chaetodactylus* are able to produce morphologically regressive, non-phoretic, heteromorphic deutonymphs. These remain in the nest cavity to infest a new generation of cells when the cavity is re-used.

Most chaetodactylids are oligoxenous, utilizing several closely related hosts. Monophyletic groups of mites are often restricted to monophyletic groups of bees, suggesting that they may share common evolutionary histories. Several bee species of the genera *Tetrapedia*, *Ceratina* and *Xylocopa* have even developed special pouches for mite transfer (acarinaria), indicating possible mutualistic relationships or means to limit damage by mites (Klimov *et al*., 2007b).

Despite the importance of mites of this family for coevolutionary and ecological studies and as pests of economically important pollinators, their systematics, host associations, and biology are poorly known. In the United States, aside from the species recently described by us (Klimov & OConnor, 2004; Klimov & OConnor, 2007; Klimov *et al*., 2007b), only two nominal species were known, and the taxonomic status of one of them is uncertain. Central and South America, the probable center of origin of the family (Klimov & OConnor, 2007), are characterized by an exceptional concentration of endemic lineages of mites and their hosts, however, only 10 species of chaetodactylids have been described (Alzuet & Abrahamovich, 1987, 1989, 1990; Baker & Delfinado-Baker, 1983; Baker *et al*., 1987; Delfinado & Baker, 1976; Fain, 1971; OConnor, 1993a; Turk, 1948; Vitzthum, 1941).

The scope of this work is to revise the chaetodactylid mites of the World from the level of family to species group and to revise the North American taxa at the species level. For three genera (*Centriacarus*, *Roubikia*, and *Chaetodactylus*), we compile keys to species of the World. For the largest genus, *Sennertia*, only a key to species of the New World is presented since many species from the Old World are undescribed or in need of revision. This monograph is an attempt to combine the traditional taxonomic approach and modern bioinformatic tools in a revisionary study of this biologically and economically important group.

Phylogenetic relationships of Chaetodactylidae were reconstructed using morphological data in PAUP* 4.0b10 (maximum parsimony) and MrBayes 3.1.1 (Bayesian analysis). Historical biogeography and host associations were analyzed in DIVA, TreeFitter, Tree Map 2.0, and ParaFit, and the results were used to explain various biogeographic and coevolutionary phenomena. A logistic regression model is used to explain the distribution of chaetodactylid mites across bee taxa and predict their presence depending on certain biological and nest architecture characteristics. Linear and non-linear multivariate morphometrics were employed to resolve complexes of cryptic species, a major obstacle in chaetodactylid systematics. Multivariate classification models are incorporated in formal descriptions and keys and some are verified using gene sequence data. Automatic classification of unknown specimens based on these models can be accomplished online at our web site.

In addition to the static data published in the monograph, taxonomic and geographic information, as well as host records, have been compiled in a continuously updated, searchable, online database. Spatial data can be automatically plotted on internal or external maps using simple and complex queries. Geographic distribution of any species described in the monograph is supplied with a link allowing automatic generation of an interactive map based on the online data. Finally, color photographs documenting the distribution of mites on the host body are linked to respective records of the database. The database and other tools are parts of a larger online project on bee-associated mites in North America available at http://insects.ummz.lsa.umich.edu/beemites.

We hope that this monograph will be useful for beekeepers, bee and mite systematists and biologists as well as researchers interested in applying innovative bioinformatic approaches in their studies.

Materials and Methods

Mites were removed from freshly collected or preserved bees, cleared in Nesbitt's fluid and mounted in Hoyer's medium using uniform methodology (OConnor & Houck, 1991). The classification and nomenclature of bees follow Michener (2000) and Engel (2005). Species of *Xylocopa* follow Hurd & Moure (1963). Idiosomal chaetotaxy of mites follows Griffiths *et al*. (1990). The terminology of coxisternal setae follows Norton (1998). The leg chaeto- and solenidiotaxy follow Grandjean (1939). All measurements are in micrometers (μm). In descriptions, unique character states or their combinations are underlined. All host specimens are labelled with unique voucher numbers. Holotypes are deposited in museums housing the host bee specimens. Museum abbreviations are given in Appendix 8 (p. 223).

Methodology used in phylogenetic, coevolutionary, biogeographic, and morphometric analyses is explained separately in the corresponding sections.

THE FAMILY CHAETODACTYLIDAE IN NORTH AMERICA: A HISTORICAL OVERVIEW

In the first reports of chaetodactylid mites in North America, the mites were identified as European species. Osborn (1893) reported the European species "*Trichodactylus" xylocopae* for *Xylocopa varipuncta* (as *Xylocopa aeneipennis*) in California. Banks (1902) reported the same species (as *Trichotarsus xylocopae*, ex *Xylocopa*, California) along with another chaetodactylid which he identified as the European *"Trichotarsus" osmiae* (New York, ex *Osmia*). The latter species probably refers to either *Chaetodactylus krombeini* or *Ch. rozeni* sp. n., the only species associated with *Osmia* in the northeastern United States. *Trichodactylus xylocopae* sensu Osborn and Banks is probably *Sennertia lucrosa* sp. n. Nininger (1916) also reported this species, as *Trichotarsus* sp., from *Xylocopa varipuncta* and *Xylocopa tabaniformis orpifex* in California. He observed this mite in the bee nests destroying a small percentage of developing bee larvae. Zachvatkin (1941) mentioned the existence of several undescribed Nearctic species of *Chaetodactylus* in his monumental monograph on free-living Astigmata of the Palaearctic region. The first description of a North American species appeared in 1962. *Chaetodactylus krombeini* was described by Baker from *Osmia lignaria* from Maryland (Baker, 1962a). This description was followed by an extensive account on the biology of both the mite and its host (Krombein, 1962, 1967). In 1976, a second new species, *Sennertia americana*, associated with *Xylocopa virginica* was described from New York and Florida (Delfinado & Baker, 1976). Three other species were subsequently described from Central America: *Sennertia shimanukii* and *S. faini* from the honeybee, *Apis mellifera*, in Guatemala (Baker & Delfinado-Baker, 1983) and *Chaetodactylus panamensis* from a nest of *Tetrapedia* in Panama (Baker *et al*., 1987). Roubik (1987) gave a short account of the biology of this host and mite. OConnor (1993a) proposed a new genus, *Roubikia*, for *Ch. panamensis* and provided a phylogenetic framework for the chaetodactylid genera. Lindquist *et al*. (1979) recorded one species of *Chaetodactylus* for Canada, but unfortunately they did not specify the name of the species. They also estimated the potential number of *Chaetodactylus* species in Canada as 10, a probable overestimate based on our data. Krantz (1978) recorded *Ch. krombeini* from Oregon as the European species, *Chaetodactylus osmiae*, and Fain (1981) suggested that *Ch. krombeini* is probably a junior synonym of *Ch. claviger* described from the Mediterranean. Therefore the taxonomic status of this single nominal North American species of *Chaetodactylus* is uncertain. OConnor (1991) found an undescribed species of *Chaetodactylus* from northern Michigan (described here as *Ch. hopliti*). Haitlinger (1999) reported *Sennertia argentina* for Guatemala from a passalid beetle. Previously, this species had been described from Argentina in association with *Xylocopa frontalis'* and Haitlinger's record is probably based on contamination. Bosch & Kemp (2001) recognized *Ch. krombeini* as a serious pest of the blue orchard mason bee (*Osmia lignaria*) commercially bred in the United States as an alternative pollinator. Finally, three cryptic species of *Chaetodactylus* associated with North American *Lithurgus* were described by Klimov and OConnor (2004) using multivariate morphometrics.

EXTERNAL MORPHOLOGY

The body of chaetodactylid mites is subdivided by the circumcapitular furrow into the gnathosoma (bearing the mouthparts) and idiosoma (the rest of the body). No other distinct division of the body[2] is present.

Gnathosoma

Gnathosoma is an anterior part of the body separated by the circumcapitular furrow. In feeding instars it bears the first two pairs of appendages, the chelicerae, enclosed in the cheliceral frame, and the pedipalps, whose fused coxae form most of the subcapitulum, a complex inferior part of the gnathosoma. The gnathosoma is a pseudotagma, a division of the body that secondarily has become mobile (Hammen, 1989). The gnathosoma of heteromorphic deutonymphs is vestigial with chelicerae absent, and probably functions as a sensory organ. It may include free palpi each bearing a solenidion and seta (*Centriacarus*), or setae absent (*Chaetodactylus*), or palpi and setae absent (*Sennertia*), or palpi absent (*Roubikia*), or the entire gnathosoma and all its elements are completely absent (*Achaetodactylus*). Chaetodactylidae lack the basal part of the gnathosoma, which is present in many acariform deutonymphs. Nomenclature used to describe parts of the gnathosoma of feeding instars of chaetodactylids below is derived from works of Akimov (1985), Evans (1992), Grandjean (1957b), Knülle (1959), and Prasse (1967).

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[2] For divisions of the body, we use the terminology of Reuter (1909) and Reuter in Oudemans (1911b) accepted in many acarological works. Grandjean (1969) developed a new terminology and changed definitions of many previously used terms, *e.g.*, propodosoma *sensu* Reuter corresponds to propodosoma+aspidosoma *sensu* Grandjean.

Chelicerae

The chelicera is chelate. It comprises the ventral element, to which cheliceral retractors are attached, the body including the fixed digit, and the movable digit. The ventral element is delimited posteriorly by a distinct oblique sclerite. Anteriorly to the sclerite, there are two cuticular folds (*at*, *pt*) (Fig. 1 *C*) that probably represent insertion sites of two groups of tendons (*at*

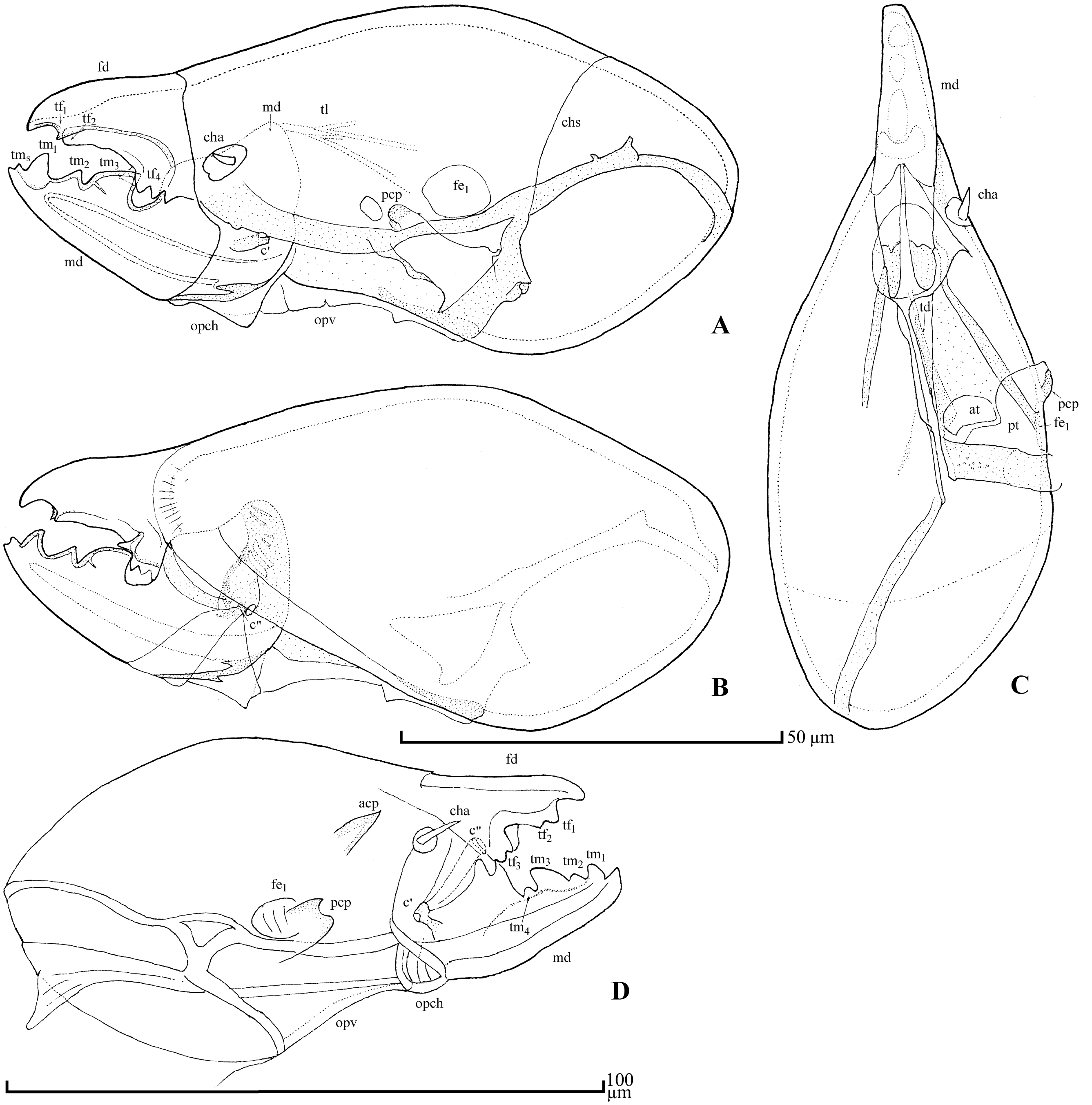

Fig. 1. Chelicera of Chaetodactylidae (males): *Chaetodactylus krombeini* (BMOC 98-1202-001) (A–C) and *Roubikia panamensis* (paratype) (D): A, D - paraxial view; B - antiaxial view; C - ventral view. **acp** - anterior cuticular process; **at** - antiaxial group of tendons; **chb** - posterior cheliceral setae; **chs** - cheliceral sheath ***c′***, ***c″*** - paraxial and antiaxial condyles for articulation of movable digit; fd - fixed digit of chelicera; **fe1** - fenestrate area of chelicera; **md** - movable digit of chelicera; **opch** - oncophysis of cheliceral body; **opv** - oncophysis of ventral element of chelicera; **pcp** - posterior cuticular process; **pt** - paraxial group of tendons; **tf1-4** - teeth of fixed digit; **td** - tendon of depressor muscle of movable digit; **tl** - tendon of levator muscle of movable digit; **tm1-3** - teeth of movable digit; **tms** - subapical tooth of movable digit.

and *pt*) (Fig. 1 *C*) described by Hammen (1989, Fig. 87 tf_i and tt_r). In Astigmata, unlike oribatid mites, these groups are not separated from each other.

The fixed digit is distinctly separated from the remaining part of the cheliceral body, with teeth arranged in two groups. The anterior group includes two teeth, situated close to each other, paraxial and antiaxial (tf'_1 and tf''_2) (Fig. 1 *A*, *B*). In *Sennertia* and *Chaetodactylus*, the latter forms a long, blade-shaped crown extending to the posterior group of teeth (Fig. 1 *A, B*). The crown is absent in *Roubikia* (Fig. 1 *D*). The posterior group is probably formed by only one strongly modified tooth (tf_3). Its body has one anterior antiaxial denticle oriented along the cheliceral axis (*Sennertia* and *Chaetodactylus*) or a vertical membranous lobe (*Roubikia*) and three posterior denticles oriented dorso-ventrally, like most other teeth (Fig. 1 *A,B,D*). Two anterior denticles (or one lobe and one denticle in *Roubikia*) form a cavity that corresponds to the third tooth of the movable digit (tm_3) (Fig. 1 *A,B,D*). In *Roubikia*, there is another tooth situated posterior to tm_3. The remaining part of the cheliceral body has a spiniform cheliceral seta *cha* situated paraxially at the base of the fixed digit (Fig. 1 *A,C,D*), membranous oncophyses (*opch* and *opv*) arising from the anterio-ventral part of the cheliceral body and covering the movable digit, anterior paraxial process *acp* (developed in *Roubikia*, absent in *Sennertia* and *Chaetodactylus*) (Fig. 1 *D*), posterior paraxial cuticular fold *pcp* (Akimov, 1985, *fc*) positionally homologous with Trägårdth's organ of oribatid mites (Fig. 1 *A, C,D*), fenestrate area fe_1 accompanying the process posteriorly (Fig. 1 *A, D*), and a distinct transverse line of attachment of the cheliceral sheath *chs* (Fig. 1 *A*). The homology of the cheliceral seta with *cha* (Grandjean, 1947) of oribatids is based on the distribution of cheliceral setae in the acarid genus *Viedebanttia*: paraxial seta (*cha*) and longer and more distal antiaxial seta (*chb*). The posterior paraxial cuticular fold *pcp* is weakly (*Chaetodactylus*, *Sennertia*) or moderately sclerotized (*Roubikia*) (Fig. 1 *A,B,D*). In *Roubikia*, the fenestrate area fe_1 is vertically striated, as in *Glycyphagus* (Akimov, 1985); in *Chaetodactylus* and *Sennertia* such striation is absent (Fig. 1 *A,B,D*).

The movable digit has three large teeth that are regularly present in other Astigmata (tm_1-tm_3) and a small subapical tooth (Fig. 1 *A,B*). The latter may be absent (*Ch. osmiae*). The movable digit is articulated to the cheliceral body by two condyles (c', c''). Two tendons of the levator (*tl*) and depressor muscles (*td*) are inserted at the posterior end of the movable digit. The latter is usually visible only ventrally (Fig. 1 *C*).

Subcapitulum

The external walls of the subcapitulum comprise fused palp coxae (see below), free palpi, and the malapophyses. The external walls are connected dorsally by the subcheliceral plate. The ventral wall is formed by the fused malapophyses, lateral lips, mentum, and rutellum. The mouth is slit-like, bordered by the fused lateral lips and the labrum and extends posteriorly to the pharynx. The preoral cavity is anterior to the mouth and flanked by the cheliceral grooves. Palpal supracoxal setae *e* are absent from the chaetodactylid subcapitulum.

Free palpi are articulated to the lateral part of the subcapitulum and comprise two distinct sections. According to Norton (1998), the palp tarsus and tibia are fused dorsally and the dorsal articulation posterior to the lyrifissure is secondary, while the ventral part of this articulation represents a true tarso-tibial articulation. Hammen (1989) believed that this is a true tarso-tibial articulation, following a fused genu-tibia. Zachvatkin (1953) and Knülle (1959) considered the whole articulation as secondary. The latter opinion is probably correct because in the relatively early derivative astigmatid genus *Megacanestrinia* (Canestriniidae), there is another articulation that is situated proximal to the tarsal lyrifissure that probably represents the true tarso-tibial articulation.

Thus, distinguishable pedipalps include at least tarsus and tibia. According to Hammen (1989) they also may include the genu. Zachvatkin (1953), based on outgroup comparison (*Epilohmannia*) and trends in palpomere fusion in oribatid mites, believed that the free astigmatid palps comprise all five ancestral palpomeres. The distal section of the palps has two distinct sensilla: a cylindrical, latero-terminal sensillum and a ventro-terminal sensillum that is spherically widened at apex (the spherical external part is continuous with cylindrical internal part that is deeply inserted into cuticle and usually not visible). In some other Astigmata, there is a third, ancestrally dorso-terminal sensillum, which is smaller than the others (Evans, 1992; Wurst & Kovac, 2003). This sensillum is probably also present in chaetodactylids (*e.g.*, *Ch. osmiae*), but not easily seen under a light microscope. Conventionally, the latero-terminal sensillum is referred to as the palpal solenidion *ω* and the other two as eupathidial setae. However, because of the structural resemblance of the three sensilla, Wurst & Kovac (2003) considered all of them as solenidia. Oribatid mites have 2–4 eupathidial setae situated distally on the palp tarsus, and the single tarsal solenidion *ω*, unlike Astigmata, is dorso-medial (Evans, 1992). In Astigmata, the two eupathidia arise ventrally and dorsally and, based on outgroup comparison, are homologous to ul' and ul'', respectively (OConnor, 1981). Setae, positionally homologous to the culminal tarsal setae (*cm*) of oribatid mites (Grandjean, 1935), are situated on the above mentioned secondary articulation of the palps (*sda*). The presence of a lyrifissure posterior to seta *cm* is the ancestral condition for Astigmata. In Chaetodactylidae, these lyrifissures are absent. The proximal section of the free palp has two setae *d* and l''; (Fig. 2 *A*). The former seta is homologous with a tibial seta of oribatid mites, while the homology of the latter is dependent on the selection of oribatid taxa for outgroup comparison. Norton (1998) considered seta l'' as tibial (Malaconothridae), but Zachvatkin (1953) considered it as femoral (*Epilohmannia*). It should be mentioned that many setal notations of oribatids, which mostly are labels referring to organ placement, lose their positional meaning when applied to the astigmatid palps.

Subcheliceral plate. The plate is composed of three parts: labrum (projecting above and anterior to the mouth in the preoral cavity), cervix (situated above the pharynx, delimited

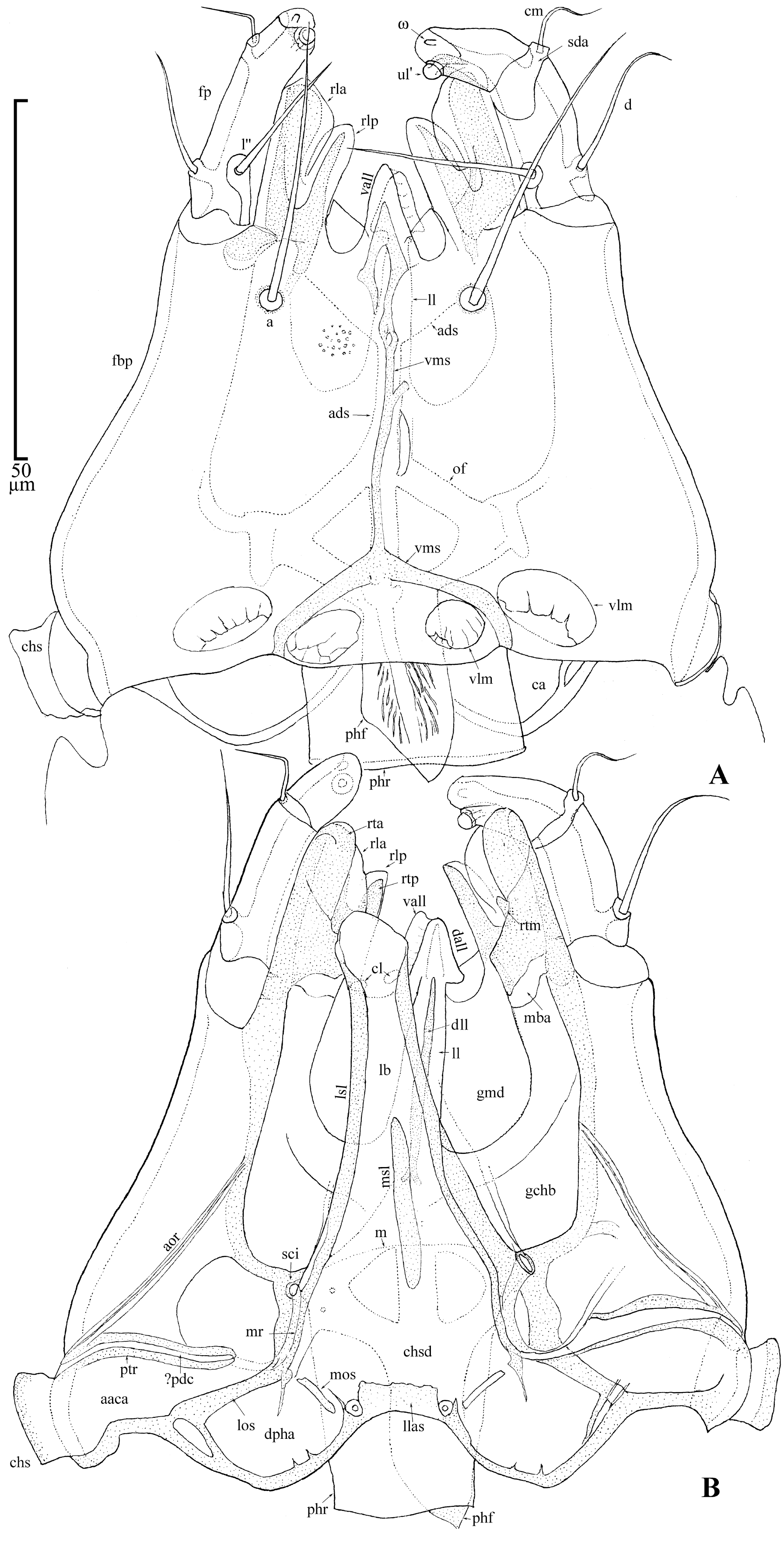

Fig. 2. *Chaetodactylus krombeini* (BMOC 98-1202-001), male gnathosoma. A - ventral view; B - dorsal view. **a** - subcapitular seta; **aaca** - antiaxial area of capitular apodeme; **ads** - adoral sclerite; **aor** - oblique anterior ridge of cervix; **chs** - cheliceral sheath; **chsd** - cheliceral saddle; **cl** - claspers of labrum; **cm** - culminal seta of palp tarsus; **d** - dorsal seta of palp tibia; **dall**-dorso-apical process of lateral lips; **dll** - dorsal sclerite of lateral lips; **dpha** - area of capitular apodeme delimited by dilators of pharynx; **fbp** - fused basal palpi; **fp** - free distal palpi; **gchb** - groove for cheliceral body; **gmd** - groove for movable digit of chelicera; **l''** - lateral seta of palp tibia; **lb** - labrum; **ll** - lateral lips; **llas** - labral levator attachment site (capitular apodeme); **los** - lateral oblique sclerite of capitular apodeme; **lsl** - lateral sclerite of labrum; **m** - mouth; **mba** - manubrial articulation; **mos** - medial oblique sclerite of capitular apodeme; **mr** - medial ridge of cervix; **msl** - medial sclerite of labrum; **of** - oral flaps of the pharyngeal floor; **pdc** - podocephalic canal; **phf** - pharyngeal floor; **phr** - pharyngeal roof; **ptr** - transverse posterior ridge of cervix; **rla**, **rlp** - antiaxial and paraxial rutellar lobes, respectively; **rta**, **rtm**, **rtp** - antiaxial, medial, and paraxial rutellar teeth, respectively; **sci** - superior commissural indurance; **sda** - secondary dorsal articulation of free palpi; **ul'** - ventral ultimal seta of palp tarsus; **vall** - ventro-apical process of lateral lips; **vlm** - areas formed by attachment sites of ventro-lateral muscles of pharynx; **vms** - ventro-medial subcapitular sclerite; *ω* - solenidion of palp tarsus.

posteriorly by a posterior, gutter-like border of the cheliceral sheath *ptr*), and subcapitular apodeme (posterior to the posterior cheliceral sheath border *ptr*).

The labrum *lb* is a long free anterior extension of the cervix and the dorsal wall of the pharynx (Fig. 2 *B*). It is smooth anteriorly and, unlike many Acaridae, does not have a proximal pectination or filtration apparatus serving for separation of solid food particles suspended in water (Akimov, 1979). The absence of these structures is well correlated with the diet of chaetodactylids, which principally feed on rather dry pollen inside enclosed bee cells. The labrum has one medial (*msl*) and two lateral sclerites (*lsl*); all these sclerites are free. The anterior end of the labrum is slightly widened and membranous. There is a pair of small ventral claspers (*cl*) at the base of the widening. Their function is unknown, but the shape of the anterior end of the lateral lips suggests that the claspers may join the anterior ends of the labrum and lateral lips when the former is depressed and the food is swallowed.

The cervix is the ventral floor of the cheliceral frame; it has distinct boundaries formed by oblique anterior (*aor*), medial (*mr*), and transverse posterior sclerotized cuticular ridges (*ptr*) corresponding to lines of attachment of the cheliceral sheath *chs* (Fig. 2 *B*). The ridges are represented by two parallel, well sclerotized, cuticular borders, between which a membranous cheliceral sheath is attached. In Chaetodactylidae, the anterior oblique ridge *aor* is well-developed, starts near the posterior transverse ridge *ptr* and extends anteriorly, meeting the internal wall of the palpcoxae (Fig. 2 *B*) (probably this is an autapomorphy for the family). In *Sancassania*, *Rhizoglyphus* (Acaridae), and *Glycyphagus* (Glycyphagidae), the anterior oblique ridge is probably absent. The position of the transverse posterior ridge *ptr* is probably constant in all Astigmata; it is distinctly wider than the anterior ridge and probably contains the podocephalic canal *pdc* (Fig. 2 *B*). The medial ridges of the cervix are continuous with lateral apodemes of the labrum (*lsl*). The capitular saddle *chsd* is situated between the medial ridges *mr*. Posteriorly it is delimited by the capitular apodeme *llas*, anteriorly it is continuous with the labrum *lb* (in *Rhizoglyphus* and *Sancassania* it is delimited by a transverse apodeme). Usually the capitular saddle is not visible as a distinct structure in dorso-ventrally mounted chaetodactylids, except for *Sennertia scutata*, where it looks like a tubercle between the chelicerae. In Astigmata, the capitular saddle serves as an attachment site for a median inter-cheliceral septum (Evans, 1992).

The capitular apodeme is divided into five parts by two pairs of oblique sclerites (*los*, *mos*) (Fig. 2 *B*) delimiting attachment sites for the ventral labral levators (median unpaired area *llas*) and pharyngeal dilators (two adjacent areas) (Prasse, 1967). Gnathosomal retractors arise from the dorsal surface of the capitular apodeme (Akimov, 1985). There are two paired antiaxial areas (*aaca*, *dpha*) that are probably not accompanied by muscles (Chaetodactylidae, *Glycyphagus*). These areas are small and indistinct in *Sancassania* and *Rhizoglyphus* because the areas of pharyngeal dilators are enlarged. Usually, the lateral oblique sclerites (*los*) are better developed than the medial oblique sclerites (*mos*). In chaetodactylids and *Glycyphagus*, the posterior-medial edge of the subcapitular apodeme (area of labral levators *llas*) is deeply concave.

The ventral wall of the subcapitulum ancestrally comprises the malapophyses (supposed endites of the palps), lateral lips, mentum, and rutellum. In Astigmata, these parts undergo fusion and form a single structure. The malapophyses are fused with the mentum (ventral surface of the subcapitulum posterior to the mouth) without any traces. The lateral lips (*ll*) are situated on the dorsal surface of the ventral wall anterior to the mouth (*m*) (Fig. 2 *B*). They are compressed laterally and fused to each other and to the malapophyses forming a ridge-like structure including three distinct sclerites. The ventral wall has a single pair of setae identified as m_1 (OConnor, 1981) or *a* of oribatids (Hammen, 1989). We provisionally accept the latter opinion because in some oribatid mites (*e.g.*, Malaconothridae, Epilohmanniidae), setae *a*, like in Astigmata, are situated more medially compared to setae *m* and the place of articulation of the free palpi. The posterior end of the subcapitulum has two pairs of rounded sigilae *vlm* (muscle attachment sites) on the cuticlule.

Lateral lips (*ll*) project ventrally from the anterior edge of the malapophyses as a pointed process (*vall*) and dorsally as an arrow-shaped process *dall* (Fig. 2 *A*, *B*, Fig. 3 *A*,*B*). The ventral process is accompanied by the ventro-medial sclerite (*vms*) and dorsally by the dorsal sclerite of the lateral lips (*dll*) (Fig. 2 *A*,*B*). The ventro-medial sclerite *vms* extends to the posterior end of the subcapitulum and bifurcates near it (Fig. 2 *A*). The bifurcation probably is not homologous to the labiogenal articulation of oribatid mites. It is very weakly developed in *Sancassania* and *Glycyphagus*. The dorsal process *dall* of the lateral lips is usually smooth but in *Sennertia scutata* it is distinctly transversely striated. The dorsal sclerite of the lateral lips *dll* (Fig. 2 *A*) is thin and does not reach the level of the mouth. There a third sclerite *ads*, probably homologous to the adoral sclerites of oribatids, arising as a bifurcated sclerotization near the anterior edge of the malapophyses and extending as two partially fused apodemes toward the mouth forming the pharyngeal floor *phf* (Fig. 3 *A*,*B*). The adoral and the ventro-medial sclerites (*ads*, *vms*) are fused at their anterior ends (Fig. 2 *A*).

Rutella are situated on the anterior edge of the ventral wall. In *Sennertia* and *Chaetodactylus*, they are formed of two membranous lobes and three dorsal teeth on each side of the subcapitulum. The two rutellar lobes are paraxial and antiaxial lobes, *rlp* and *rpa* respectively (Fig. 2, Fig. 3, Fig. 4 *A,B*). The paraxial lobe is always ventral, with an incorporated paraxial tooth (*rtp*) that looks like an internal sclerite. The antiaxial lobe is the largest in these two genera, forming the lateral and, along with the paraxial lobe, medial walls of the rutellum. The lobe forms distinct anterior edges or folds (Fig. 4 *B*) that give a false impression that it comprises multiple lobes but, in fact, represent its complex three-dimensional structure, including small secondary folds (*e.g.*, rla_v, rla_d). In *Roubikia*, the two lobes (*rlp* and *rpa*) are fused ventrally, and the paraxial lobe is

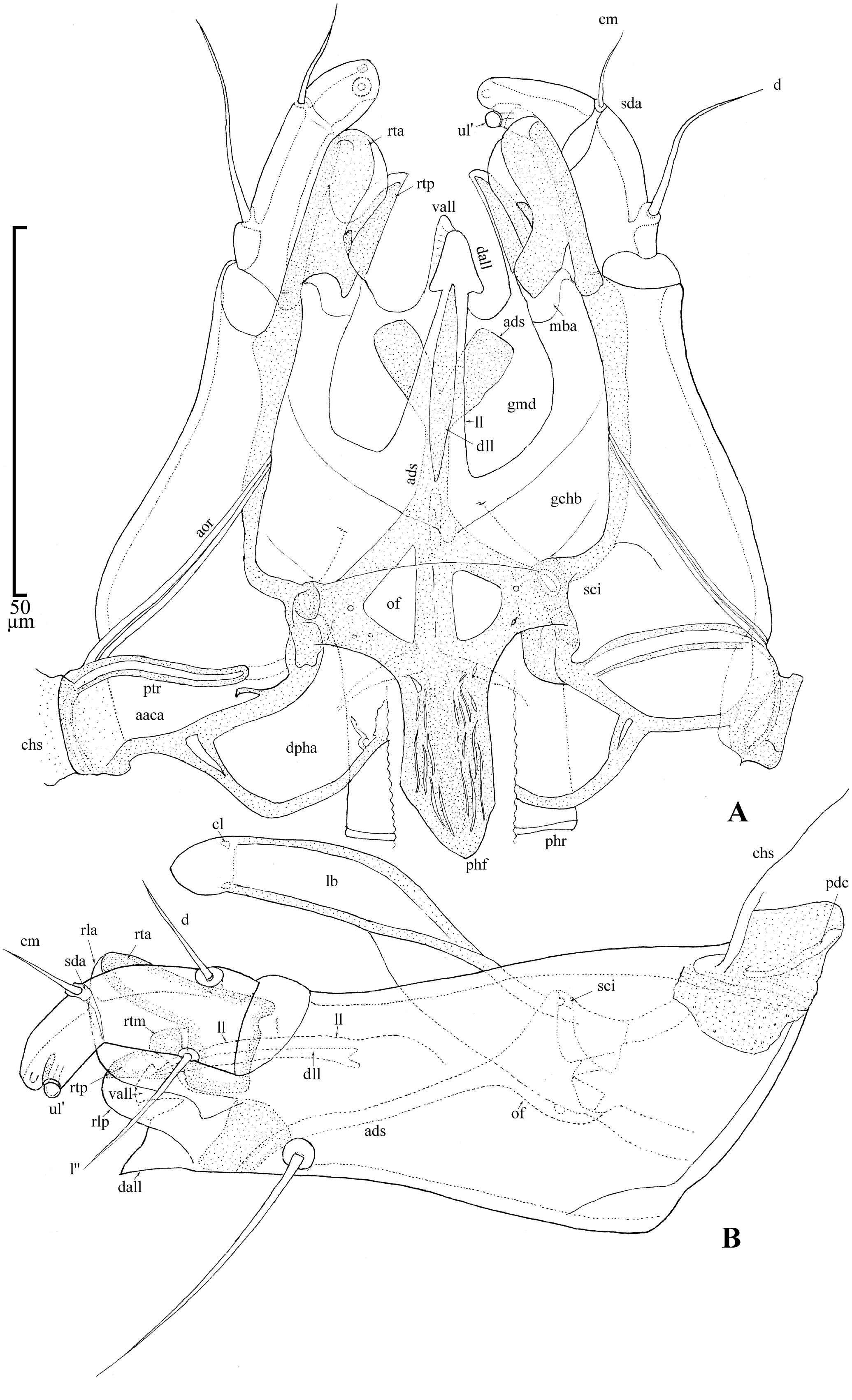

Fig. 3. *Chaetodactylus krombeini* (BMOC 98-1202-001), male gnathosoma. A - dorsal view, labrum removed; B - lateral view (proximal structures are distorted). Abbreviations as on Fig. 2.

Fig. 4. Rutellum (A–C) and subcapitulum (D) of adult chaetodactylid mites. A, B - *Chaetodactylus osmiae* (ex *Osmia rufa*, Belgium), ventral and dorsal view, respectively; C - *Roubikia panamensis* (paratype), ventral view; D - *Sennertia americana* (BMOC 82-0521-017), ventral view. Abbreviations as on Fig. 2.

distinct only dorsally (Fig. 4 *C*). The dorsal wall of the antiaxial lobe has two teeth and forms a longitudinal gutter. The two teeth include a large, lateral, antiaxial tooth (*rta*) and a smaller, medial tooth (*rtm*) situated ventrally with respect to the former (Fig. 2 *B*, Fig. 3 *B*, Fig. 4 *B*). The base of the antiaxial tooth extends ventrally as a short band covering a base of the medial tooth (Fig. 4 *A*). In *Roubikia*, the medial tooth is distinctly smaller (Fig. 4 *C*) than in *Chaetodactylus* and *Sennertia* (Fig. 4 *B*,*D*). Posterior to the antiaxial lobe, there is a distinct manubrial articulation *mba* (Fig. 2 *B*, Fig. 3 *A*). The two above-described rutellar lobes are also found in Canestriniidae, Heterocoptidae and some other astigmatid families. This condition is probably plesiomorphic for Astigmata. In Acaridae and, probably Glycyphagidae, the paraxial lobe is incorporated into the axial lobe, forming a single lobe (the two families are different in the structure and position of rutellar teeth, suggesting that the fusion may not be homologous). This may be an apomorphic condition, although Norton (1998), discussing the homology of this type of rutellum with rutella of oribatid mites, suggests the opposite. The rutella form the anterior part of the grooves *gmd* for movable digits of the chelicerae (Fig. 2 *B*, Fig. 3 *A*). The grooves extend into the subcapitulum. The lateral walls of the groove are distinct but not sclerotized (Fig. 2 *B*), unlike in *Megacanestrinia* where they are sclerotized.

The homology of the astigmatid rutellum is unclear (Akimov, 1985; Evans, 1992). Knülle (1959) considered it as an extension of malapophyses and therefore, not homologous to the rutellum of oribatid and Prostigmata mites, which has a setal origin. Based on the positional similarity and the presence of the manubrial articulation, OConnor (1984) and Norton (1998) believed that the structure is a derivative of the true rutellum that secondarily lost birefringence.

The pharynx is the portion of the fore-gut extending from the mouth to the esophagus. In transverse section, it appears as a wide, slit-like lumen formed by dorsal and ventral sclerites, the roof and the floor. The roof *phr* of the pharynx is a weakly and evenly sclerotized plate (Fig. 2 *B*) representing the ventral wall of the cervix. The floor *phf* is a posterior continuation of the well-sclerotized adoral sclerites *ads* (see above). At the beginning of the mouth (*m*) the sclerites are widened forming oral flaps *of*, each with two subtriangular orifices (small in *Sennertia*), and then extending to the posterior part that has a pattern of characteristic linear fissures (Fig. 3 *A*). The oral flaps also have a smaller orifice that probably has some functional role (Fig. 3 *A*). The oral flaps of the pharyngeal floor are connected to the roof by two superior commissures on each side of the mouth. The commissures have distinct sclerotization (superior commissural indurance *sci*, Fig. 2 *B*, Fig. 3 *A*), each with an orifice. In *Sennertia americana*, there are two other distinct orifices situated at the junction between the oblique cuticular ridge of the capitular apodeme and the transverse posterior cuticular ridge of the cervix (Fig. 4 *D*). Similar orifices were also observed in *Glycyphagus*.

Idiosoma

Ancestrally, the idiosoma of astigmatid mites is subdivided by the sejugal furrow into two pseudotagmata: propodosoma (anterior) and hysterosoma (posterior). In chaetodactylids a complete sejugal furrow is not developed, and some hysterosomal elements may be shifted to the prodorsal area (*e.g.*, the progenital chamber in females and hysterosomal setae c_p, c_2 in *Sennertia*, *Chaetodactylus*, and *Achaetodactylus* deutonymphs), or some propodosomal elements may be shifted to the hysterosomal area (*e.g.*, posterior apodemes II in *Sennertia*). The following elements of the chaetodactylid idiosoma are distinguishable and will be briefly described below: idiosomal cuticle; idiosomal setae (p. 10); cupules (p. 11); prodorsal shield (p. 12); supracoxal sclerites and associated structures (p. 13); hysterosomal shield (p. 15); opisthosomal glands (p. 21); coxisternal region with setae (p. 16); Claparède's organs (larval) (p. 20); reproductive organs (p. 24); anal opening (p. 31); lateral longitudinal hysterosomal sclerites (p. 15) and attachment organ (p. 21) developed only in heteromorphic deutonymphs.

Idiosomal cuticle

The idiosomal cuticle outside sclerotized shields is usually strongly modified and may serve as a good diagnostic character at the species level. The unsclerotized idiosomal surface can be lineate, lineolate, striate, ruminate, rugose, sulcate, granulate, tuberculate, pusticulate, aculeate or a combination of these patterns (terminology follows Evans, 1992). Idiosomal shields may have smooth, falsifoveate (prodorsal shield of *Sennertia koptorthosomae*), or various modifications of colliculate (heteromorphic deutonymphs) surfaces. Sometimes, there is a substantial sexual dimorphism in modifications of the idiosomal cuticle. In males of *Sennertia* and *Chaetodactylus*, elements of the cuticular pattern are smaller and less dense than in females, or they may be differently arranged (see below).

Ancestrally, heteromorphic deutonymphs of Chaetodactylidae have a striate dorsal idiosoma. The linear pattern formed by invaginated cuticular folds is parallel to the lateral edges of the idiosoma and transverse in the sejugal region. The two idiosomal shields, prodorsal and hysterosomal, are foveolate and bear the same striate pattern as on the unsclerotized cuticle; the lines are longitudinal or transverse (posterior portion of prodorsal shield in *Roubikia, Centriacarus*, and *Chaetodactylus*). In some deutonymphs, the idiosomal cuticle has undergone several modifications. In *Sennertia loricata* sp. n., *S. indica*, *S. leei*, *S. ceratinarum*, *S. latipilis*, and *S. spinifera*, the cuticle outside the hysterosomal shield has sclerotized bands situated between striae, and the bands appear as continuations of the hysterosomal shield. In some species of *Sennertia* (*Afrosennertia*), striae are distinctly uneven in length, accompanied by thick foveolate sclerotization, and are absent from the central and posterio-lateral areas of the hysterosomal shield (*S. jeanalexi*, *S. basilewskyi*). In the latter species, the entire idiosomal cuticle has foveolate sclerotization that is slightly less developed than on the hysterosomal shield or nearby striae. In *Sennertia* *vitzthumi*, the dorsal cuticle is completely punctate and bears thick folds instead of striations (Fain, 1981a). In *Centriacarus* and *Chaetodactylus*, unlike *Roubikia*, *Achaetodactylus*, and *Sennertia*, cuticular folds forming a striate pattern on the cuticle outside shields are substantially different from those on the idiosomal shields. They are usually much shorter and their spacing is much wider, creating a pattern of short unsclerotized grooves. The groove outlines range from nearly linear and long (*Chaetodactylus melitomae*) to lens-like and short (*Centriacarus turbator*, *Chaetodactylus osmiae*). In the genus *Chaetodactylus*, the propodosoma, including the prodorsal shield, is almost completely transversely striated in the central part, while almost lacking longitudinal medial striation. The whole prodorsal shield of *Achaetodactylus* is longitudinally striated. The prodorsal shield of *Roubikia* and *Centriacarus* has two distinct regions of striation: anterior with longitudinal, and posterior with transverse striation. This shield is absent in *Sennertia*. The hysterosomal shield is usually longitudinally striated in all chaetodactylids.

In adults of *Roubikia*, the idiosoma is transversely striated (longitudinally on lateral propodosoma and a small portion anterior to the opisthosomal glands and around the progenital folds) or smooth on ventral propodosoma; the lines are close to each other (ca. 1.2) and bear conical papillae: 4.0–5.0 × 2.0–2.5 (height × diameter). In adults of *Sennertia koptorthosomae*, the dorsal cuticle is aculeate, conical papillae are about 6.5–5.5 × 6.0–5.5; in the dorsal metapodosomal area, there are small granulate areas (diameter about 1.3) between the conical papillae. The ventral part of the idiosoma, excluding the smooth area anterior to anterior apodemes I, has smaller conical papillae (about 1.5) and is slightly striate. In females of *Sennertia scutata*, most of the opisthosomal region has a tuberculate (4.0 × 4.0) pattern that gradually transforms to aculeate (2.5 × 2.5) at the posterior end of the body. The whole ventral opisthosoma, the lateral area of the opisthosomal area posterior to the opisthosomal glands, and the dorsal area between the transverse levels of *si* and *d* are striate (distance between lines 4.0). The latter area also has very small (0.3 × 2.0) tubercles arranged along the lines. The males differ in having less developed striate and tuberculate patterns (1.5 × 2.0 on dorsal opisthosoma). The dorsal and ventral idiosoma of *Sennertia americana* females is covered by more or less uniform (2.5 × 2.0) tubercles arranged along transverse or longitudinal (lateral opisthosoma) striae. The dorsal region of the opisthosoma situated above the anus is longitudinally striated and without tubercles. Such a pattern is absent in the males, and the idiosomal tubercles are smaller (2.0 × 2.0) and less developed ventrally. *Sennertia faini* is distinct in the absence of any cuticular tubercles. The dorsal idiosoma and ventral hysterosoma are striate, whereas the ventral propodosoma is almost smooth. No sexual dimorphism in the cuticular surface was detected in this species. The dorsum of *Chaetodactylus krombeini* and *Ch. hopliti* is densely aculeate. The pattern is more strongly developed on the opisthosoma, where the conical mammillae are very dense, approximately 1.2 × 1.5 in the female and 0.9 × 0.9 in the males. It also is present on the lateral sides of the ventral opisthosoma, where it gradually turns to a linear pattern. The rest of the ventral idiosoma is almost smooth. In females of *Chaetodactylus micheneri*, only the dorsal opisthosoma is tuberculate, and the tubercles (1.3 × 2.0) are arranged in transverse lines; the ventral opisthosoma is slightly striate and the remaining idiosoma is almost smooth or with sparse tubercles. In the males, the pattern is less dense and represented by tubercles or conical mammillae (1.0 × 1.5). In females of *Chaetodactylus zachvatkini*, the dorsal opisthosoma is tuberculate (papillae 2.0–2.5). The remaining idiosoma is striate. In the males, the tubercles are smaller (ca. 1.5 × 2.0) and less dense. In females of *Chaetodactylus reaumuri* the posterior dorsum and the ventral podosoma posterior to the progenital chamber is tuberculate. The tubercles (1.5–1.8 × 2.5–3.0) are fleshy and sometimes fused to each other and are arranged in more or less distinct transverse rows. The tuberculate pattern turns to a striate pattern on the ventral and lateral sides of the dorsal opisthosoma and anterior to setae d_1. The propodosoma and the region of the progenital chamber are almost smooth. In the males, the modifications of the idiosomal cuticle are less developed: tubercles on the posterior opisthosoma are smaller (ca. 1.3–1.5 × 1.5–2.0) and less dense, not fused to each other and not arranged in distinct transverse rows. Both striate and smooth areas of females are smooth in the males.

Idiosomal setae

Idiosomal setae are traditionally grouped as prodorsal, hysterosomal (including the anal region), coxisternal, and genital setae (Griffiths *et al*., 1990). Although there is no distinct boundary between the chaetodactylid propodosoma and hysterosoma, setae pertaining to the former can be homologized with the prodorsal setae of the ancestral astigmatid type and are considered as such. Coxisternal and genital setae are described in the sections Coxisternal region (p. 16) and Reproductive system (p. 24), respectively. Supracoxal setae (*scx*), situated on lateral edges of propodosoma, usually above trochanters I, are described in the section Supracoxal sclerites and associated structures (p. 13).

Prodorsal setae include four pairs of setae (*ve*, *vi*, *se*, *si*). All of them are larval. Setae c_2, c_p, and c_3 may also be present in the prodorsal area (*Achaetodactylus*, *Chaetodactylus*) but they originate from the hysterosoma. The shape and the arrangement of the prodorsal setae in different chaetodactylids is shown on Fig. 22, Fig. 47, Fig. 66, and Fig. 84, and the position of some setae on the prodorsal shield is discussed in the section Prodorsal shield (p. 12). Setae *ve* are always represented only by alveoli (they are not distinctly seen in *Achaetodactylus*, but small areas at the anterior end of the prodorsal shield probably represent these alveoli). There is a correlation between the positions of setae *se* and c_2 in all instars. They either both occupy their normal ancestral position (*se* are nearly on the same level as *si*, c_2 are nearly on the same level as c_1 in *Centriacarus* and *Roubikia*), or they are shifted anteriorly (*se* are distinctly anterior to the level of *si*, c_2 are distinctly anterior to the level of c_1 in *Achaetodactylus*, *Chaetodactylus*, and *Sennertia*).

Hysterosomal setae include a maximum of 12 pairs of setae situated on the dorsal or dorso-lateral hysterosoma, and a maximum of 6 pairs of setae in the paraproctal region. All the dorsal hysterosomal setae are invariably present in chaetodactylids. Ten pairs of these setae are larval (c_1, c_2, c_3, c_p, d_1, d_2, e_1, e_2, h_1, h_3), and two pairs (h_3 and f_2) are protonymphal. Their length, shape, and relative position may serve as diagnostic characters at the level of genus or species (Fig. 47, Fig. 66, Fig. 22, and Fig. 84).

In feeding instars, the homology of setae h_2 and h_3 is questionable. Both of these setae are usually ventral and one of them is long and the other one short. In *Roubikia*, the short seta is distinctly anterior and medial to the long one (Fig. 49 *A*), while in *Sennertia* and *Chaetodactylus* the short seta is always external and slightly anterior (*Ch. micheneri*, *S. vaga*) (Fig. 27, Fig. 38), at the same level (*S. americana*) or posterior (*S. koptorthosomae*) to the long seta. It is interesting that in the latter case, the protonymph has the reverse condition, the more medial seta is anterior and the more external seta is posterior (in this species, both setae are approximately of the same length in protonymphs; but in adults, the external one is the longest). This might suggest that the anterior position of the short seta is the ancestral condition for the family. We identify, therefore, the more anterior and usually short seta as h_3, and the more posterior and usually long seta as h_2. The anal region of feeding instars is surrounded by three pairs of pseudanal setae and 0–3 pairs of adanal setae. Adanal setae or their alveoli, when present, are more medial and usually shorter than pseudanal setae. Pseudanal setae are protonymphal, while the adanal setae in feeding instars first appear in tritonymphs as alveoli (*Sennertia*) or in adults as filiform setae (*Chaetodactylus*). Pseudanal setae ps_3 are shifted anteriorly, away from the anus in all known chaetodactylid females. In *Roubikia* and some *Sennertia* (*S. vaga*), they are slightly posterior to coxal fields IV. In *Chaetodactylus*, these setae are situated at the level of setae *4a*, slightly posterior to the progenital folds. In several *Sennertia* (*S. americana*, *S. scutata*, *S. augustii, S. splendidulae*, *S. koptorthosomae*), setae ps_3 follow the anterior shift of the progenital chamber and are situated near its posterior border at the level of coxal fields III. These setae occupy their ancestral position in all immature instars, as well as in males of *Chaetodactylus* and *Sennertia*. In both homeo- and heteromorphic males of *Roubikia*, ps_3 are shifted away from the anus and lie posterior to coxal fields IV (Fig. 12 *A*). In adults of *Roubikia*, setae ps_2, like ps_3, are shifted anteriorly, midway between the levels of the anus and coxal fields IV. In other known chaetodactylids, ps_2 are inserted at the middle or posterior level of the anus. Tritonymphs of *Sennertia* have three pairs of adanal alveoli, while females have 1–3 pairs of adanal setae or alveoli and males 0–1 pairs. Tritonymphs of *Chaetodactylus* lack any traces of adanal setae; females have three pairs of *ad* and males have only ad_1 (see details in Table 6). Females of *Roubikia* have only one pair of adanal setae (ad_3) and two pairs of ad_1 and ad_2 alveoli, and the males have probably only one pair of alveoli (?ad_1) (tritonymphs are unknown).

In heteromorphic deutonymphs, pseudanal and adanal setae are strongly modified and incorporated into the attachment organ, where the former appear as conoids and the latter as alveolar suckers (p. 21).

Lyrifissures

Lyrifissures are sense organs thought to be mechanoreceptors (Evans, 1992). There are hysterosomal cupules (rounded lyrifissures) and tarsal slit-like lyrifissures. Palpal lyrifissures, common in other acariform mites, are absent in Chaetodactylidae. Chaetodactylids have four pairs of hysterosomal cupules situated on the hysterosoma, all of which are ancestral in the Astigmata: *ia*, *im*, *ip*, and *ih* (Fig. 38 *A*). In heteromorphic deutonymphs of all chaetodactylids, there is another pair of cupule-like structures (*ix*) near the opisthosomal gland openings (Fig. 47 *B*). These structures are also present in deutonymphs of other astigmatid mites, for example, in the family Acaridae. A normally developed cupule (*e.g.*, feeding instars and heteromorphic deutonymphs of *Roubikia*, *Sennertia*, and *Chaetodactylus*) is cup like, situated in the soft cuticle or may form a short, slit-like opening in this place (*e.g.*, heteromorphic deutonymphs of *Chaetodactylus* and *Sennertia*) (Fig. 5 *A*,*B*,*D*). At the bottom of the cup, there is also a small, ring-like sclerite, probably representing the receptor canal (Evans, 1992). A cupule, viewed from the plane parallel to the surface of the cuticle, looks like a sclerotized ring with a smaller ring-like sclerite in the center. In *Achaetodactylus*, *Chaetodactylus*, and *Sennertia*, as a rule, cupules that are inserted on the hysterosomal shield in heteromorphic deutonymphs are usually less developed, lacking the small ring-like sclerites, and look like a small perforation in the shield. A distinct ring-like sclerite may be absent (*Centriacarus*, *Achaetodactylus*).

In feeding instars, cupules *ia* are dorsal, lying slightly posterior to setae c_2; cupules *im* are ventro-lateral (*Roubikia*), ventral (*Chaetodactylus*), or dorsal (*Sennertia*) (this character state is correlated with that in heteromorphic deutonymphs), usually anterio-distal to the opisthosomal gland opening; cupules *ip* are dorso-lateral, anterior (*Roubikia*) or posterior (*Chaetodactylus*, *Sennertia*) to setae f_2 (this state is correlated with that in heteromorphic deutonymphs); cupules *ih* are always ventral, situated on the anterior sides of the anus. In females of *Roubikia*, the distance between them distinctly exceeds the length of the anus, while in the males of *Chaetodactylus* and *Sennertia* the distance does not exceed the length of the anus.

In heteromorphic deutonymphs, cupules *ia* are situated in the area delimited by the lines between the bases of setae c_2, c_p, and d_2, usually closer to the former two setae. Only in *Roubikia* and *Centriacarus* are they inserted on the hysterosomal shield; in all other genera they lie on the soft cuticle. *Roubikia* is distinct from other chaetodactylids in that well-developed cupules (*ia*, *im*) have a transverse sclerotized ridge that connects an elongated ring-like sclerite and inner walls

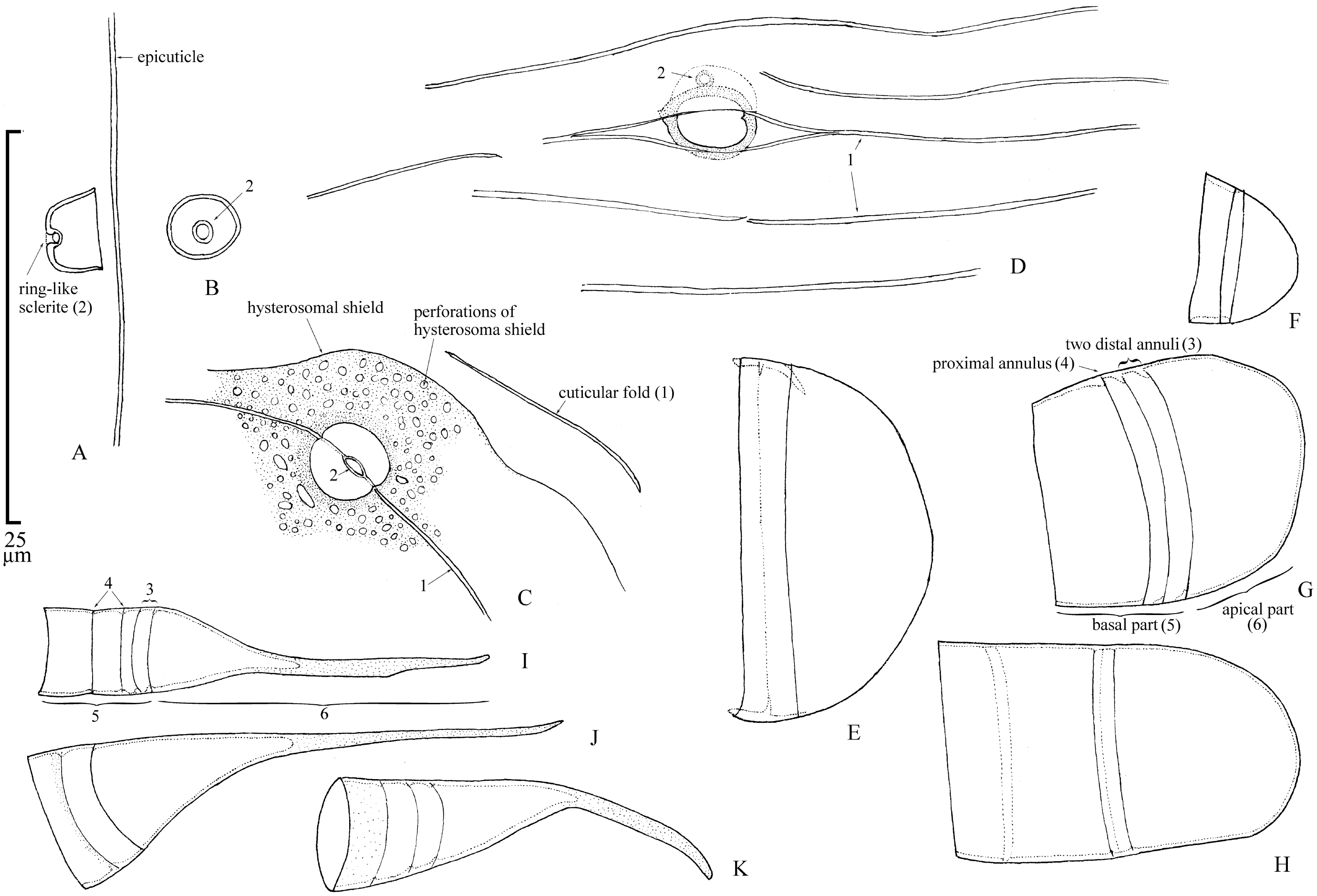

Fig. 5. Cupules (A–D) and posterior genital papillae (E–K) of Chaetodactylidae. A - *im*, lateral view (*Roubikia panamensis*, female); B - *ia*, dorsal view (*R. panamensis*, female, paratype); C - *ia*, dorsal view (*R. panamensis*, heteromorphic deutonymph); D - *ia*, dorsal view (*Sennertia americana*, heteromorphic deutonymph, BMOC 90-1212-025); E - *R. panamensis* (female); F - *Chaetodactylus krombeini* (male, BMOC 98-1202-001); G - *Ch. krombeini* (female, BMOC 79-0312-001); H - *Sennertia koptorthosomae* (female, ex *Xylocopa latipes*, Malaysia); I - *R. panamensis* (heteromorphic deutonymph, BMOC 91-0103-007); J - *Chaetodactylus azteca* (heteromorphic deutonymph, BMOC 96-0510-139#1); K - *S. americana* (heteromorphic deutonymph, BMOC 90-1212-025).

of the cap of the cupule (Fig. 5 *C*). The direction of this ridge usually follows the direction of the cuticular folds. Cupules *im* are associated with lateral longitudinal hysterosomal sclerites (p. 15). In *Sennertia*, these cupules are situated dorsally or dorso-laterally at the level of leg acetabula III, approximately at the middle of the line between setae d_2 and e_2. In *Chaetodactylus melitomae*, *im* are also dorsal, but they are inserted at the level of leg acetabula IV and setae e_2, lateral to the latter. In all other *Chaetodactylus*, *Centriacarus*, and *Roubikia*, *im* are ventral and situated between leg acetabula III and IV. Cupules *ip* are invariably inserted on the hysterosomal shield, usually close to its lateral edges (*Centriacarus*, some *Sennertia*, *Chaetodactylus*), anterior (*Centriacarus*, and *Roubikia*) or posterior (*Chaetodactylus*, *Sennertia*, *Achaetodactylus*) to setae f_2. Cupules *ih* are ventral, situated on the sides of the attachment organ (*Achaetodactylus*, *Centriacarus*, *Roubikia*, *Sennertia*) or are incorporated into its lateral sclerotized border (*Chaetodactylus*). In most chaetodactylids, cupules *ih* are inserted at the level of the central suckers (ad_{1+2}) of the attachment organ, while in *Centriacarus* they are posterior and in *Achaetodactylus* they are anterior to this level.

The tarsal lyrifissure is situated on the anterior-dorsal surface of the base of tarsus I only. It is slit-like in both feeding instars and heteromorphic deutonymphs. In some adults, we were able to observe the central ring-like sclerite (Fig. 14 *A*). No other variation occurs in the position or appearance of the tarsal lyrifissure. Tarsal lyrifissures II, which are present ancestrally in acariform mites (*e.g.*, *Megacanestrinia*) are absent in chaetodactylids.

Prodorsal shield

The prodorsal shield in feeding instars varies in shape, proportions, and position of the alveoli of *ve*. In *Roubikia*, *Chaetodactylus*, and some *Sennertia* (*S. vaga*), the shield is subquadrate (length/width ratio is 0.8–1.4), while in certain *Sennertia*, it is distinctly elongated, with the length exceeding the width by about 1.7–2.4 times (*Sennertia koptorthosomae*, *S. ameri-*

cana). The anterior edge of the shield is always concave, with contiguous bases of setae *vi*. The alveoli of setae *ve* are situated at the lateral edges of the shield, paramedially in the posterior part of the shield. These alveoli are inserted inside (*Roubikia panamensis*) or outside the shield (*S. vaga*), or touching the shield (all other known species). The lateral edges of the prodorsal shield are concave anterior to alveoli *vi*. The part of the shield posterior to this point is rounded (*Roubikia*), tongue-like (*S. scutata*, *S. americana*), rounded-triangular (*S. vaga*, *Chaetodactylus*), or trapeziform (*S. koptorthosomae*). Males of the latter species are distinct in the presence of a rough falsifoveate pattern on the prodorsal shield; in all other feeding instars of chaetodactylids, the propodosomal shield is evenly foveolate.

The prodorsal shield in chaetodactylid heteromorphic deutonymphs is developed in all genera except for *Sennertia*. It is triangular and covers only part of the prodorsal surface (except in *Achaetodactylus*). The relative size and outlines of the shield vary substantially. In *Achaetodactylus ceratinae* and *A. leleupi*, the prodorsal shield extends laterally to the level of setae c_2, and anteriorly it reaches or almost reaches the rostral projection. In *Chaetodactylus lassulus*, the prodorsal shield is very small, not extending to the level of c_2 laterally and the level of *si* anteriorly. In *Centriacarus, Roubikia*, and most species of *Chaetodactylus*, it is intermediate, almost extending to the level of c_2 laterally (not extending in *Centriacarus, Roubikia*) and *scx* anteriorly. In most cases *(Roubikia*, *Chaetodactylus*, *Achaetodactylus*), the width of the prodorsal shield exceeds its length. In *Centriacarus*, however, it is longer than its width. The number of setae situated on the prodorsal shield varies from 0 to 3 (excluding alveoli *ve*): no setae (*Ch. lassulus*); *si* (most *Chaetodactylus*, *Centriacarus*, *Roubikia*); *si* and c_2 (*claviger*-group); or *si*, *se*, and c_2 (*Achaetodactylus ceratinae*, *A. leleupi*). The alveoli of setae *ve* are situated at the anterio-lateral edges of the prodorsal shield (*Centriacarus*; *Roubikia*; most species of *Chaetodactylus*) or on unsclerotized cuticle (*Sennertia*, *Ch. lassulus*). Ornamentation of the prodorsal shield in heteromorphic deutonymphs is described above (p. 9).

Supracoxal sclerites and associated structures

Supracoxal sclerites are situated on the dorso-lateral edges of propodosoma (Fig. 6) above the acetabula of legs I. Each sclerite has a supracoxal gland opening surrounded by large cuticular ridges and flaps, a podocephalic canal, a supracoxal seta, and a ventral gutter-like canal. Grandjean's organ is absent. Supracoxal gland openings are slit-like, situated at the posterior end of the sclerites, dorsal to trochanters I. They are surrounded by cuticular ridges and, unlike some free-living and parasitic Astigmata, covered by two distinct cuticular flaps. There are two narrow rings with heavily sclerotized ridges, outer and inner. The latter is situated deeper and close to the supracoxal gland opening. The former extends to two longitudinal external protective flaps. The flaps are thin and transversely striated, covering the inner ridges and the supracoxal gland opening. The outer flap is usually larger and more visible. The outer ridge is open at the anterior end extending to the anterio-lateral ridge and podocephalic canal. The two are touching medially, the ridge is outer and the canal is inner. Topologically the anterio-lateral ridge could be a place where salivary glands (Brody *et al*., 1976, glands *Gt* (Grandjean, 1937a, 1937b)) open and the ventral gutter-like canal (Brody *et al*., 1976) starts. Although the latter is obviously associated with the anterio-lateral ridge, we were unable to find any opening inside the ridge. Relative length of the anterio-lateral ridge is a useful character in species diagnostics (Fig. 6). The podocephalic canal progresses anteriorly in the supracoxal sclerites. It extends to the unsclerotized cuticle of the propodosoma at the anterior end of the sclerite, makes two folds at the propodosoma-gnathosoma border and enters the sclerotized lateral part of the cheliceral sheath. A transverse posterior ridge of the cervix, representing an attachment site for the cheliceral sheath (see above) is probably accompanied by the podocephalic canal (Fig. 6 *D*). We did not clearly see where the canal discharges on the subcapitulum. The orifice in the superior commissural induration, situated at the lateral sides of the mouth, is possibly such a place, as was observed for *Sennertia americana* (Fig. 6 *D*) and *Chaetodactylus krombeini* (Fig. 2 *B*). This coincides with the observations of Prasse (1967) on *Sancassania*. Secretions of the supracoxal glands are rich in salts and hygroscopic. As it moves through the external podocephalic canal to the preoral cavity (Prasse, 1967) it absorbs atmospheric water (Wharton & Furumizo, 1977; Wharton, 1979). The ventral gutter-like canal starts ventrally from the anterior end of the anterio-lateral ridge and progresses over the dorsal edge of trochanters I. The supracoxal seta is filiform or spiniform (*Roubikia)*, lateral to the outer flap (*Roubikia*, *Sennertia vaga*), anterio-lateral (*Sennertia scutata* and *S. americana*) or situated on the flap (*Chaetodactylus*).

The supracoxal sclerite of *Roubikia* differs from the above description by much longer outer and inner ridges (distinctly longer than half of the supracoxal sclerite), by being more than 3 times longer than the orifice of the supracoxal gland, and by the absence of an anterio-lateral ridge. The medial edge of the outer ridge has a distinct denticle that is probably homologous with the denticles at the open anterior end of the outer ridge of *Sennertia* and *Chaetodactylus*. In *Roubikia*, however, the compartment anteriorly following this denticle is probably not homologous to the anterio-lateral ridge of *Sennertia* and *Chaetodactylus* because it is situated medial to the podocephalic canal.

Some adult chaetodactylids display sexual dimorphism in the length of the outer ridge (Fig. 6 *F,G*). We measured both the absolute length of the ridge and, because males are usually smaller than females, its length relative to the length of the idiosoma. As the female idiosoma can substantially enlarge due to egg production, comparison of the latter values is not entirely appropriate. Nevertheless, both absolute and relative measurements suggest that in *Chaetodactylus krombeini*, *Ch. hopliti*, and *Ch. osmiae*, the outer ridge is significantly ($p<0.05$)

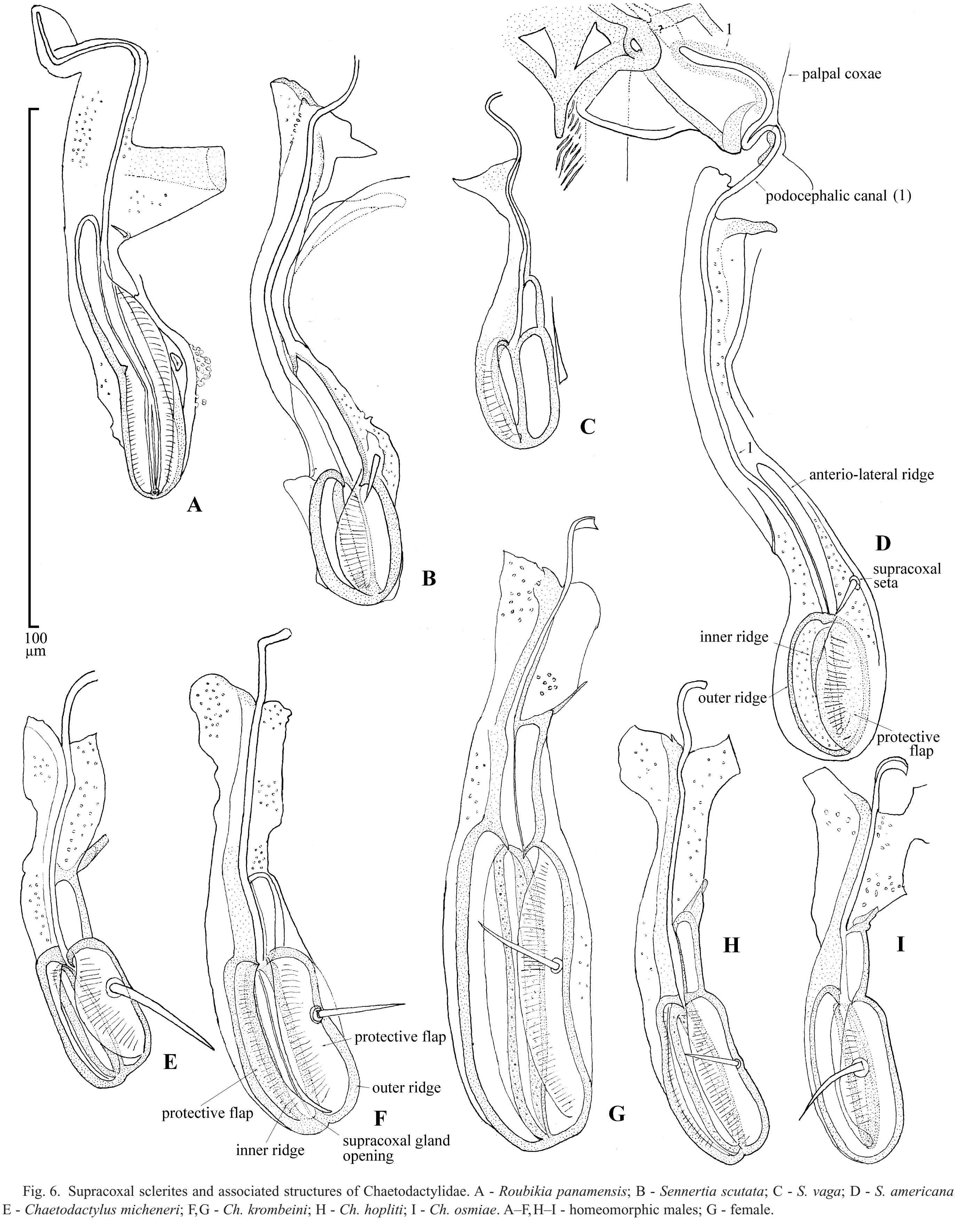

Fig. 6. Supracoxal sclerites and associated structures of Chaetodactylidae. A - *Roubikia panamensis*; B - *Sennertia scutata*; C - *S. vaga*; D - *S. americana*; E - *Chaetodactylus micheneri*; F,G - *Ch. krombeini*; H - *Ch. hopliti*; I - *Ch. osmiae*. A–F, H–I - homeomorphic males; G - female.

smaller in males. This is probably also true for *Ch. zachvatkini* and *Sennertia vaga*, for which we have smaller sample sizes. In *Sennertia scutata*, in turn, data suggest that the outer ridge is larger in males than in females ($p = 0.033$). In *Sennertia americana* and *Ch. micheneri* relative measurements, unlike absolute ones, do not show any significant differences between the sexes. We suspect this is also true for *Sennertia koptorthosomae*.

In heteromorphic deutonymphs of *Roubikia*, an orifice probably homologous to the supracoxal gland opening, is situated on a dorsal extension of the anterior coxal apodeme. This may indicate that the supracoxal sclerites are incorporated into these extensions in heteromorphic deutonymphs. However, in some chaetodactylids, a very small, dark area topologically homologous to the supracoxal gland opening is present on the soft cuticle (*e.g.*, *Sennertia americana*, *Chaetodactylus claudus*). If this homology is correct, then the supracoxal sclerites are not developed in the heteromorphic deutonymphs of the chaetodactylids. The supracoxal setae *scx* are always vestigial; short (ca. 2–5); with a slightly rounded tip; rod-like, conical, or clavate. They are situated on a small separate sclerite deeply embedded into cuticle (*Centriacarus*, *Roubikia*, *Chaetodactylus*, many *Sennertia*) or on the distal extension of posterior apodeme I (*Sennertia surinamensis* and related species). Grandjean's organ and the podocephalic canal are also absent in this stage.

Hysterosomal shield

A hysterosomal shield is developed only in heteromorphic deutonymphs. The hysterosomal shield is usually in the form of an inverted trapezium with the outlines following those of the hysterosoma, although the shield may not cover it completely (*Centriacarus*, *Chaetodactylus*, some *Sennertia*, *e.g.*, *S. surinamensis*, *S. koptorthosomae*, *S. horrida*). In contrast, in many *Sennertia*, the shield is distinctly smaller than the hysterosomal area, leaving a large area of unsclerotized hysterosomal cuticle. The shape of the shield in this genus varies substantially and may be used to distinguish infrageneric lineages. In many species of *Sennertia* with small hysterosomal shields, the shield is elongated, exceeding half of the body length, with more or less parallel lateral edges and a rounded anterior margin (almost transverse in *S. congoicola*), or it is ovoid (with the widest part situated on the anterior hysterosoma) (*e.g.*, *S. madagascarensis* and *S. koptorthosomae*), or subtriangular (*e.g.*, *S. zhelochovtsevi*, *S. argentina*). If the shield is distinctly shorter than half of the body length, then it is subtriangular (subgenus *Afrosennertia*) or suboval (*e.g.*, *S. oudemansi*, *S. delfinadoae*). There is a distinct concavity surrounded anteriorly by a sclerotized area in *S. hipposideros* and *S. koptorthosomae* (Fig. 13). In both species, fungal spores were found in this hysterosomal pouch suggesting that this structure is probably analogous to sporothecae of other mites, *e.g.*, *Trochometridium* or *Siteroptes* (Lindquist, 1985). In some *Sennertia* associated with *Ceratina*, the hysterosomal shield expands onto the prodorsal part of the idiosoma almost touching setae *si* (*S. indica*), or these setae are inserted on the shield (*S. bifida*). Usually, the hysterosomal shield has a well-sclerotized posterior longitudinal apodeme. Positions of some hysterosomal setae (c_1, d_1, d_2, e_1, e_2) and opisthosomal gland openings on the shield or outside are good diagnostic characters separating infrageneric groups in *Sennertia* and *Chaetodactylus*.

The hysterosomal shield in heteromorphic deutonymphs is a place for insertion of muscles of the attachment organ (p. 20) and the ventro-dorsal muscles (p. 15). If the hysterosomal shield is reduced as in many *Sennertia* and *Chaetodactylus*, the ventro-dorsal muscles usually insert on unsclerotized cuticle lateral to the shield. The muscles of the attachment organ retract suckers of the attachment organ creating vacuum ensuring the attachment of the mites to the host cuticle during phoresy. The ventro-dorsal muscles create hydraulic pressure, a very important component in the mite locomotion. Mites lack protractor muscles, and protraction/extension of various appendages, including locomotory ones, is accomplished solely by hydraulic pressure. As the two types of muscles are essentially antagonistic, their partial structural separation in *Sennertia* and *Chaetodactylus* probably ensures their relative independence and the possibility to operate simultaneously.

Lateral longitudinal hysterosomal sclerites

Lateral longitudinal hysterosomal sclerites are developed only in the heteromorphic deutonymphs of all chaetodactylids except for *Sennertia* and some *Chaetodactylus*. They are narrow, band-like sclerites situated on the sides of the hysterosoma and are always associated with cupules *im* (Fig. 70 *A*). Well-developed lateral hysterosomal sclerites are present in *Roubikia*, most *Chaetodactylus*, and weakly developed in *Centriacarus turbator* and *Achaetodactylus*. In most *Chaetodactylus* (*e.g.*, *Ch. krombeini, Ch. osmiae*), the sclerites are ventro-lateral, with the anterior end situated at the anterior level of coxal apodemes III and the posterior end at the attachment organ, touching it or fused to its outer sclerotization. In *Ch. melitomae*, however, the sclerites are dorsal, split onto three small, separate sclerites, one of them posterior to cupule *im*, and two anterior (Fig. 52 *A*). These sclerites were not observed in *Ch. antillarum* and *Ch. furunculus*. In *Roubikia*, the lateral hysterosomal sclerites are almost ventral, with the anterior end slightly posterior to anterior coxal apodemes III and with a separate, distinctly widened posterior end. In *Centriacarus turbator*, the sclerites are extremely narrow (narrower than cupule *im*), extending approximately from the levels of the middle of leg acetabula III to the middle of leg acetabula IV. In contrast, in *C. guahibo* it is well developed, extends anteriorly almost to the level of *ia*, and posteriorly to the attachment organ where it distinctly widens. In *Achaetodactylus*, these sclerites are represented by a small sclerotized area surrounding *im* and extending slightly posteriorly. Probably because cupules *im* are dorsal, the lateral hysterosomal sclerites are absent in *Sennertia*.

Coxisternal region

The coxisternal region comprises four pairs of coxal fields (epimera) associated with legs I–IV (in larvae leg and coxal fields IV are absent) and various locomotory and non-locomotory muscles. Each of coxal fields I–II or III–IV are situated close to each other, while coxal fields II and III are separated. There are a maximum of four pairs of coxisternal setae. Anterior and posterior borders of the coxal fields are accompanied by a maximum of six pairs of coxal apodemes (*ap*): *ap*′ I, *ap*″ I+*ap*′ II, *ap*″ II, *ap*′ III, *ap*″ III+*ap*′ IV, and *ap*″ IV[3]. Each anterior apodeme, especially in heteromorphic deutonymphs, has a distinct longitudinal furrow, while posterior apodemes do not have such a furrow and are incorporated with the subsequent anterior apodeme (*ap*″ II, which may be incorporated with the sejugal apodeme, and *ap*″ IV are exceptions). The leg trochanters are inserted in the acetabular cavities. They are thought to be articulated to the body by horizontal bicondylar joints (Evans, 1992). Knülle (1957) figures only one condyle (he calls it the ball joint) for trochanters I–II and two condyles for trochanters III–IV in *Trimalaconothrus novus* (Malaconothridae). Woodring & Carter (1974) described a bicondylar body-trochanter joint in heteromorphic deutonymphs of *Sancassania boharti* (Acaridae), while Wurst (1993) reported this articulation as monocondylar in the adults of *Sancassania "berlesei"* (Acaridae) and as bicondylar for *Listrophorus leuckarti* (Listrophoridae). In chaetodactylids, we were able to observe only a well developed anterior condyle of this joint at the antiaxial part of the anterior apodemes. The posterior part of the trochanters and corresponding posterior parts of the apodemes probably form a very specific joint, with the "condyle" situated on the former and the "cotyloid" cavity (if present) situated on the latter. This articulation is usually weakly developed and difficult to observe, but in feeding instars of *Sennertia* af. *alfkeni* (BMOC 86-0406-010) of the *japonica*-group, both elements are distinct at the body-trochanter articulation of legs III, with the "cotyloid" cavity appearing as a groove. At this point, the body-trochanter joint of chaetodactylids may be considered as a bicondylar horizontal joint. More detailed studies are necessary to confirm this observation. Cotyloid and pedotectal walls are absent. The acetabular cavity is formed by proximal and distal folds that are connected to each other at the body-trochanter joint. Distal and anterio-distal walls of acetabular cavities I–II are better developed and almost cover trochanters I–II. The acetabular cavity is flanked by sclerotized acetabular extensions of the coxal apodemes. We propose to distinguish their two parts, proximal and distal, situated on each side of the line connecting the anterior condyle and the posterior end of the trochanter. The proximal acetabular extension always extends from the anterior condyle; it is situated ventrally and completely (heteromorphic deutonymphs of *Centriacarus* and *Roubikia*) or partially (all known chaetodactylid adults) borders the antiaxial margins of the coxal fields. In the former case, they are also fused to the subsequent apodeme. The distal extension is usually dorsolateral and formed by two parts originating from the anterior and posterior apodemes of a coxal field, at the anterior and posterior condyles, respectively. With a few exceptions (Table 1), the two parts are separate.

In feeding instars, acetabular extensions of *ap*′ I extend dorsally flanking trochanter I and may have a distinct furrow and be fused to the supracoxal sclerite (Fig. 6 *A*,*B*,*H*). In phoretic heteromorphic deutonymphs, the anterio-distal portion of *ap*′ I extends dorsally forming paired lateral sclerites on the rostral projection of the propodosoma. The relative sizes of these sclerites vary substantially from small (compared to the rostral projection of the propodosoma) and inserted in the basal portion of the rostral projection (as in *Centriacarus*); as narrow bands situated near the lateral sides of the rostral projection (as in *Sennertia hurdi*); or large, occupying almost the whole rostral projection (as in *Chaetodactylus claudus* and *Ch. krombeini*). There are no distinct boundaries between these morphological conditions, however.

In the feeding instars, mobile and immobile heteromorphic deutonymphs, apodemes *ap*′ I are fused medially forming a sternum. The sternum of chaetodactylids is usually simple. Only in the heteromorphic deutonymphs of *Chaetodactylus krombeini* and *Ch. claviger*, it is distinctly bifurcated. Females of *Sennertia* are an exception; the proximal ends of *ap*′ I are separated from each other by a large pregenital sclerite (see Female genitalia, p. 24) and are fused to the lateral parts of this sclerite (Fig. 10 *G*, Fig. 38*A*). Females of *Chaetodactylus* have a normally developed sternum with its posterior end fused to the pregenital sclerite. The two are separate in females of *Roubikia*. Males and immature feeding instars of *Sennertia* are characterized by a very short sternum, which is distinctly shorter than the free parts of *ap*′ I.

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[3] A prime (′) and double prime (″) means an apodeme pertaining to the anterior or posterior border of a coxal field, respectively. There is substantial disagreement in terminology of the coxisternal region of acariform mites (*e.g.* Zachvatkin, 1941; Grandjean, 1952; Woodring & Carter, 1974; OConnor, 1982; Evans, 1992). Grandjean (1952) conducted a detailed study on this subject, but his terminology cannot be easily adapted to Astigmata. The application of Evans (1992) is incorrect with regard to "apodemes 3 and 4" of adult brachypiline oribatids, which actually correspond to the posterior portions of coxal fields III and IV of astigmatid mites. Woodring & Carter (1974) derived their terminology from a hypothetical ancestor not corresponding to that proposed by Grandjean (1952). Parts of the invaginated borders of a coxal field were recognized depending on whether a structure is free or fused to the paired or adjacent structure. Because of this, their terminology may use different names for homologous structures (*e.g.*, for oribatids with mentotectum and for Astigmata with separated coxal fields II and III). Zachvatkin (1941) and OConnor (1982) proposed their terminologies based on the position of the coxal borders relative to the trochanter. The two terminologies were extensively used in the descriptive literature. Unfortunately, the term "epimera" of the former author is not entirely semantically correct. In the present work, we adopt the terminology developed by OConnor. Here, the term "apodema" is different from its traditional definition (Grandjean, 1952; Van der Hammen, 1980) in several points: 1) it includes acetabular sclerites surrounding, in the general case, the leg acetabula; 2) it may include accompanying sclerotization of the ventral cuticle; 3) it may refer only to a part (posterior or anterior) of an apodeme *sensu* Grandjean; 4) it may include a condyle. However, in the present work, the sclerites mentioned in 1–2) will be referred to as apodemal extensions. Apodemes *sensu* Grandjean were observed in chaetodactylids near the anterior borders of coxal fields I.

Table 1. Characters of coxisternal apodemes in five genera of Chaetodactylidae (if different, character states pertaining to heteromorphic deutonymphs and adults are separated by a slash "/", respectively. Centr = *Centriacarus*, Roub = *Roubikia*, Achaet = *Achaetodactylus*, Chaet = *Chaetodactylus*, Senn = *Sennertia*).

Character	**Centr**	**Roub**	**Achaet**	**Chaet**	**Senn**
Coxal fields I–II medially: closed (0); open (1)	1	1	1	1	1
Coxal fields III medially: closed (0); open (1)	0	0	1	1/0	1/0,1
Coxal fields IV medially: indistinctly closed (0); open (1)	1	0/1	1	1	1
ap′ I fused medially forming sternum (0); fused to pregenital sclerite (1)	0	0	0	0	0/1/0
Proximal acetabular extensions of *ap′* I completely (0) border antiaxial margins of coxal fields I; partially (1)	0	0/1	1	0/1	0/0,1
Distal acetabular extensions of *ap′* I and *ap″* I fused (0); separate (1)	1	1	1	1	1
Proximal acetabular extensions of *ap′* II completely (0) border antiaxial margins of coxal fields II; partially (1)	0	0/1	1	0/1	1/0,1
Distal acetabular extensions of *ap′* II and *ap″* II fused (0); separate (1)	1	0/1	1	1	1/0,1
Distal acetabular extensions of *ap″* I and apodeme *ap′* II separate or former is absent (0); fused (1)	0	1/0	0	1/0	0
Proximal acetabular extensions of *ap′* III completely (0) border antiaxial margins of coxal fields III; partially (1)	0	0/1	0	0/1	1/0,1
Distal acetabular extensions of *ap′* III and *ap″* III fused (0); separate or not developed (1)	1	1	1	1	1/0,1
Proximal acetabular extensions of *ap′* IV completely (0) border antiaxial margins of coxal fields IV; partially (1)	0	0/1	0	0,1/1	0,1
Distal acetabular extensions of *ap′* IV and *ap″* IV fused (0); separate or not developed (1)	1	1	0	0,1/1	0,1
Posterior part of *ap″* II not displaced posteriorly to *ap′* III (0); displaced posteriorly to *ap′* III (1); absent (2)	0	0	1	0,2/2	0,1/0,1
Transverse medial extension of *ap″* IV well-developed (0); absent (1)	0	0	0	1	1

Coxal fields I–II are open in all chaetodactylids. In heteromorphic deutonymphs, *ap′* II never reaches the level of coxal fields III. Apodeme *ap′* IV may be absent in heteromorphic deutonymphs and feeding stages of some *Sennertia* (*e.g.*, *Sennertia americana*). Distribution of characters of coxisternal apodemes in chaetodactylids is summarized in Table 1.

Coxal fields I and III–IV have 4 pairs of setae (Fig. 27 *A*, Fig. 22 *A*), two of which (*1a* and *3a*) are larval and the other two are deutonymphal (*4a* and *4b*). Setae *1a*, *3a*, and *4a* are located on coxal fields I, III, and IV, respectively. In the heteromorphic deutonymphs of *Centriacarus* and *Roubikia*, these setae are shifted to the posterior coxal field border and usually lie on their cuticular sclerotization. This tendency also exists in *Achaetodactylus* and *Chaetodactylus* for setae *1a* and *3a* but, with the exception of *1a* in *Chaetodactylus hopliti* and *1a* and *3a* in *Ch. krombeini* and *Ch. claviger*, these setae are shifted anteriorly and do not lie on sclerotization at the posterior borders. In heteromorphic deutonymphs of *Sennertia* and in feeding instars of all three genera where they are known, setae *1a* and *3a* are situated on the central part or anterior part of the respective coxal fields. Coxal setae are usually filiform but are basally widened in several taxa in heteromorphic deutonymphs of *Sennertia* and *Chaetodactylus*. In *Chaetodactylus krombeini* and *Ch. claviger*, setae *1a*, *3a*, and *4b* have a short inflated basal part and a long filiform part, which is often broken off (Fig. 70 *A*). Some of these setae may be similarly modified in other species of the *claviger*-group. All coxal setae are spiniform in *S. varicosa* and *Sennertia* (*Spinosennertia*) (Fig. 78 *A*); setae *1a*, *3a* and *4b* are inflated and almost rounded and setae *4a* are almost spiniform in *Sennertia devincta* phoretic in the metasomal acarinarium of *Ceratina* sp. in Peru; in *S. madagascarensis* and *S. latipilis* only setae *4b* are spiniform.

Muscles of the coxisternal region may be subdivided into non-locomotory and locomotory. The former include muscles associated with various structures of the progenital opening and dorsoventral and transverse hysterosomal constrictors. Locomotory muscles comprise depressors and ventral portions of levators of trochanters as well as femoral remotors (Table 2, Fig. 7). We also include here dorsal levators of trochanters originating from the endosternite (=central suspensory ligament, Woodring & Cook, 1962; ventral muscle mass, Kuo & Nesbitt, 1970) and functionally associated with locomotory coxisternal muscles. Below, we describe muscles of the coxisternal region based on the female of *Chaetodactylus micheneri* (BMOC 03-0310-001) and compare these data with *Roubikia panamensis* and *Sennertia* sp. 1 from South Africa, the only properly preserved material we have. It should be noted that in the above species of *Sennertia*, the coxisternal region is modified. In some early derivative species (*e.g.*, *S. vaga*), it is not modified and similar to that of *Chaetodactylus* and *Roubikia*.

The locomotory muscles of the coxisternal region and the endosternite include levators (*ltd*) and depressors of trochanters (*dt*) as well as femoral remotors (*rf*) (Table 2, Fig. 7). With the exception of the separation of apodeme III into two functional parts in some *Sennertia*, their structure and position are rather constant but substantially different from published accounts of other astigmatid mites. The most remarkable feature of free-living taxa is the presence of well-developed muscles originating from the endosternite (Woodring & Carter, 1974; Kuo & Nesbitt, 1970). The endosternite and attached trochanteral muscles are also known in oribatid and endeostigmatid (*Pachygnathus*) mites (Akimov & Yastrebtsov, 1989; Hammen, 1989), but are apparently absent in the parasitic astigmatid mite *Listrophorus leuckarti* (Wurst, 1993) and the pyroglyphid genus

Table 2. Locomotory muscles of the coxisternal region of females *Roubikia panamensis*, *Chaetodactylus micheneri* (s. lat.) (BMOC 03-0310-001), and *Sennertia* sp. 1. *ap′* and *ap″*- anterior and posterior coxal apodemes, respectively. See Fig. 7 to identify muscles by their numeric or letter designations.

Muscle	**Origin**	**Direction**	**Insertion**
Remotor of femur I (1)	Sternum (also *Roubikia*) or posterior part *ap′* I (*Sennertia*)	Anteriad	Posterio-proximal angle of femur I
Remotor of femur I (2–3)	Free *ap′* I	Anteriad	Posterio-proximal angle of femur I
Remotor of femur II (1)	*ap′* II	Anteriad	Posterio-proximal angle of femur II
Remotor of femur II (2)	*ap′* II	Anteriad	Posterio-proximal angle of femur II
Remotor of femur III (1–3)	*ap′* III (*Chaetodactylus* and *Roubikia*) or proximal part of *ap′* III (*Sennertia*)	Posteriad	Posterio-proximal angle of femur III
Remotor of femur IV (1–2)*	*ap′* IV	Posteriad	Posterio-proximal angle of femur IV
Depressor of trochanter I (1–3)	*ap′* II	Anteriad	Ventro-proximal edge of trochanter I
Depressor of trochanter II (1–2)	*ap′* III, ventral edge (*Chaetodactylus* and *Roubikia*) or proximal part of *ap′* III (*Sennertia*)	Anteriad	Posterior part of ventro-proximal edge of trochanter I
Depressor of trochanter III (1–2)	Ventro-distal part of *ap′* III	Posteriad	Anterior part of ventro-proximal edge of trochanter III
Depressor of trochanter III (b)**	Ventro-proximal part of *ap′* III connecting *ap′* III and IV	Laterad	Submedian part of ventro-proximal edge of trochanter III
Depressor of trochanter III (a)	Ventral part of *ap″* III	Anteriad	Submedian part of ventro-proximal edge of trochanter III
Depressor of trochanter IV (1–2)***	*ap′* IV, ventral edge	Posteriad	Anterior part of ventro-proximal edge of trochanter IV
Dorsal levator of trochanter I	Endosternite	Anteriad	Dorso-proximal edge of trochanter I
Vventral levator of trochanter I	Proximal end of *ap′* II	Posteriad and slightly ventrad	Dorso-proximal edge of trochanter I
Levator of trochanter II, dorsal part	Endosternite	Anteriad	Dorso-proximal edge of trochanter II
Levator of trochanter II, ventral part	Proximal end of *ap′* III (*Chaetodactylus* and *Roubikia*) or proximal part of *ap′* III (*Sennertia*)	Posteriad and slightly ventrad	Dorso-proximal edge of trochanter II
Levator of trochanter III	Endosternite	Posteriad	Dorso-proximal edge of trochanter III
Levator of trochanter IV	Endosternite	Posteriad	Dorso-proximal edge of trochanter IV

*A third (most distal) remotor is probably developed in *Sennertia* and *Roubikia*; **not observed in *Sennertia*; ***A third (most distal) depressor is developed in *Sennertia*.

Dermatophagoides (our data, unpublished). In chaetodactylids, muscles originating from the endosternite (*ltd*) always insert on the dorso-proximal rim of trochanters I–IV (Table 2, Fig. 7). Judging from their position, we believe that they are levators with the principal function of elevation (abduction) of the trochanters. They also may serve as remotors, since trochanters are lacking the posterior condyle (except probably trochanter III) and are situated obliquely forward (I–II) or backward (III–IV) in both horizontal and vertical planes. Exactly the same muscles were described in adults of *Sancassania* "*mycophaga*" (Kuo & Nesbitt, 1970). Woodring & Carter's (1974) description of the heteromorphic deutonymph of *Sancassania boharti* is different in that the muscles originating from the endosternite insert on the ventro-proximal rim of the trochanters (their p. 280, Fig. 3). On Figs 6 and 8, however, these authors show these muscles inserting on the dorso-proximal edge of the trochanters, which is consistent with the observations of Kuo & Nesbitt (1970) and our observations. In the oribatid species, *Nothrus palustris*, probably homologous muscles were described as the external remotors of trochanters, inserting on their anterior-lateral surface (Akimov & Yastrebtsov, 1989). In *Listrophorus leuckarti*, these muscles were described as abductors inserting on the dorsal rim of trochanters (as in free living Astigmata) but attached to various parts of the ventral coxal endoskeleton (Wurst, 1993). Chaetodactylids are probably unique in the presence of ventral trochanteral levators I–II (*ltv*) (but see discussion on trochanteral depressors of Kuo & Nesbitt (1970) below). These muscles are attached to the proximal portions of posterior apodeme II and anterior apodeme III, respectively and operate as synergists of the dorsal trochanteral levators I–II. Posterior apodeme II is reduced and probably incorporated into anterior apodeme III. In some *Sennertia*, this complex anterior apodeme III is split into proximal and distal parts. The anterior side of the proximal part serves as an attachment site for trochanteral depressors II, ventral extensions of trochanteral levators (situated more proximally), and dorsoventral muscles. In this genus, the insertion sites of the trochanteral levators I–II and sometime III–IV (*S. koptorthosomae*) form a distinct pattern of three bulges and correspond with four concavities on the sclerotized dorsal surface of the trochanters.

Depressors (adductors) of the trochanters (*dt*) insert on their ventro-proximal rims. Depressors of trochanter I attach to the posterior apodeme of the corresponding coxa, depressors III–IV to the anterior apodemes. There are two additional depressors III attached to the proximal part of anterior apodeme III and posterior apodeme III (posterior group of trochanteral depressors) (Table 2, Fig. 7). However, in *Sennertia*, where coxal

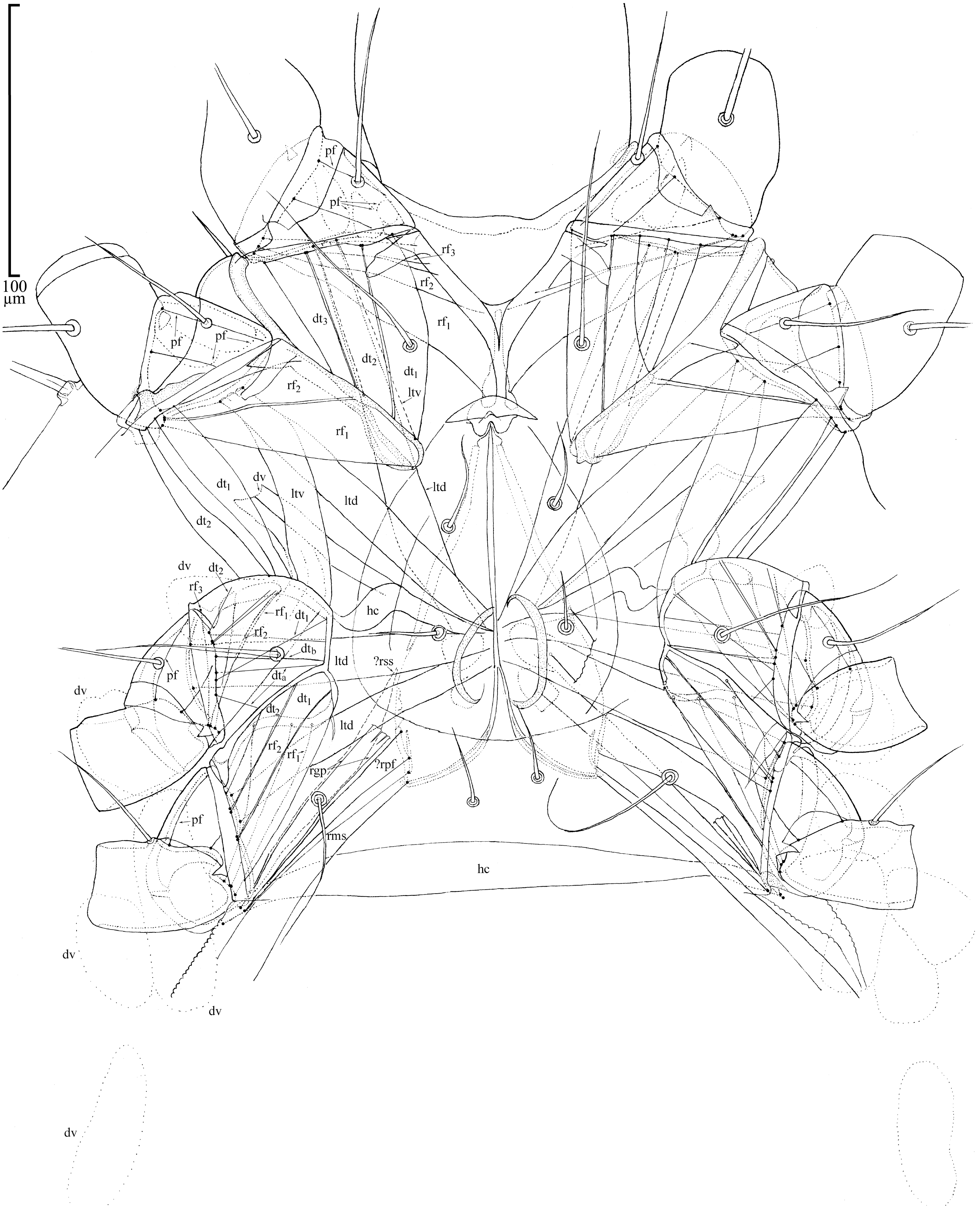

Fig. 7. Coxisternal region of *Chaetodactylus micheneri* s. lat. (BMOC 0310-001). **dt** - depressor of trochanter; **dv** - dorso-ventral muscle; **hc** - hysterosomal constrictor; **lap** - levator of apodeme IV; **ltd** - dorsal levator of trochanter; **ltv** - ventral levator of trochanter; **pf** - promotor of femur; **rf** - remotor of femur; **rgp** - retractors of genital papillae; **rms** - retractor of medial sclerite; **rpf** - retractor of progenital fold; **rss** - retractor of dorsal supporting sclerite of ovipore.

fields III are open, the most anterior depressor in this group is probably absent. As indicated above, in some *Sennertia*, the complex anterior apodeme III is split into proximal and distal parts; trochanteral depressors II attach to the anterior side of the proximal part; the anterior group of trochanteral depressors III attach to the distal part. Nearly the same muscles were described as trochanteral "abductors" (Woodring & Carter, 1974). Those authors state that the muscles insert on dorso-proximal edges of trochanters but on their Figure 6, they depict the muscles inserting on the ventral edges of trochanters. It is difficult to homologize the trochanteral depressors described by Kuo & Nesbitt (1970). According to those authors, the muscles insert on the anterior-dorsal edges of trochanters and always originate from the corresponding anterior apodemes. The points of insertion of "depressors" I–II may suggest that they are homologous to the ventral trochanteral levators I–II described above, however their attachment sites are different. Despite the above discrepancies, the attachment, insertion, and direction of the trochanteral depressors of chaetodactylids almost exactly correspond to those of *Listrophorus leuckarti* (Wurst, 1993), suggesting that this pattern may be conserved in Astigmata.

Anterior apodemes I–IV serve for attachments of well developed femoral remotors (extensors) *rf* (Table 2, Fig. 7). Their antagonists, femoral promotors (flexors) *pf*, originate on the trochanters and are discussed in section on Legs (p. 31). Femoral remotors insert on posterio-proximal angles of femora I–IV. On coxae III–IV, trochanteral depressors overlap femoral remotors and the latter are situated more dorsally. Coxa III of many species of the genus *Sennertia* is an exception, because anterior apodemes III are separated into proximal and distal parts, and the latter serves for attachment of femoral remotors. Our observations are consistent with the descriptions of femoral remotors and promotors of *Sancassania boharti* and *L. leuckarti* (Woodring & Carter, 1974; Wurst, 1993). In *Nothrus palustris*, femoral extensors are also more or less similar, but femoral flexors attach to the coxal apodemes (Akimov & Yastrebtsov, 1989). The latter was also described for *Sancassania "mycophaga"* (Kuo & Nesbitt, 1970), but the identity of the femoral muscles was probably misinterpreted in this species.

Non-locomotory muscles of the coxisternal region include muscles operating various structures of the progenital opening and some muscles that supposedly create hydraulic pressure: dorsoventral and transverse hysterosomal constrictors. Posterior apodeme IV is the smallest apodeme, but it serves as an attachment site for a large number of various muscles, principally muscles of different structures of the progenital chamber. In some *Sennertia*, this apodeme is spit into distal and proximal parts, and the latter is shifted anteriorly and is the attachment site for the above muscles. We were able to find at least five such muscles with unclear insertion points: one probably inserts on the posterio-lateral edge of the progenital folder, another one on the stick-like supporting sclerites, the remaining three muscles usually group together and are probably retractors of the genital papillae. The only other pair of muscles associated with the progenital opening, posterior retractors of the medial fold, attach to the anterio-ventral opisthosoma or to the proximal part of posterior apodeme IV on the posterior-ventral podosoma (some *Sennertia*). A pair of muscles originating on the endosternite, just posterior to trochanteral levators IV, is also connected to posterior apodeme IV. The function of these muscles is unknown, but they probably are constrictors or fixators. A well developed transverse muscle connecting the two posterior apodemes IV (Fig. 7) is probably a constrictor. The dorsal surface of the posterior apodeme serves for the attachment of two bundles of dorsoventral constrictors. The proximal part of apodeme III is also an attachment point for a complex of dorsoventral muscles and a transverse muscle connected to the endosternite (Fig. 7). This also applies to some *Sennertia*, where the proximal part of the apodeme is separated from the distal one.

Claparède's organs

Claparède's organs are paired, usually cylindrical structures, situated on the prosoma of the prelarva and larva but not in other instars of acariform mites. Although Claparède's organs originate on coxal fields I, they actually derive from the coxal region of legs II (Thomas & Telford, 1999). It was also demonstrated that Claparède's organs are homologous to the lateral organs of other arachnids (Thomas & Telford, 1999), and Fashing (1984) and Fashing & Marcuson (1996) indicated their possible homology with the axillary organs of aquatic astigmatid mites of the family Algophagidae. Claparède's organs and genital papillae (see p. 30) have a similar ultrastructure and are considered to be water uptake or osmoregulatory organs in terrestrial or aquatic Acariformes, respectively (Alberti, 1979; Fashing, 1988). Typical Claparède's organs have been studied in Astigmata only in *Naiadacarus arboricola* (Acaridae), which is an aquatic species (Fashing, 1988). Like genital papillae, it is a cylindrical shaft terminating in a dome with an apical cavity. The organs are unicellular, with numerous placations of the plasma membrane and associated mitochondria in the distal region, while the nucleus is in a cellular extension below the cuticle of the prosoma; neural connections are probably absent. Claparède's organs differ from genital papillae by some ultrastructural details and the lack of musculature (Fashing, 1988).

In chaetodactylids, Claparède's organs are developed in larvae of *Roubikia* and *Chaetodactylus* and absent in all studied *Sennertia*. In the former two genera the organs are situated nearly in the middle of each coxal field I, in close association with setae *1a* (Fig. 14 *I*, *J*, Fig. 19 *A*). Their external morphology corresponds to that outlined above, with the shaft and dome (Fig. 14 *I*, *J*). The shaft in *Roubikia* is slightly asymmetrical, distinctly narrowing terminally and ending in a button-shaped dome. In *Chaetodactylus*, the shaft is more or less cylindrical, constricted apically, and ending in a spherical, transparent dome with a distinct apical cavity (Fig. 14 *I*).

Opisthosomal glands

Opisthosomal glands are paired, relatively large unicellular structures situated under the cuticle on each side of the opisthosoma in all active instars. An opisthosomal gland includes a large vesicular portion filled with highly refractive liquid and a duct that opens to the outside by a crescent-shaped orifice that is covered by a cuticular flap. Both the vesicular portion and duct are lined with cuticle. Hypodermal cytoplasm underlying the cuticle of the vesicular part has several characteristics of a secretory cell. Muscle fibers associated with the gland are probably involved in the intermittent expulsion of the volatile and liquid component of the glands. The gland secretion is best characterized as a dilute solution of non-hydrocarbons (mostly oxygenated terpenes) in hydrocarbon solvents (Howard *et al*., 1988). The cuticular flap ("hinged trapdoor") is probably capable of opening and closing the gland orifice, and its "hinge" portion ensures that upon depression of the "trapdoor" the glandular components will be discharged over the rear part of the mite body (Howard *et al*., 1988). Opisthosomal glands are shed and the new glands are formed from undifferentiated embryonic cells in the hypodermis at each molt (Brody & Wharton, 1970). Sakata & Norton (2001) speculated that the opisthosomal glands had evolved in the "glandulate" oribatids and ancestrally their secretion had a repugnatorial function. In derived taxa, most notably the Astigmata, the functions of the glands have diversified, as they contain substances that act as alarm pheromones or attractants (Nishimura *et al*., 2002; Hiraoka *et al*., 2003), aggregation (Kuwahara *et al*., 1982; Shimizu *et al*., 2001) and sex pheromones (Ryono, 2001), and antifungal agents (Kuwahara *et al*., 1989).

In feeding instars of chaetodactylids, opisthosomal gland openings are usually anterio-medial to setae e_2, but not more anterior than the transverse level half way between the levels of setae e_2-d_2 (*Roubikia*, *Chaetodactylus*, and *Sennertia vaga*). In derived *Sennertia*, the orifices of the opisthosomal glands tend to shift posteriorly. In females of *Sennertia americana*, the gland orifices are posterio-medial to e_2, in males and tritonymphs, they are situated nearly at the same level as e_2, and in earlier instars they retain the ancestral anterio-medial condition. In adults of *S. scutata* and *S. koptorthosomae*, the gland orifices are situated nearly at the same transverse level as e_2. In *S. splendidulae*, the opisthosomal gland orifices are distinctly posterior to e_2.

In chaetodactylid deutonymphs, the opisthosomal gland orifices are anterior-medial to e_2 in all the genera. The trend of posterior displacement described for adults of *Sennertia* above is evident in the deutonymphs as well, and the gland orifices are situated very close to setae e_2 but usually not posterior to them. The orifices of the glands are situated on the hysterosomal shield in all genera, although in some species of *Sennertia* they are situated on a soft cuticle outside the hysterosomal shield.

Attachment organ

The attachment organ is developed only in heteromorphic deutonymphs. It serves for attachment to smooth cuticular surfaces using low pressure created by its setal alveolar derived suckers and probably adhesive forces created by its cuticular "suckers" (Woodring & Carter, 1974). Ancestrally, the attachment organ comprises two pairs of suckers (modified alveoli of adanal setae) and surrounding sclerotized supporting flanges, two pairs of conoids and a pair of alveoli (modified pseudanal setae), five apodemes with exterior surfaces forming five cuticular suckers, a small anal opening, and a transparent marginal cuticular membrane. In addition, the posterior part of the progenital chamber may be incorporated into the attachment organ (p. 30). The apodemes of the attachment organs are often complemented by corresponding apodemes protruding ventrally from the hysterosomal dorsum, most notably for the lateral and posterior unpaired apodemes of the attachment organ. Anteriorly the attachment organ is bordered by the progenital chamber and, in *Roubikia*, *Centriacarus*, and *Achaetodactylus*, by posterio-median extensions of posterior apodeme IV. Posteriorly it is bordered by the posterio-lateral sclerite. This sclerite also connects apodemes associated with conoidal setae ps_1 and ps_2. The outlines of the attachment organ (including the marginal membrane) vary from transversely elongated (*Achaetodactylus*), subpentagonal or subrectangular (*Roubikia*, *Centriacarus*, some *Sennertia*), to longitudinally elongated (some *Sennertia* and to a lesser extent, *Chaetodactylus*) (Fig. 8).

Two pairs of suckers of the attachment organ are derived from alveoli of three pairs of anal setae. Two of them, ad_1 and ad_2, are fused together forming a single sucker on each side, while ad_3 forms the other pair. The central sclerite of the latter has one perforation, and the sclerite of the former has two (Fig. 8). The two sclerites formed by ad_1+ad_2 and ad_3 are attachment sites for retractor muscles originating from the dorsal wall of the hysterosoma (Woodring and Carter, 1974). Contraction of these muscles creates inward bowing of the sucker and the low pressure necessary for attachment. Suckers ad_3 are usually smaller than ad_{1+2} and positioned posterior to the progenital chamber, with suckers ad_{1+2} posterior to ad_3. The suckers are attached to sclerotized flanges by flexible cuticle, sometimes forming large transparent cuticular rings (Fig. 8 *D*). The sclerotized flange of the median sucker (ad_{1+2}) is socket-like, always well developed and sclerotized, with alveoli of ps_3 on its anterior edge (Griffiths *et al*., 1990). In contrast, flanges of suckers ad_3 are less developed. They are always fused to the anterior edge of supporting flanges of ad_{1+2} and their visible sclerotized part surrounds at most only the anterior and outer area of the sucker (Fig. 8 *A,D,E*). In *Achaetodactylus*, the anterior part is not developed (Fig. 8 *B*). In the genus *Chaetodactylus*, the development of flanges of sucker ad_3 substantially varies. In species belonging to early derivative lineages (*Ch. azteca, Ch. melitomae, Ch. ludwigi*) the flanges are present; in *Ch. osmiae*, the anterior and lateral parts of the flange are "interrupted"; and in many other species (*e.g.*, *Ch. krombeini*, *Ch. micheneri*) the whole structure is weakly sclerotized and difficult to see.

Conoids are hollow, pear-shaped, birefringent structures otherwise similar to setae (Fig. 8). Unlike the suckers they do not have any muscles. The function of the conoids is unknown.

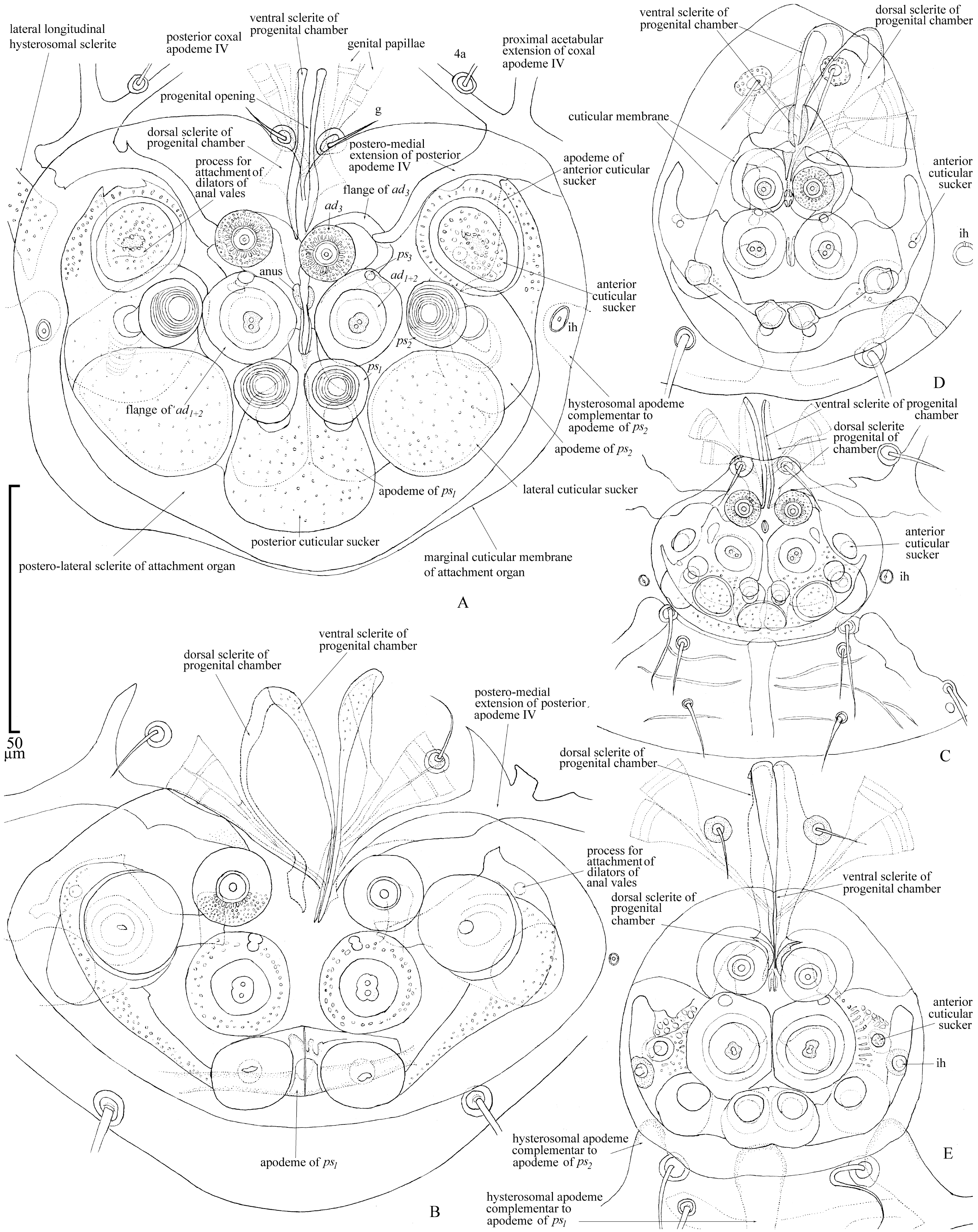

Fig. 8. Attachment organ in Chaetodactylidae: A - *Roubikia panamensis* (BMOC 91-0103-007); B - *Achaetodactylus leleupi* (BMOC 04-0508-279); C - *Centriacarus turbator* (BMOC 04-0508-237); D - *Sennertia americana* (BMOC 90-1212-025); E - *Chaetodactylus azteca* (BMOC 96-0510-139).

Woodring & Carter (1974) found nerves entering conoids of the attachment organ of *Sancassania boharti* (Acaridae) and speculated that they may have a sensory function, while Fain (1973, 1985) believed that conoids serve to detach mites from their hosts. Conoids ps_1 and ps_2 are usually rounded in outline, but in some *Sennertia* or *Chaetodactylus* they have two lateral concavities (*e.g.*, *S. argentina*, *S. surinamensis*, *Ch. krombeini*) or two lateral bulges (*e.g.*, *S. americana*, *S. faini*). Conoids ps_1 are invariably posterior to the median suckers, either inserted far from the posterior border of the attachment organ (*e.g.*, *Roubikia*) or close to it (*e.g.*, *Achaetodactylus*), depending on whether their apodemes are developed or not. The relative position of conoids ps_2 varies greatly. They may be at the same level as ps_1 and touching them, with their respective apodemes fused (*e.g.*, *Sennertia tanythrix*), anterior to the level of ps_1 and posterior to the central level of the median suckers (*Centriacarus*, many *Chaetodactylus* and *Sennertia*), at the central level of the central suckers (*e.g.*, *Roubikia*, *Ch. osmiae*), or anterior to this level (*Achaetodactylus*; *Ch. nipponicus*). In the latter three cases, apodemes ps_1 and ps_2 are usually connected by the posterio-lateral sclerite. Alveoli of setae ps_3 are always apparent, situated on the anterio-central (*e.g.*, *Roubikia*, *S. americana*), anterio-proximal (*Achaetodactylus*), or anterio-distal (*e.g.*, *Centriacarus*) edge of the supporting flange of the median suckers.

Apodemes of the attachment organ include the unpaired posterior apodeme and the pared lateral and anterior apodemes. The former two are associated with conoids ps_1 and ps_2, respectively; the latter is not associated with any setal derivatives. The posterior and lateral apodemes are connected by the posterio-lateral sclerite that delimits sclerotized borders of the attachment organ in this region. The surfaces of each apodeme may form a maximum of five cuticular "suckers" (Fig. 8 *A*), probably contributing to the mechanism of adhesion (Woodring & Carter, 1974). The posterior apodeme may comprise two separate apodemes of ps_1 (*Centriacarus*). These apodemes are partially fused anteriorly in *Roubikia* and are completely fused in the remaining genera, forming a single unpaired apodeme. *Roubikia* is unique in that apodemes of ps_1 form a distinct medial process extending between the median suckers; *Achaetodactylus* is unique in that these apodemes are very narrow, band-like and transverse (Fig. 8 *A*, *B*). The position of the lateral apodemes follows that of conoids ps_2 (see above). The cuticular suckers of apodemes ps_1 and ps_2 may be absent (*Achaetodactylus*, *Chaetodactylus*, *Sennertia*) or developed (*Roubikia* and *Centriacarus*). In *Roubikia*, they are larger than the central suckers, while in *Centriacarus* they are distinctly smaller. The position and development of the anterior cuticular suckers and their apodemes is generally correlated with the above character. It is present and well developed in *Roubikia*, *Centriacarus*, and some *Chaetodactylus* (*e.g.*, *Ch. ludwigi*, *Ch. melitomae*) and vestigial or absent in all *Achaetodactylus*, *Sennertia*, and several *Chaetodactylus*. In the latter three genera (including all species of *Chaetodactylus*), the base of the sucker is incorporated to the posterio-lateral sclerotized border of the attachment organ, while in the former two genera it is inserted on a separate apodeme, which may touch or overlap the border (*Roubikia*). Irrespective whether the anterior apodeme is separate or incorporated, there is a distinct process serving as an attachment site for the dilators of the anal valves. This process is conspicuous in large species (*Roubikia*, *Achaetodactylus*) and inconspicuous in small ones (*Centriacarus*, *Sennertia*, *Chaetodactylus*) as well as in large *Sennertia* (*e.g.*, *S. surinamensis*). Species of the genus *Chaetodactylus* are distinct in having cupule *ih* incorporated into the posterio-lateral sclerite (Fig. 8 *E*). In all other genera, these cupules are lateral to the attachment organ. *Sennertia horrida* is distinct in having long, thin anterior extensions of the posterio-lateral (marginal) sclerite and apodemes of ps_2. The former almost touch each other at the progenital chamber, forming a characteristic semicircular outline. The extensions of ps_2 apodemes are almost straight, converging toward the midline and leaving large areas of unsclerotized cuticle between them and the extensions of posterio-lateral sclerite.

The anus is fully incorporated into the attachment organ and is described in the corresponding section (p. 28). Characters discussed above are summarized in Table 3.

Table 3. Distribution of characters of the attachment organ and neighboring structures in five genera of Chaetodactylidae. Centr = *Centriacarus*, Roub = *Roubikia*, Achaet = *Achaetodactylus*, Chaet = *Chaetodactylus*, Senn = *Sennertia.*

Character	**Centr**	**Roub**	**Achaet**	**Chaet**	**Senn**
Conoids ps_1 and ps_2: smooth (0); with concentric pattern (1)	0	1	0	0	0
Conoids ps_1 and ps_2 in outline: rounded (0); 2 lateral concavities (1); 2 lateral bulges (2)	0	0	0	1	0,1,2
Cuticular suckers of apodemes ps_1 and ps_2: developed (0); absent (1)	0	0	1	1	1
Apodemes of ps_1: separated (0); partially fused anteriorly (1); completely fused (2)	0	1	2	2	2
Anterior cuticular suckers: well-developed (0); vestigial or absent (1)	0	0	1	0,1	1
Bases of anterior cuticular suckers (if developed): inserted on a separate apodeme (may touch or overlap posterio-lateral sclerotized border of the attachment organ) (0); incorporated to the border or absent (1)	0	0	1	1	1
Ventral longitudinal sclerites of progenital chamber conspicuous, evenly developed on their full length (0); better developed in posterior part (1), inconspicuous on their full length (2)	0	0	0	2	1
Anus situated: at level of ad_{1+2} (0); ad_3 (1); at level between these suckers (2); ? absent (3)	2	0	3	1	1
Cupule *ih* free, lateral to attachment organ (0); incorporated to posterio-lateral sclerite of attachment organ (1)	0	0	0	1	0

Reproductive system

The external genitalia of Astigmata supposedly have an epidermal origin. They include three groups of structures associated with the male aedeagus, female ovipore and inseminatory canal. Despite the fact that these structures are of great importance for both species and supraspecific systematics, there is no generally accepted terminology. Several terms are conventionally used in descriptive papers but sometimes they may refer to different structures or may be inconsistent with the terminology in anatomical papers. To describe external genitalia of chaetodactylids and find structural homologies in both males and females and among other Astigmata, we use terminology derived from the works of Baker & Krantz (1985), Grandjean (1938), Evans (1992), Knülle (1959), Prasse (1970), and Witaliński *et al*. (1990). Knülle (1959) and Prasse (1970) applied the term epigynum to homologous structures of both females and males. In the latter case, the use is semantically incorrect, as the second root of the compound word indicates that it pertains to a female. To preserve uniform notations for these structures, we follow Evans (1992) and use the term medial lip.

Female Genitalia include two distinct systems associated with the ovipore and the copulatory opening. The ovipore is ventral, situated in the progenital chamber between coxal fields II–IV (*Roubikia*) or I–IV (*Chaetodactylus*, *Sennertia*) (Fig. 27). Structures associated with the ovipore include progenital folds, diachilous cavities with genital papillae (p. 30), genital setae, supporting sclerites of the preoviporal canal, unpaired medial fold with shield, anterogenital sclerite, and undulate lamina continuous with the preoviporal canal[4] (Fig. 10 *G*). Except for retractors of the medial fold, muscles operating various structures associated with the ovipore are attached to the posterior apodeme IV (see p. 20). Progenital folds (progenital lips, genital valves) form the ventral wall of the progenital chamber in acariform mites (Evans, 1992); they cover the ovipore and, partially, the medial sclerite in Astigmata. Anteriorly they are close to each other and fused to the pregenital sclerite, and posteriorly they are diverging and forming an inverted "V" or "Y". The pregenital sclerite (=anteroventral sclerite, epigynal apodeme or epigynum in descriptive papers but not in anatomical papers), is represented by a transverse, somewhat arched sclerite situated at the anterior end of the ovipore. In *Sennertia*, its lateral ends are fused with anterior coxal apodemes I. In descriptive papers, progenital folds are called the genital valves. The pregenital sclerite and posterior ends of the progenital folds are insertion sites for muscles that retract the extruded the ovipositor and associated sclerites (Prasse, 1970). The progenital folds have paired cavities that open ventrally (diachilous slits) and divide the folds into outer and inner progenital folds. The edges of the cavities are transparent so the opening is difficult to see when the genital papillae are protracted. Diachilous sclerites (Fig. 10 *G*) are situated at the outer side of the diachilous slit; they are well-developed, relatively short, and measure about one third (*Roubikia*) or one forth (*Sennertia*, *Chaetodactylus*) the length of the progenital folds. Two pairs of eversible genital papillae are situated at the bottom of the diachilous cavities. External progenital folds in Chaetodactylidae are transparent, whereas the ventral and dorsal sides of the inner folds are partially sclerotized, and these sclerites are connected to the posterior lobes of the medial sclerite (see below) (Fig. 11, Fig. 10 *G*). Posteriorly, the inner fold flanks and partially covers the medial fold, and anteriorly it covers (in repose) the undulate lamina of the ovipositor and the ovipore itself. The medial fold is accompanied by a large medial shield that has the shape of an inverted "V" and is the most distinctive part among other structures associated with the ovipore (Fig. 10 *G*, Fig. 11). The anterior point of the medial shield almost reaches the pregenital sclerite, and in *Chaetodactylus* its two posterior parts form a distinct posterior boundary as in *Glycyphagus* (*Lepidoglyphus*) (see Knülle, 1959, Fig. 410). In *Sennertia* such a boundary is not developed. The undulate lamina of the ovipositor normally does not extend externally and is hidden by the inner progenital folds at the level of the genital papillae; it is continuous with the preoviporal canal (=vagina, meatus ovi, see Evans (1992)). Well-developed supporting sclerites of the preoviporal canal are not known outside Chaetodactylidae. The sclerites are paired, long, rodlike structures situated under the medial sclerite and diverging posteriorly according to the diverging progenital folds and the posterior lobes of the medial sclerite (Fig. 10 *G*). Their anterior ends are slightly posterior to the pregenital sclerite, and they are probably connected to the latter by means of transparent, tendon-like bars; their posterior ends have the same tendon-like bars and are situated near posterior edges of the progenital folds (*Sennertia*) or near the diachilous slits (*Roubikia*, *Chaetodactylus*). These sclerites may somehow participate in expanding or retracting the preoviporal canal. Positionally, the supporting sclerites of the preoviporal canal are probably homologous to sclerites *Tp* described for males of *Glycyphagus destructor* by Prasse (1959). They also may be homologous to the long sclerites at the base of the aedeagus of many males of *Sennertia* ("dorsal supporting sclerites") (Fig. 10 *A*).

The *copulatory opening* is situated at the posterior end of the opisthosoma at the base of a shallow depression formed by sclerotized cuticle. In *Sennertia vaga* and *Ch. osmiae*, the depression and the opening are situated on the top of an external copulatory tube. The copulatory opening leads through a relatively narrow inseminatory canal to the spermatheca. The shape of the copulatory opening is species-specific (Walzl, 1992). In *Roubikia panamensis*, the inseminatory canal is well-sclerotized, cylindrical, wide (about 10 μm), and distinctly protrudes inside the spermatheca. In *Chaetodactylus* and *Sennertia*, the inseminatory canal is usually transparent, trumpet- or funnel-shaped, narrow (less than 10 μm), and widened at the spermatheca but not protruding inside it. A short portion of the inseminatory canal near the copulatory opening is well sclerotized and transversely striated (Fig. 9 *B*, *E*, *F*), indicating the possi-

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[4] The undulate lamina is probably homologous to the ovipositor of oribatid mites, cf. Fig. 63 (Hammen, 1989) and Fig. 9 (Prasse, 1970).

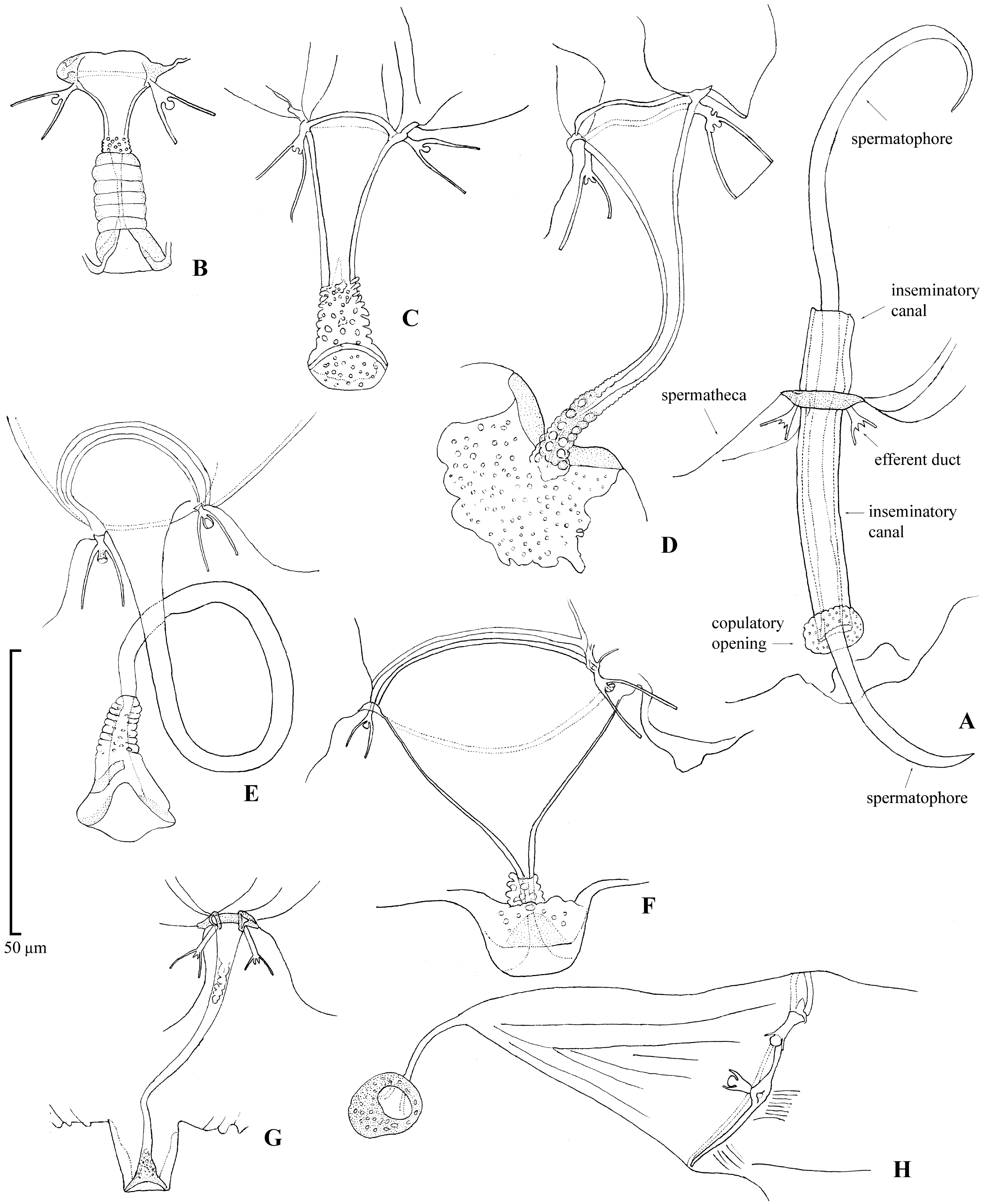

Fig. 9. Spermatheca and inseminatory canal of Chaetodactylidae. A - *Roubikia panamensis*; B - *Chaetodactylus reaumuri*; C - *Ch. zachvatkini*; D - *Ch. krombeini*; E - *Ch. micheneri*; F - *Ch. osmiae*; G - *Sennertia vaga*; H - *S. americana*.

ble presence of constrictor muscles. These striated areas were not observed in *Roubikia*, the only known genus for which endospermatophores are known (see below). The shape of the inseminatory canal is an important diagnostic character for chaetodactylid species. The basal (ventral) part of the spermatheca is connected with the ovaries via two efferent ducts (sclerites of ovaries) and transitory cones. The efferent ducts, appearing as "Y"-shaped sclerotized structures in conventionally mounted mites, are situated on the sides of the inseminatory canal entering the spermatheca. Two small, variously shaped valves (Fig. 9 *G*, *H*, *E*) are located at the bottom of the lateral prongs of the "Y". In *Sennertia americana*, the lateral prongs are very short and the valves globular and as large as the prongs.

In *Acarus siro*, part of the spermatheca at the entrance of the inseminatory canal is a distinct structure called the basal part of the spermatheca (Witaliński *et al*., 1990). These authors state that both the inseminatory canal and the basal part of the spermatheca are lined by cuticle indicating that they have the same origin. Unlike these structures, the wall of the saccular part of the spermatheca is formed by cells covered only by long, numerous microvilli. In *Sennertia* and *Chaetodactylus*, the basal part of the spermatheca is continuous with the inseminatory canal without any distinct boundaries (Fig. 9 *B–H*). In *Roubikia*, there is a basal sclerite with two efferent ducts at the place where the inseminatory canal enters the spermatheca (Fig. 9 *A*).

Spermatophores (Griffiths & Boczek, 1977) are present in *Roubikia*, but they are probably absent in other genera of chaetodactylids with known females. In *Roubikia panamensis*, we found 2–4 spermatophores in each of four known females. Spermatophores were situated in the spermatheca, and in each female, one spermatophore projected through the inseminatory canal and copulatory opening to the outside. The spermatophores are transparent, filariform, 204–289 μm long and 4 μm wide, with one distinctly pointed end. Based on their shape, length and the presence of a filariform "esophagus", OConnor (1993a) suggested that these structures are nematodes of the order Oxyurata. However, after restudying the same material, we were unable to verify a distinct esophagus and now believe these to be spermatophores. Although *Roubikia* spermatophores are exceptionally long, their shape and, especially, the presence of a pointed tail are consistent with some other astigmatid spermatophores (for example, Fig. 11 in Griffiths & Boczek, 1977).

Male genitalia include progenital folds with sclerites, genital papillae (p. 30), genital setae, aedeagus, dorsal supporting sclerite, and a genital capsule that presumably is homologous to the medial fold of females (Fig. 10 *A–F*, Fig. 12).

In *Roubikia* and *Chaetodactylus*, unlike some other astigmatid mites (*Sancassania*, *Glycyphagus*), progenital folds cover only a small anterior portion of the genital capsule and aedeagus (this is probably also true for *Sennertia*, for which distinct medial boundaries of progenital folds were not observed). The folds have a pair of sclerites, which are probably homologous to the sclerites of the inner progenital fold of females (these sclerites are also present in other Astigmata, for example in *Sancassania* and *Glycyphagus*). The shape and position of these sclerites relative to the genital capsule provide valuable phylogenetic information. In *Roubikia*, they are much smaller than the progenital folds and look like two bands folded and touching each other in the middle and situated anteriorly to the genital capsule (Fig. 12 *A*). In some *Sennertia*, progenital sclerites are large, presumably expanding onto the entire progenital fold, distinctly separated or slightly touching anteriorly, and situated on the anterior sides of the genital capsule (Fig. 10 *B,C,E*). Finally, in *Chaetodactylus*, these sclerites are fused to a large, single sclerite that greatly expands anteriorly from the level of the genital capsule (Fig. 10 *F*, Fig. 12 *A–E*). A diachilous slit is probably present in all males of chaetodactylids, but it is difficult to see because of its transparent edges. We were able to observe a distinct slit on the progenital folds only in *Roubikia* (Fig. 12 *A*). In *Chaetodactylus micheneri*, fused progenital folds form two transparent flaps that flank the anterior part of the genital capsule (Fig. 10 *F*).

A distinct pregenital sclerite is absent in males of Chaetodactylidae (present in *Glycyphagus*). We also were unable to find its characteristic fork-like process described by Knülle (1959) for *Glycyphagus* (*Lepidoglyphus*) *destructor*.

The position of genital setae *g* and pseudanal setae ps_3 substantially varies among the chaetodactylid genera. In *Roubikia*, genital setae are represented by a transparent disk situated on well-sclerotized alveoli in front of the progenital sclerites, while pseudanal setae ps_3 are lateral to these sclerites. In *Chaetodactylus* and some *Sennertia*, setae *g* are short, transparent mammillae situated on distinct alveoli on the progenital shields; setae ps_3 are distinctly posterior to the progenital sclerites, usually situated on their own sclerites. The latter may be fused with the progenital sclerites (some *Sennertia*, Fig. 10 *B–E*). Setae *g* may be filiform in other *Sennertia* (*Sennertia faini, S. scutata*; males of *S. koptorthosomae*). Pseudanal setae ps_3 are filiform (Fig. 10 *A,D,E*) or spiniform (Fig. 10 *B,C*).

The genital capsule is probably a derivative of the medial fold and, in general, it extends posteriorly from the progenital sclerites. Its ventral wall is formed by a large, flat ventral shield (medial sclerite, Fig. 12 *A*). Its lateral walls are formed by lateral sclerites that usually are fused anteriorly, forming a fulcrum that supports the aedeagus during its protraction. If the aedeagus is long, the dorsal side of the ventral wall of the genital capsule often forms a groove that fits the aedeagus and provides additional support (Fig. 12 *D*). At the ventral side of the fulcrum, there are two pairs of small mammillae, often appearing as alveoli in dorsoventral view. In *Sancassania*, the anterior pair of mammillae is called the tactile organs and the posterior pair is called the suction caps (Prasse, 1970). Walzl (1991) suggested that the two pairs of terminal organs located on the genital capsule ("transmission sclerites") are both sensory organs in *Dermatophagoides farinae* and *D. pteronyssinus*. He also reported that nerves passed through the dorsal supporting sclerite ("basal sclerite"). In these species, the aedeagus and the terminal organs ("tips of transmission sclerite") are inserted into the copulatory opening of the female during

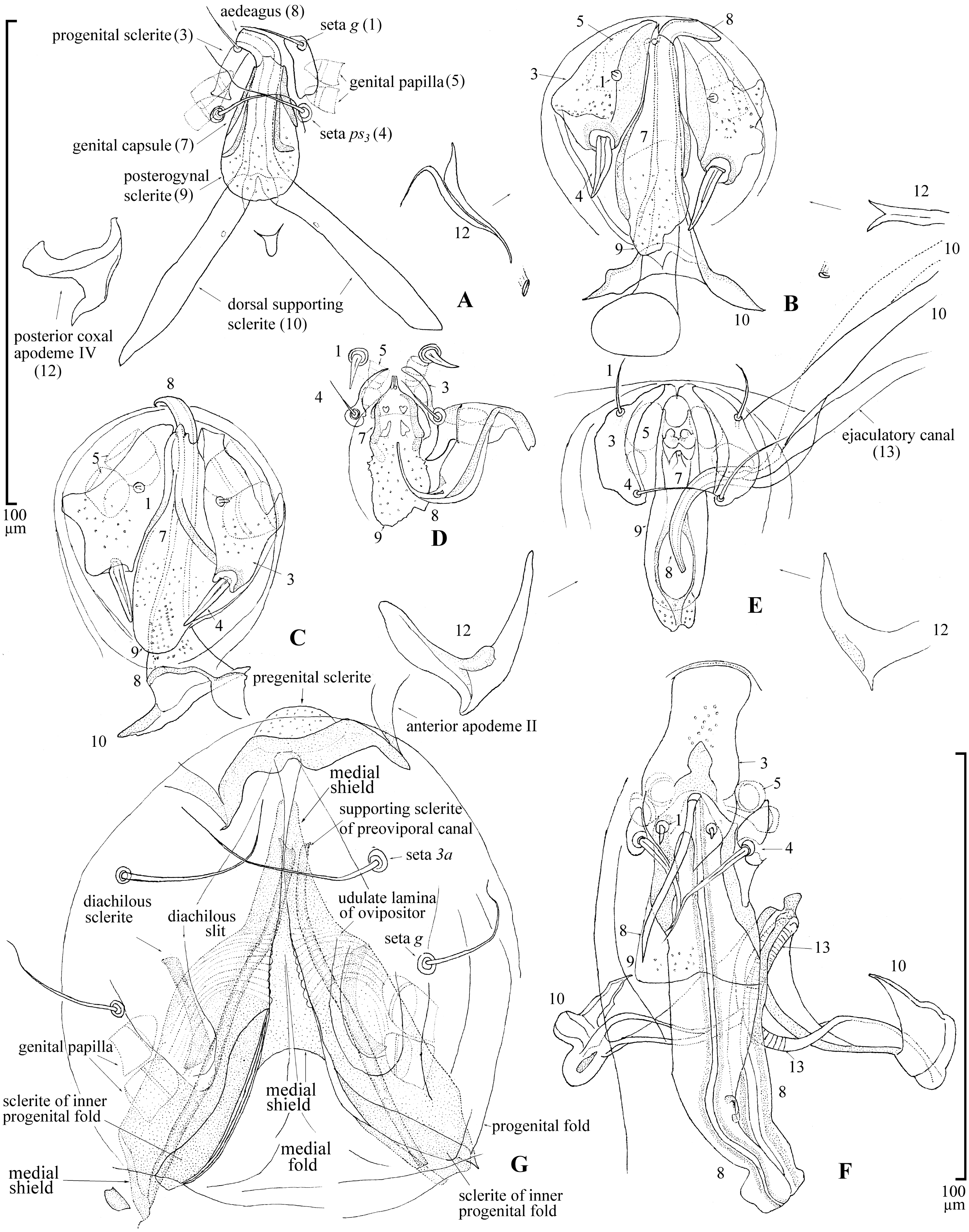

Fig. 10. Male and female external genitalia. Male: A - *Sennertia scutata*; B,C - *S. americana*; D - *S. vaga*; E - *S. koptorthosomae*; F - *Chaetodactylus micheneri*. Female ovipore: G - *Sennertia scutata*. Scale bars: top left corner: A-E,G; right bottom: F. B-E - aedeagus is artificially displaced.

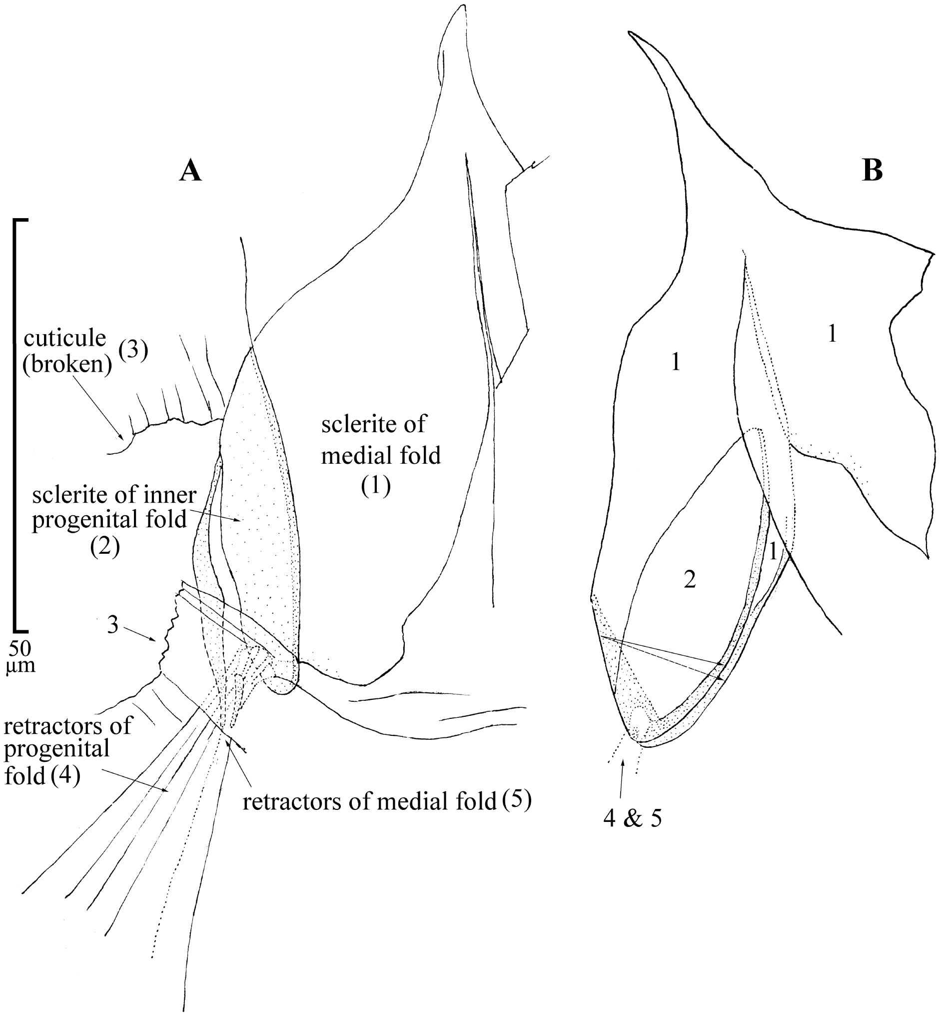

Fig. 11. Progenital and medial folds of female progenital opening: A, B - *Sennertia scutata* (right part of medial sclerite is broken).

mating (Walzl, 1992). In chaetodactylids these structures are exceptionally small, often appearing only as alveoli on the sclerotized wall of the genital capsule (Fig. 12 *B, E*). The aedeagus is a strongly sclerotized intromittent organ. The shape and length of the aedeagus varies substantially in the family. In *Roubikia* it is straight, short and wide, with a blunt external end and a clearly visible ejaculatory duct and external orifice (Fig. 10 *E,F*). In *Chaetodactylus*, the aedeagus is often bent, long and thin, with a sharply pointed external end to the lateral ejaculatory orifice; the ejaculatory duct is not visible in the aedeagus. *Sennertia* have thin or thick aedeagi but, unlike *Roubikia*, they are always bent (Fig. 10 *A–E*). Some *Chaetodactylus* have the aedeagus consisting of two distinct parts: a more widened distal part and a thin proximal part (Fig. 12 *B,E*). In other species of Chaetodactylidae, aedeagi are uniform in width, or there is no abrupt boundary between the widened distal and the thin proximal part. *Chaetodactylus micheneri* has a unique aedeagus, exceptionally long, bent twice and accompanied by a band-like sclerite. Probably, like in *Glycyphagus*, the aedeagus is extruded forward suggesting proconjugate copulation.

The dorsal supporting sclerite is most developed in *Chaetodactylus*, where it has at least two paired lateral processes that superficially give the sclerite the appearance of a vertebra in superior or inferior view. *Chaetodactylus micheneri* is an exception, with lateral processes of the dorsal supporting sclerite spirally twisted, band-like, and the sclerite not having an appearance of a vertebra. In *Sennertia*, there is only one pair of lateral processes, and they are usually short. It is unknown whether these structures are homologous to the dorsal supporting sclerite or whether they are transverse extensions of the base of the aedeagus. In *Sennertia scutata*, however, these processes are very long (Fig. 10 *A*) and resemble the supporting sclerites of the preoviporal canal of the female. As was mentioned above, these sclerites are probably not homologous to the forked sclerite described by Knülle (1959) for *Glycyphagus destructor*. In *Roubikia*, the lateral processes of the supporting sclerite are not developed at all, and muscle retractors are probably attached to the wide base of the aedeagus. Chaetodactylids are distinct compared to acarids or glycyphagids by the disassociation of the dorsal supporting sclerite from the medial sclerite. In *San-*

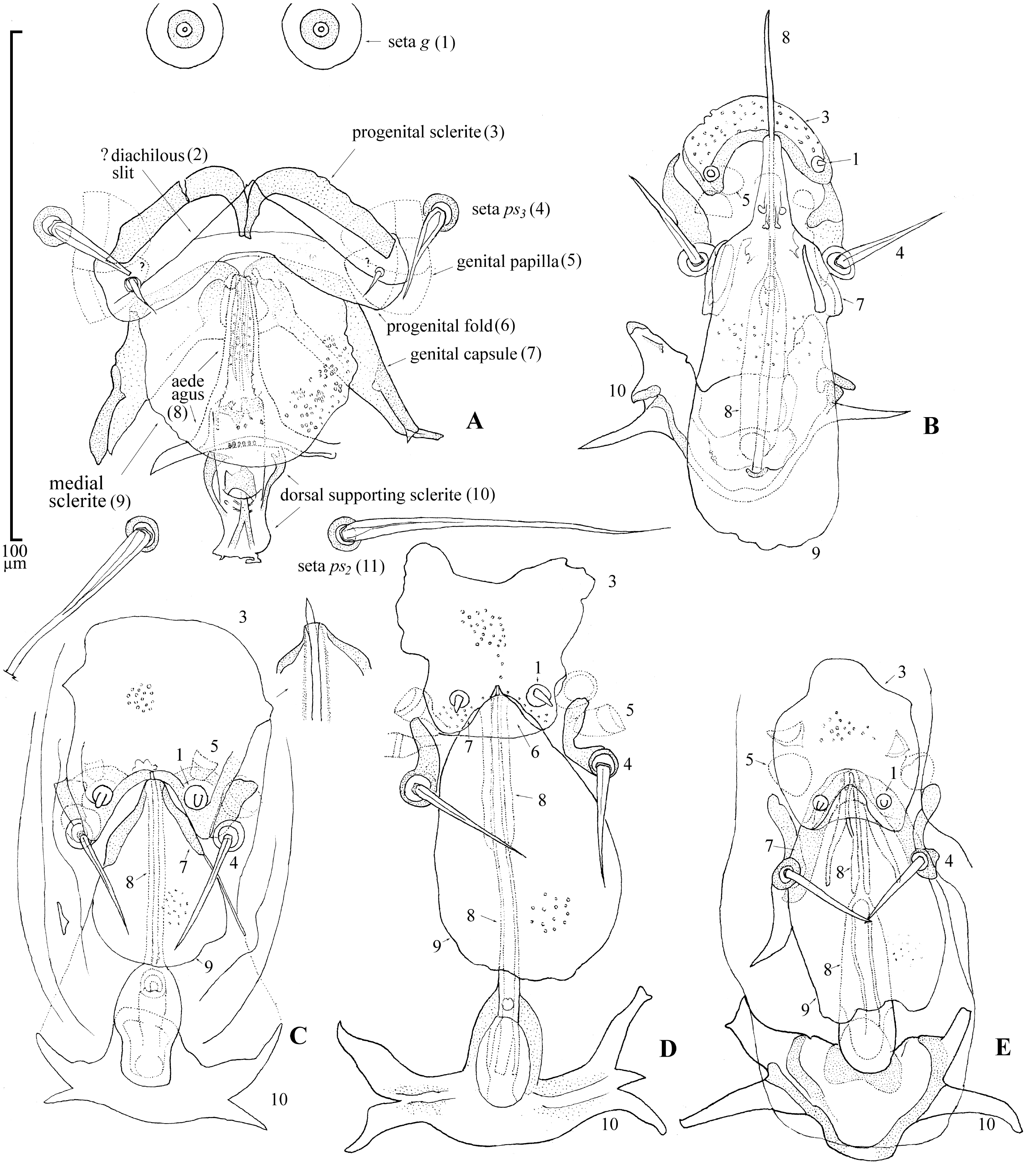

Fig. 12. Male external genitalia: A - *Roubikia panamensis* (homeomorphic male); B - *Chaetodactylus reaumuri*; C - *Ch. osmiae*; D - *Ch. zachvatkini*; E - *Ch. krombeini*.

cassania and *Acarus* (Acaridae), this sclerite is connected to the dorsal surface of the ventral wall of the medial sclerite (Prasse, 1970). According to Knülle (1959), in *Glycyphagus destructor*, the medial ("epigynal") and dorsal supporting ("basal") sclerite also form a hinge-like joint, although, in our view, homologies in this case are not fully established. The dorsal supporting sclerite is connected to the aedeagus and has an orifice through which the ejaculatory duct enters the aede-

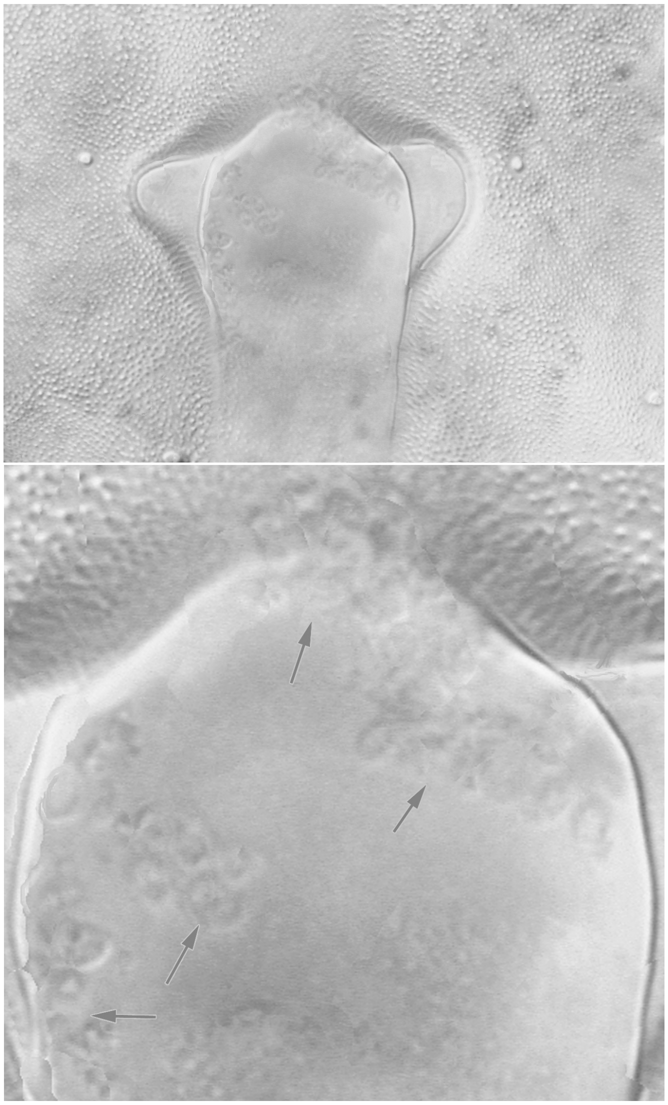

Fig. 13. Hysterosoma pouch of *Sennertia koptorthosomae* (BMOC 90-1212-006) (top); its anterior part at a large scale, arrows show fungal spores (bottom).

agus. The orifice is usually visible in dorso-ventral aspect, but sometimes the sclerite or its body is transverse and the orifice is not visible (Fig. 10 *A*). The ejaculatory duct, at its entrance to the dorsal supporting sclerite, is not or only poorly visible, smooth or distinctly transversely striated (*Chaetodactylus micheneri*, Fig. 10 *F*). A small bell-shaped sclerotized structure posterior to the aedeagus in *Sennertia scutata* (Fig. 10 *A*) is probably also associated with the ejaculatory duct. In *Sancassania*, at the place of articulation of the dorsal supporting sclerite and the aedeagus, Prasse (1970) also found another sclerotized structure that he called the "sclerite field of the penis". We could not find any homologous structure in chaetodactylids, probably because of the disassociation of the dorsal and medial sclerites.

External genitalia in immature instars

Genitalia in nymphal instars are represented by the progenital chamber that opens to the outside by the progenital slit bordered by narrow, longitudinal progenital folds with progenital sclerites, 1–2 pairs of genital papillae (p. 30), and 1 pair of associated genital setae. The homology of the progenital sclerites with that of the female is unclear. They may represent the diachilous sclerites as well. The progenital chamber, genital setae, and one pair of genital papillae are protonymphal. All subsequent instars have two pairs of genital papillae.

In feeding stages, the progenital chamber is situated at the anterior level of coxal fields IV and not associated with the anus. Lateral walls of the chamber have paired progenital sclerites. The genital papillae resemble those of the female.

In heteromorphic deutonymphs, the progenital chamber is situated at the level of the posterior part of coxal fields IV, with its posterior end incorporated into the attachment organ (Fig. 8). The well developed paired sclerites and elongated genital papillae are distinct features of this instar. The paired sclerites are better developed in early derivative genera (Fig. 8 *A*,*B*,*C*), where each forms a distinct ventral part at the inner edges of the progenital slit. The ventral part is continuous anteriorly with the dorsal part that is situated at the roof of the progenital chamber. At the lateral aspect, the sclerites have an elliptical outline with separated posterior ends (Fig. 8 *B*). The ventral longitudinal sclerites of the progenital chamber are evenly developed and conspicuous along their full length (*Centriacarus*, *Roubikia*, *Achaetodactylus*) or these sclerites are more or less developed in their posterior parts. The main anterior part is probably present but weakly developed and not visible (*Sennertia*), or the sclerites are weakly developed along their full length (*Chaetodactylus*). The homology of the sclerites with elements of the progenital chamber of the feeding instars is unclear. Probably the dorsal sclerites are derived from the medial fold and the ventral sclerites from the progenital fold. A comparison of the chaetodactylid progenital chamber structure and that of acarid mites (Woodring & Carter, 1974) suffices to show the existence of substantial variation that may be of potential phylogenetic value. *Sancassania boharti*, the only astigmatid species where this structure is described, has only one dorsal unpaired sclerite situated along the upper wall of the progenital chamber (Woodring & Carter, 1974). The genital papillae (Fig. 8) are inserted at the posterior end of the dorsal sclerites and probably fused to them.

Genital papillae

Genital papillae are semispherical, cylindrical or conical organs situated in repose on the inner walls of the progenital folds. In chaetodactylid females, each progenital fold has a distinct cavity (diachilous cavity) separating the fold into inner and outer progenital folds (Fig. 10 *G*). Genital papillae consist of an apical part and a cylindrical basal part that attaches to the mite body. They can be extruded to the outside by hydraulic pressure of the body or retracted by muscles inserted on their basal part. The basal part has annulations and corresponding internal cuticular rings. Ultramicroscopic studies demonstrated that it contains a single (*Naiadacarus arboricola*) or multiple cells (*Acarus siro*), with mitochondria in close association with cell membrane plications; while the apical part is cell free and is covered with two layers of cuticle, which also can be seen under a light microscope (Fashing, 1988; Witaliński *et al*., 1990). The structure of the cells in the basal part indicates that they have active transport functions. Alberti (1979) suggested that in terrestrial mites these cells serve for water uptake.

The majority of Astigmata have one pair of genital papillae in the protonymph, two pairs in adults, tritonymphs, and heteromorphic deutonymphs. Genital papillae are lacking in the larva. The ontogenetic sequence of expression of genital papillae is unknown, but in the brachypyline oribatid *Oppia nitens*, it is hypothesized to be a posterio-anterior direction (Behan-Pelletier, 1991).

In the feeding instars of chaetodactylids, genital papillae are semispherical (*Roubikia*) or cylindrical with a dome-shaped apical end (*Sennertia*, *Chaetodactylus*) (Fig. 5 *E*,*G*,*H*). There are at least two annuli situated close to the base of the papilla in *Roubikia* (Fig. 5 *E*) or shifted distally in the remaining two genera (Fig. 5 *F–H*). A third annulus may be present between the two distal annuli and the base of the papilla in both these genera. The three annuli may be separated from each other by the same distance (*e.g.*, *Sennertia americana*) or the proximal annulus is far from the two distal ones (Fig. 5 *H*). It appears that the degree of development and the position of the third proximal annulus is a highly homoplastic character. The genital papillae of the male are much smaller than those of the female and may have a smaller number of distinct annuli (cf. Fig. 5 *F* and *G*).

In the heteromorphic deutonymphs, the apical part of each genital papilla is conical with a long attenuated, lumenless tip (Fig. 5 *I–K*). In some species, a short apical portion of the tip is split forming two short, fiber-like processes (*e.g.*, *Sennertia surinamensis*). There are two distinct distal annuli, probably homologous to those of the feeding instars. A distinct third, proximal annulus may be present (*e.g.*, *Roubikia*, *S. americana*, Fig. 5 *I,K*) or absent (*Chaetodactylus azteca*, Fig. 5 *J*). *Roubikia* is distinct in the presence of a forth proximal annulus (Fig. 5 *I*).

Anal opening

The anal opening (Fig. 14 *H*) is a longitudinal slit situated ventrally at the posterior end of the body in a cavity formed by the cuticle of the body wall. The cavity is formed from two distinct cuticular folds on each side of the anus. Internally, the anal opening leads to the anal atrium lined by a thin cuticular layer. The anal atrium connects the postcolon to the anal opening. Two well developed anal valves flank the anus and give an elliptical outline to the whole structure in ventral aspect. In mounted specimens of feeding instars, each side of the anus may undulate in dorso-ventral aspect. This pattern probably represents muscle insertion sites, although the strong undulation itself is perhaps an artifact of fixation. For example, both males and females of *Sennertia koptorthosomae* may have four pairs of such muscles. In adults of *Chaetodactylus micheneri* (Michigan) and males of *Roubikia*, we observed three pairs of these muscles attached to paramedial sides of the anus and they did not form any distinct undulations (Fig. 27, Fig. 29, Fig. 49 *B*). These muscles originate from the medio-lateral region of the ventral opisthosoma and probably are dilators of the anus. It is worth noting that in males of *Roubikia*, muscles operating the dorsal supporting sclerite of the aedeagus are also attached to the medio-lateral region of the ventral opisthosoma and are probably functionally associated with the anal dilators (Fig. 49 *B*). In *Chaetodactylus micheneri* (Michigan), however, the three anal dilators and the muscles of the dorsal supporting sclerite are disassociated (Fig. 29 *A*). In lateral aspect, the sides of the anus usually have a distinct striate pattern. The cuticle at the posterior and anterior ends of each side of the anus is well sclerotized and serves as an attachment site for the thin cuticular layer of the anal atrium. The anus and the progenital opening are spatially disassociated. However, in males of *Sennertia* (except for *S. splendidulae* and *S. vaga*), the anal opening is shifted anteriorly, and the relative distance between the anus and progenital opening is distinctly shorter than in other feeding instars.

In heteromorphic deutonymphs, the anus and progenital chamber are situated close to each other, and the former is incorporated into the attachment organ (p. 21). The anus is small (Fig. 8 *A*), situated at the level of ad_{1+2} (*Roubikia*), ad_3 (*Chaetodactylus*, some *Sennertia*, *e.g. S. americana*), or at the level between these suckers (*Centriacarus*, some *Sennertia*, *e.g.*, *S. surinamensis*). It has not been observed in *Achaetodactylus*.

Legs

Chaetodactylids have three pairs of legs in the larva and four pairs of legs in the postlarval instars. Each leg includes six podomeres articulated by joints (from proximal to distal): trochanter, femur, genu, tibia, tarsus, and apotele (Evans, 1992) (Fig. 15, Fig. 14 *A*). The apotele, condylophores, and flexible distal extension of the tarsus constitute the ambulacrum (Hammen, 1989; Evans, 1992). The five proximal podomeres are rather uniform, although a few differences, especially on the tarsus, occur. The differences involve different sets of setae or solenidia on a particular podomere (Table 4), different proportions of podomeres, modification of setae and pretarsal elements, the presence or absence of bulges, modifications of joints and associated elements, and muscle attachment sites. Below, we give a comparative analysis of legs of adults and heteromorphic deutonymphs only. Most ontogenetic differences concerning leg setae or solenidia are discussed in the section on Ontogeny (p. 43). We also briefly discuss here leg differences associated with sexual dimorphism and andropolymorphism.

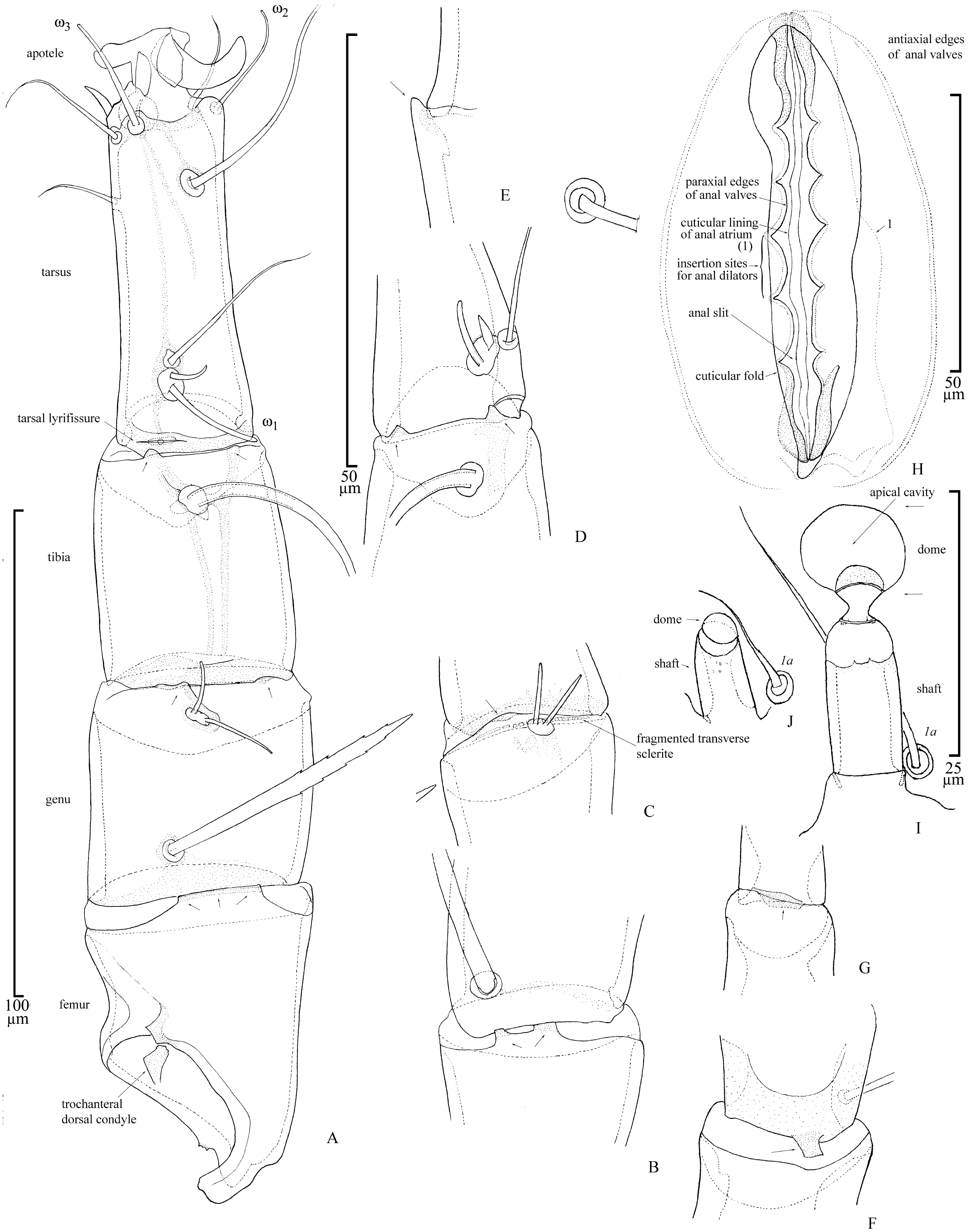

Fig. 14. Leg joints (A–G), anus (H), and Claparède's organs (I–J) of chaetodactylid mites. A - leg I, dorsal view, *Sennertia scuatata* (BMOC 79-1125-002); B - femur-genu I, *Sennertia scuatata* (BMOC 79-1125-004); C - genu-tibia I, *Chaetodactylus osmiae*; D - tibia-tarsus I, *Ch. reaumuri*; E - longitudinal optical section of condyle-like tubercle on tibia IV, *Ch. reaumuri*; F - femur-genu III articulation, *Sennertia americana* (BMOC 09-1212-025); G - femur-genu IV articulation, *Sennertia americana* (BMOC 09-1212-025); H - anus, *Sennertia koptorthosomae*; I - *Chaetodactylus micheneri* (BMOC 03-0310-001); J - *Roubikia panamensis* (paratype). Scale bars: A–D - 100 μm; E - 50 μm (middle); 50 μm (top left) - H; 25 μm - I–J. Unless otherwise noted, arrows indicate condyle-like tubercles or plates.

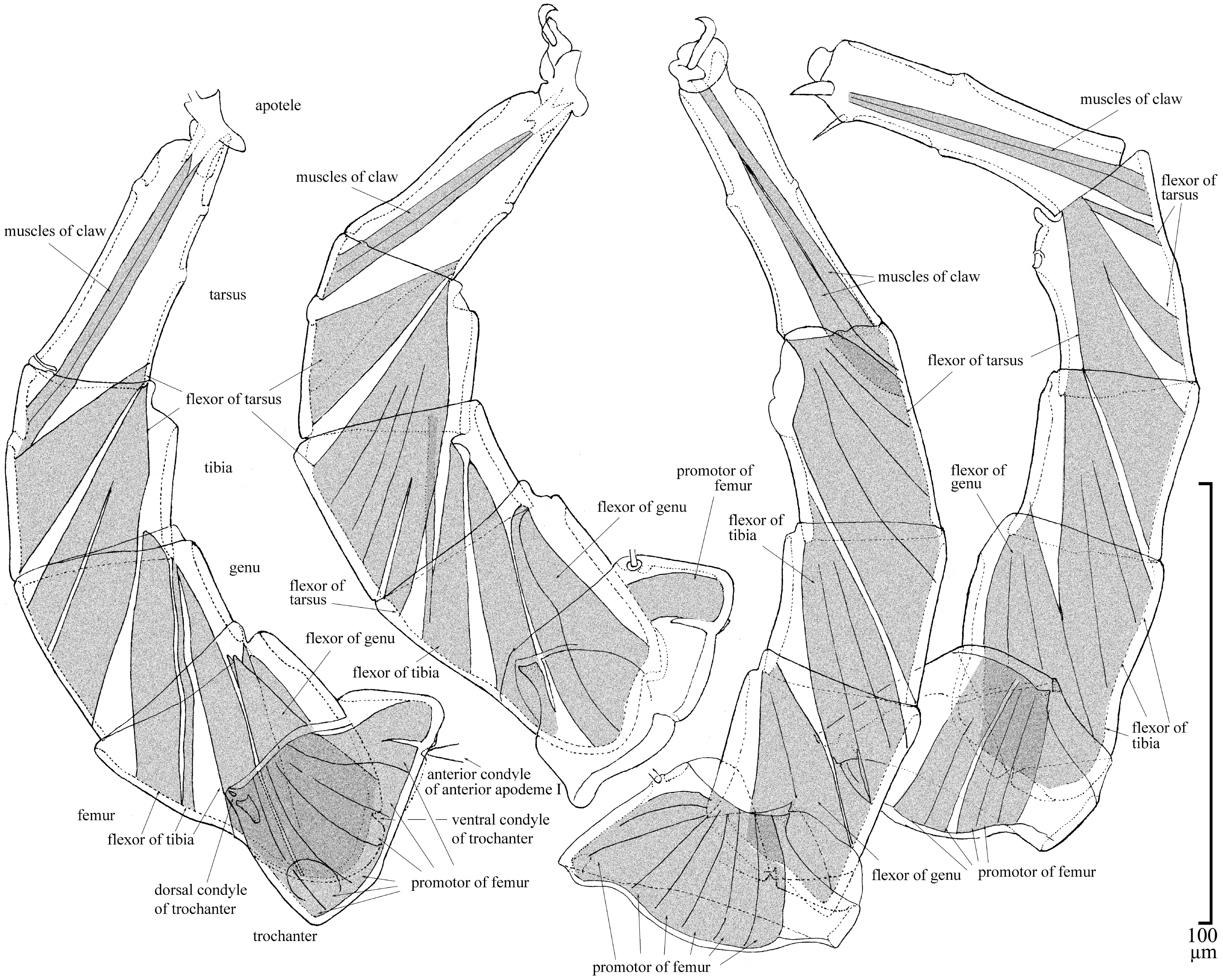

Fig. 15. Muscles of legs I–IV of *Roubikia panamensis* homeomorphic male. Trochanters I–II are distorted. Not all femoral promotors II are shown.

Trochanters, femora, genua I–IV, and tibiae I–III are the most morphologically conservative podomeres with no variation in chaetotaxy in adults (Table 4). With the exception of the presence of a specific pattern of bulges and grooves on the dorso-proximal surface of trochanters in *Sennertia* (see section on the Coxisternal region, p. 16), there is virtually no other discrete variation of this podomere in the family. Femora of chaetodactylids vary principally in their proportions. *Sennertia americana* is conspicuous by a very short femur (about 14–15% of leg III measured from femur to tarsus, in other chaetodactylids it is 19–28%). In this species and *S. koptorthosomae*, the femora are distinctly widened distally (the genu continues to widen and the tibia and tarsus gradually narrow). Genu I of *Sennertia vaga* has a distinct dorsal swelling or bulge in the protonymph (Fig. 32 *O*). Its function is unknown and no other studied species has the same bulge in any instar. In *Roubikia*, the setation of tibiae IV is complete, while in *Chaetodactylus* and *Sennertia* tibial seta *kT* IV is missing (Table 4). The tarsus and the apotele (see separate section below) are the most character-rich podomeres. Tarsi of chaetodactylids are different in their proportions, thickness of cuticle, and the number and position of setae and solenidia. Variation in proportions of the tarsi is quantitative and difficult to score as discrete characters. Tarsi of *Roubikia, Chaetodactylus*, and *S. vaga* are short (*e.g.*, tarsus III is 29–37% of femur-tarsus length) and almost cylindrical (proximal/distal height of tarsus III is 0.9–1.8), while tarsi of derived *Sennertia* are long (41–49% of femur-tarsus III length), slender and attenuated apically (proximal/distal height of tarsus III is 2.0–2.6). Tarsi of *S. scutata* are intermediate; they are long (tarsus III is 41–49% of femur-tarsus III length) but not attenuated (proximal/distal height of tarsus III is 1.6). Tarsi of *S. americana*, *S. koptorthosomae*, and *Sennertia* sp. 1

are unusual in having a disproportionately thickened cuticle. On the dorsal side of the tarsus it is several times thicker than on the ventral side. Early derivative species of *Sennertia* (*S. vaga*, *Sennertia* associated with *Ceratina*), as well as representatives of other chaetodactylid genera, have evenly thickened cuticle on both the dorsal and ventral side of their tarsi. Leg chaetotaxy and solenidiotaxy are presented in Table 4 and Table 5.

In heteromorphic deutonymphs, trochanter-tibia I–IV generally resemble those of adults in the structure of joints and setation (musculature was not studied); tarsi I–III, and especially IV, are the most specialized podomeres compared to adults. The differences include displacement of setae principally along the tarsal length and the absence of some setae (Table 5). The former set of differences is potentially very homoplastic because the feeding instars usually retain alternative

Table 4. Chaeto- and solenidiotaxy of adult chaetodactylids. + = present/true, ± = present or absent, blank = absent; an = anterior, dr = dorsal, ds = distal, fam = famulus, pr = proximal, ps = posterior, set = seta, sm = submedial, sol = solenidion, vr = ventral. Shading: ▓ = among-taxon variation; ░ = sexual dimorphism; ▒ = sexual and male dimorphism; ■ = male dimorphism, among-taxon variation; no shading = constant.

			Position							Leg				
Podomere	**Structure**	**Type**	**an**	**ps**	**dr**	**vr**	**pr**	**ds**	**sm**	**I**	**II**	**III**	**IV**	**Comment**
Tarsus	ω_1	sol			+		+			+	+			
	ω_2	sol		+	+			+	+	+	±			1
	ω_3	sol	+	+	+			+		+				2
	ε	fam	+		+		+			+				3
	ba	set	+		+		+			+	±			4
	e	set		+	+			+		+	+	±	±	5
	f	set	+		+			+		+	+	+	+	6
	d	set			+			+	+	+	+	+	+	7
	s	set				+		+		+	+	+	+	8
	p	set		+		+		+		+	±	±	±	9
	q	set	+			+		+		±	±	±	±	10
	wa (*w*)	set				+		+	+	+	+	±	+	11
	ra (*r*)	set		+		+			+	+	±	±	±	12
	la	set	+			+			+	+	±			13
Tibia	ϕ	sol			+			+		+	+	+	+	
	gT (*kT*)	set	+			+			+	+	+	+	±	14
	hT	set		+		+			+	+	+			15
Genu	σ'	sol	+		+			+		+	+	+		16
	σ''	sol		+	+					+				
	cG	set			+		+			+	+			
	mG	set		+		+			+	+	+			
	nG	set	+			+	+					+		
Femur	*vF* (*wF*)	set				+			+	+	+		+	
Trochanter	*pR* (*sR*)	set	+			+			+	+	+	+		

Comments: **1** - ω_2 I subapical (*Chaetodactylus*, derived *Sennertia*), submedial (*Roubikia*) or intermediate (*S. vaga*). Solenidion ω_2 II (positional notation, = ω_3 II ontogenetic notation) anterior to *ba* II, in common cuticular field with *ba* and ω_1 II; present in females and homeomorphic males of *Roubikia*, absent in *Sennertia* and *Chaetodactylus* and heteromorphic males of *Roubikia*; **2** - ω_3 displaced on posterior side of tarsus in females; **3** - Immediately distal to ω_1, in common cuticular field with ω_1 and *ba*; lanceolate (*S. vaga*), cylindrical (*Roubikia*), or spiniform (*Chaetodactylus micheneri*); **4** - On tarsus I either distal to famulus ε (*Roubikia*, *Ch. micheneri*) or anterio-distal to ω_1 (*S. vaga*); in common cuticular field with ω_1 and famulus ε (except for heteromorphic male of *Roubikia* where *ba* is separate and position of famulus ε variable). On tarsus II immediately distal to ω_1; in common field with ω_1 (and ω_2 in *Roubikia*). absent in *S. americana*. Setae *ba* I–II very short in *S. scutata* (as long as famulus ε or shorter). In other taxa it is longer than famulus ε; **5** - always filiform; *f* III–IV absent in *Roubikia* males; **6** - always filiform; **7** - *d* I–II proximal to *e* and *f* I–II; *d* I–II are subapical, *d* III–IV are submedial. Setae *d* I–IV always filiform; **8** - *s* I–IV subapical and filiform in *Sennertia* and *Chaetodactylus*; *s* I–II more proximal and spiniform in *Roubikia*. *s* III–IV subapical and spiniform in *Roubikia*; **9** - *p* II absent in males of *S. scutata* and *S. americana*, present in *Chaetodactylus* and *Roubikia* and males of *S. vaga*; *p* III is absent in males of all the three genera; **10** - *q* I absent in males of *S. scutata*. Setae *q* II absent in males of *Sennertia* and *Chaetodactylus*, heteromorphic males of *Roubikia*, but present in homeomorphic males of this species. *q* III–IV absent in males of *Sennertia* and *Chaetodactylus* but present in *Roubikia*; **11** - *w* III absent in *Chaetodactylus* and *Sennertia*, present in *Roubikia*. Setae *w* IV are shifted distally in males of *Chaetodactylus* and *Sennertia* and close to *s*; **12** - *ra* II absent in *S. vaga*; *r* III–IV present in *Roubikia*, absent in *Chaetodactylus* and *Sennertia*; **13** - *la* I–II are more distal than *wa* and *ra*. Setae *la* II absent in *S. vaga*; **14** - present in *Roubikia*, absent in *Chaetodactylus* and *Sennertia*; **15** - *hT* I–II usually more thick and massive than *gT* I–II; **16** - homology of σ' and σ II–III not positively established.

Table 5. Chaeto- and solenidiotaxy of mobile heteromorphic deutonymphs of chaetodactylids. + = present/true, ± = present or absent, blank = absent, an = anterior, dr = dorsal, ds = distal, fam = famulus, pr = proximal, ps = posterior, set = seta, sm = submedial, sol = solenidion, vr = ventral. Shading: ■ = deutonymphs and females with same pattern of presence/absence (see comment); ░ = always present in females (see comment); □ = absent, but present in some females (see comment); ▨ = position different from that of female.

			Position							Leg				
Podomere	**Structure**	**Type**	**an**	**ps**	**dr**	**vr**	**pr**	**ds**	**sm**	**I**	**II**	**III**	**IV**	**Comment**
Tarsus	ω_1	sol			+		+		▨ +	+	+			1
	ω_2	sol		+	+		▨ +		+	±	□			2
	ω_3	sol	+		+		▨ +	+	▨ +	+				3
	ε	fam	+		+		+	▨ +	▨ +	+				4
	ba	set								░	░			
	e	set		+	+			+		░	░	+	+	5
	f	set	+		+			+	▨ +	+	+	+	+	6
	d	set	+				▨ +	+	▨ +	+	+	+	+	7
	s	set		▨ +		+	▨ +	+	▨ +	░	░	+	+	8
	p	set		+		+		+		░ ±	░ ±	±	±	9
	q	set	+			+		+		░ ±	░ ±	±	±	10
	wa (*w*)	set				+		+	+	+	+	■ ±	+	11
	ra (*r*)	set		+		+		▨ +	+	+	+	■ ±	■ ±	12
	la	set	+			+		▨ +		+	+			13
Tibia	ϕ	sol			+			+	▨ +	+	+	+	░ ±	14
	gT (*kT*)	set	+			+			+	+	+	+	■ ±	15
	hT	set		+		+			+	+	±			16
Genu	σ'	sol			+			+		+	+	░ ±		17
	σ''	sol								░	░			
	cG	set			+		+			+	+			18
	mG	set		+		+			+	+	+			19
	nG	set	+			+	+		▨ +			+		20
Femur	*vF* (*wF*)	set				+			+	+	+		±	21
Trochanter	*pR* (*sR*)	set	+			+			+	+	+	+		22

Comments: 1 - ω_1 I usually proximal, but in *S. argentina* group it almost submedial. **2** - ω_2 I usually present, absent in *Achaetodactylus decellei* (feeding instars unknown); situated approximately at same level as ω_1, sometimes slightly anterior (North American examples: *S. pirata*, *S. lucrosa*, *S. americana*, *Ch. krombeini* group, *Ch. claudus*), almost submedial (*S. surinamensis* and *S. argentina* groups). Solenidion ω_2 II only preset in females and homeomorphic males of *Roubikia*. **3** - ω_3 situated closer to ω_1 than to f_I and almost proximal in *Afrosennertia*, it is closer to *f* I and distal (*Centriacarus*, *Roubikia*) or submedial (*Achaetodactylus*, *Chaetodactylus*, *Sennertia*). **4** - famulus ε proximal and situated in common cuticular field with ω_1 in *Centriacarus*, in other taxa it is usually disassociated from ω_1, ranging from proximal (*S. loricata*) to submedial (*e.g.*, *S. pirata*, *S. surinamensis* group). *S. argentina* group exceptional in having subapical famulus ε. **5** - *e* III subapical and usually foliate. It may be submedial and almost filiform (*e.g.*, *S. hurdi*) or intermediate in both location and degree of apical widening (some *Sennertia* and *Chaetodactylus*). Variation in *e* IV appearance is usually correlated with that of *f* IV (see below). **6** - *f* I–II subapical in *Centriacarus*, *Roubikia*, *Achaetodactylus*, some *Sennertia* (*e.g.*, *surinamensis* group, *argentina* group, *Ch. antillarum*) or submedial (*e.g.*, *S. americana*, *Ch. micheneri*). Foliate in *Centriacarus*, *Roubikia*, *Achaetodactylus*, some *Sennertia* and *Chaetodactylus* (*e.g.*, *surinamensis* and *argentina* groups, *S. pirata*, *Ch. antillarum*) or almost filiform (*e.g.*, *S. loricata*, *Ch. azteca*). *f* III subapical (*Roubikia*, *Centriacarus*, *S. argentina* and *surinamensis* groups, *Ch. antillarum*), submedial (*S. lucrosa*, *Ch. kouboy*) or intermediate. *f* IV is always subapical, foliate and medium sized (*Centriacarus*, *Roubikia*), very short, ranging from needle-like to spiniform (*Achaetodactylus*, *Sennertia*, some *Chaetodactylus*), or long and filiform (*e.g.*, *Ch. krombeini*, *Ch. claudus*) or needle-like (*Ch. melitomae*), or absent (*e.g.*, *Ch. kouboy*). **7** - *d* I–II subapical (*e.g.*, *Centriacarus*, *Roubikia*, *Achaetodactylus*, *Ch. antillarum*, *S. surinamensis* and *argentina* groups) or submedial (*e.g.*, *Ch. kouboy*, *S. loricata*). *d* III is submedial (*e.g. Centriacarus*, *Achaetodactylus*, *Ch. micheneri*, *S. americana*) or proximal (*Roubikia* and several *Sennertia*, *e.g.*, *S. loricata*, *Afrosennertia* group) (character difficult to score). *d* I–III filiform in *Roubikia* and *Centriacarus* or foliate in *Achaetodactylus*. In *Sennertia* and *Chaetodactylus*, they range from almost filiform (*e.g.*, *S. loricata*, *Ch. claudus*) to foliate (*e.g.*, *S. surinamensis* group, *Ch. antillarum*). *d* IV are always apical and extremely long in chaetodactylids. **8** - *s* III usually subapical in chaetodactylids. In *Centriacarus* and *Roubikia*, *s* III slightly foliate, while on other taxa it filiform (*Achaetodactylus*, many *Chaetodactylus* and *Sennertia*) or spiniform (*S. argentina* group, *Ch. krombeini*, *S. lucrosa*). *s* IV in early derivative taxa situated on midline in proximal part of tarsus, in *Centriacarus* it is between *w* and *r* IV, while in *Roubikia* slightly posterior to these setae. Homology of *s* IV in derived chaetodactylids (*Achaetodactylus*, *Chaetodactylus*, *Sennertia*) is tentative and based on facts that this seta situated near midline of tarsus and in common cuticular field with *w* (*e.g.*, *Ch. claudus*, *S. lucrosa*, *S. loricata*; in some taxa, *e.g.*, *Ch. krombeini*, *Ch. antillarum* *s* and *w* separated). In some species, *s* IV it slightly posterior to tarsal midline (*e.g.*, *Ch. melitomae*, *S. argentina*), indicating that it could be homologous to *r* IV. Length of *s* IV variable across chaetodactylid taxa. In derived chaetodactylids, *s* IV usually submedial (*e.g.*, *Ch. melitomae*) or subapical (*e.g.*, *S. recondita*). **9** - *p* I–II present in *Centriacarus*, foliate, absent in all other genera. *p* III–IV present in *Centriacarus* and *Roubikia* (*p* III foliate, *p* IV foliate in *Roubikia* and slightly foliate in *Centriacarus*), absent in other genera; always present in females. **10** - *q* I–III present in *Centriacarus*, foliate, absent in other genera; *q* IV present in *Centriacarus* (slightly foliate) and *Roubikia* (foliate). *q* I–IV always present in females. **11** - *wa* I–II submedial (*Centriacarus*) or subterminal and anterior (*Roubikia*, *Achaetodactylus*, most *Chaetodactylus*, *Sennertia*) or at level (*Ch. melitomae*) of *f* I–II. *wa* I–II filiform, with ventral denticle in *Centriacarus* and *Roubikia*, in other genera it is always smooth, filiform or spiniform (*S. argentina* and *frontalis* groups, *Ch. krombeini* group). *w* III present in *Centriacarus* and *Roubikia*, absent in other genera; present in females of *Roubikia* (and probably *Centriacarus*). Appearance of *w* IV correlated to *s* IV (see above); except for *Roubikia*, *w* IV usually longer than *s* IV. **12** - *ra* I–II subapical; foliate (*Centriacarus*, *Roubikia*), relatively short, filiform (*Chaetodactylus*, some *Sennertia*), flattened and simple (*S. loricata*, *S. hurdi*) or bifid apically (*S. faini* group). Setae *r* III–IV present in *Centriacarus* and *Roubikia*; absent in other genera; present in females of *Roubikia* (and probably *Centriacarus*). *r* III foliate, subapical (*Roubikia*) or submedial (*Centriacarus*). *r* IV filiform, submedial. **13** - *la* I–II almost submedial (*Centriacarus*) or subterminal (all other taxa); foliate (*Centriacarus*, *Roubikia*) or filiform (all other genera). In *S. argentina* group, *la* I–II exceptionally small, microsetae. **14** - Position of ϕ I–III ranging from subterminal (*e.g.*, *Roubikia*) to submedial (*e.g.*, *Centriacarus*, *S. argentina* group); in remaining taxa, it usually intermediate, shifted from distal end of tibia. ϕ IV absent (alveolus) in all genera except for *Chaetodactylus* where it subterminal; it is present in all adult chaetodactylids. **15** - *gT* I–II and *kT* III filiform, rarely spiniform (*S. argentina* group). *gT* I–II always smooth, longer or shorter than *hT*. *kT* III filiform, serrate (*Centriacarus*) or smooth (other taxa). Smooth and filiform *kT* IV present in *Centriacarus* and *Roubikia* but absent in all other genera; adults have same pattern of presence/absence. **16** - *hT* I–II serrate in *Centriacarus* and *Roubikia*, smooth in other genera, filiform (except for *S. argentina* group with spiniform *hT* I–II). - *hT* I–II absent is *Sennertia bifida*. **17** - homology of single genual solenidion I–II is based on *Chaetodactylus furunculus* that has vestigial σ'' solenidion; σ III absent (alveolus, submedial in *Roubikia* and *Centriacarus*) in deutonymphs of all genera except for *Sennertia* and *Chaetodactylus furunculus* (vestigial), it present in all adults. **18** - *cG* I long while *cG* II distinctly shorter and smooth (*Roubikia*, *Centriacarus*, *Achaetodactylus*, *Chaetodactylus*). In *Sennertia cG* I–II short, subequal. *cG* I serrate and usually flattened (*Roubikia*, *Centriacarus*, some *Chaetodactylus*, *e.g.*, *lithurgi* group) or smooth (*e.g.*, *Ch. krombeini*). Short *cG* I–II of *Sennertia* always smooth. **19** - *mG* I serrate in *Centriacarus*, *Roubikia*, some *Sennertia* and *Chaetodactylus* (*e.g.*, *S. bifida*, *Ch. lithurgi* group), smooth in other taxa. *mG* II serrate in *Centriacarus* and some *Chaetodactylus* and *Sennertia* (*e.g.*, *Ch. lithurgi* group, *S. bifida*) and smooth in *Roubikia* and other taxa. *Roubikia*, some *Chaetodactylus* and *Sennertia* (*e.g.*, *Ch. krombeini*, *S. argentina*, *S. loricata*) display disproportional elongation and often widening of *mG* II. *mG* I–II bifurcated in *S. surinamensis* group. **20** - *nG* III serrate in *Centriacarus*, smooth in all other taxa; submedial in all taxa except for *S. argentina* group where it proximal as in adults. **21** - *vF* I–II filiform; *wF* IV usually filiform (spiniform in *S. argentina* group); *wF* IV absent in *Sennertia bifida*. **22** - Trochanteral setae usually filiform (spiniform in *S. argentina* group).

states (Table 5, cells shadowed with diagonal stripes), which may influence reversals and further evolutionary changes "independent" from ancestral deutonymphal morphology. The apotele of deutonymphs is also very divergent from that of the feeding instars and its structure is discussed in the corresponding section (p. 38).

In the heteromorphic deutonymphs of *Roubikia*, *Chaetodactylus*, *Achaetodactylus*, and *Sennertia*, the ventral setae of tarsi I–II (*wa* and often *ra*, *la*) are shifted proximally to the apices of the tarsi. The shift appears to be correlated with shortening of the tarsi (except for the *S. surinamensis* group) and with the development of the apical tarsal extension causing setae *d*, *f* I–II, and often solenidion ω_3 to be proximal to the level of *wa* I–II and far from the tarsal apices (Fig. 64 *A–B*, Fig. 77 *A–B*). Presumably, *Centriacarus* retains the ancestral condition, with tarsi long, setae *wa* I–II submedial, the distal tarsal extension absent, and setae *d* and *f* I–II situated near the dorsal edges of the tarsal apices (Fig. 48 *A*,*B*,*F*,*E*). The same process probably took place on tarsus III, which is similar to tarsi I–II, except for the absence of topologically homologous seta *w* III. Only three apical tarsal setae I–II of chaetodactylids can be positively identified based on their topology and shape: *f* (all taxa), *d* (all taxa), and *q* (present only in *Centriacarus*). In the early derivative genus, *Centriacarus*, there is a foliate seta situated on the posterior side of the tarsal apex (Fig. 48 *A*). The homology of this seta (either *e* or *p*) cannot be positively established. Given the relative length of the seta and the fact that the proral setae are most prone to reduction in astigmatid heteromorphic deutonymphs and in chaetodactylid adults, it could be setae *e*. However these setae are positionally homologous to setae *q*, and there is a weakly visible alveolus dorsal to them (Fig. 17 *I*). We tentatively identify the dorsal alveolus as vestigial seta *e*, and the more ventral seta as *p*. Legs IV are generally shorter than any other leg, lack ambulacra (except in *Roubikia*, where it is vestigial), and have at least one long terminal seta (*d*). The distribution of setae and solenidia on podomeres as well as comments on their morphology are given in Table 5.

Ambulacrum

The apotele, condylophores, and flexible membranous distal extension of the tarsus constitute the ambulacrum. The apotele is the terminal element of the postcheliceral limbs of Chelicerata (Dunlop, 2000). In acariform mites, it is present only on the legs as a claw and basilar piece. The latter forms an eudesmatic bicondylar joint with two condylophores arising from the distal end of the tarsus. In Astigmata, the basilar piece is considered to be fused to the claw, and its ventral part, as well as the condylophores, is surrounded by the caruncle, a pad-like, membranous cuticle originating from the flexible distal extension of the tarsus (Grandjean, 1943). The caruncle is morphologically similar to the synarthrodial membrane between other leg podomeres and we use this term as synonymous with the terms articulating membrane and conjunctiva (Atyeo, 1979). In some parasitic Astigmata (Canestriniidae and Psoroptidia), the ambulacrum (including the caruncle) is clearly divided by the point of articulation of the condylophores and the basiliar piece on the ambulacral stalk and more distal ambulacral disk (Atyeo, 1979). Unfortunately the term ambulacral stalk and disk are inappropriate for the remaining astigmatid taxa as the articulating membrane forming the ambulacral stalk seemingly extends beyond the condylophore-basiliar piece articulation (Atyeo, 1979).

The ambulacrum of the feeding instars of chaetodactylids is rather conservative (Fig. 16 *A-J*) and includes elements of the typical ambulacra of free-living Astigmata outlined above. The caruncle is divided into three parts, sometimes with unclear boundaries: proximal, medial, and distal. The proximal part is cylindrical or slightly conical, and typically contains sclerotized portions of condylophores; it is homologous to the ambulacral stalk (Atyeo, 1979). In females it is longer and distinctly expanded disto-laterally forming distinct lateral subtriangular lobes; in males it is shorter and not expanded distally (cf. Fig. 16 *H* and *F*). The median part forms a sucker (ambulacral disk of Atyeo, 1979) and usually contains unsclerotized distal portions of condylophores (see below). This part is much smaller in the female than in the male, and in the latter its ventral surface is flat and unlike the female, is not deformable (cf. Fig. 16 *H* and *G*). The distal part of the caruncle surrounds the ventral part of the apotele and is more or less similar between the sexes (Fig. 16 *H* and *F*); in *Chaetodactylus* and *Sennertia* it extends distally to the claw, forming a characteristic small lobe (Fig. 16 *C*). The lobe seems to be absent or underdeveloped in *Roubikia*. The insertion point of the superior tendon is situated on the dorsal caruncle between its medial and lateral parts (Fig. 16 *A*). When the claw is elevated, the caruncle becomes greatly compressed and folded, with the three parts indistinct (except for the sucker in males). In both sexes of chaetodactylids, distal portions of the condylophores, sometimes transparent and difficult to see, are connected to the claw (Fig. 16 *E*,*H*). In some species (*Sennertia vaga* and *Chaetodactylus micheneri*), they are almost as well sclerotized as their proximal portions. Proximally, condylophores are articulated to the tarsus. The exact location of the articulation could not be observed in all studied species. In *Sennertia vaga*, the proximal ends of the female condylophores are bent upward and attach to a sclerite situated dorsally, posterior to the distal sclerotized margin of the tarsus (Fig. 39*A*). In other species, the proximal ends of the condylophores are probably transparent and poorly visible. The dorsal sclerite may be absent (*Roubikia*). The length and width of the condylophores vary in different species of chaetodactylids (Fig. 16 *E*,*H*). Chaetodactylids are characterized by a strong sexual dimorphism in condylophore morphology. In females they are less modified compared to the ancestral type, appearing as long and thin, paired sclerites. In males of *Chaetodactylus* and *Sennertia*, the posterior condylophore is thick and short (compared to females), and the anterior condylophore is modified forming a bilobed sucker extending from the caruncle. The degree of development of this pretarsal sucker varies (cf. Fig. 16 *F*,*D*), and this is a good character for species diag-

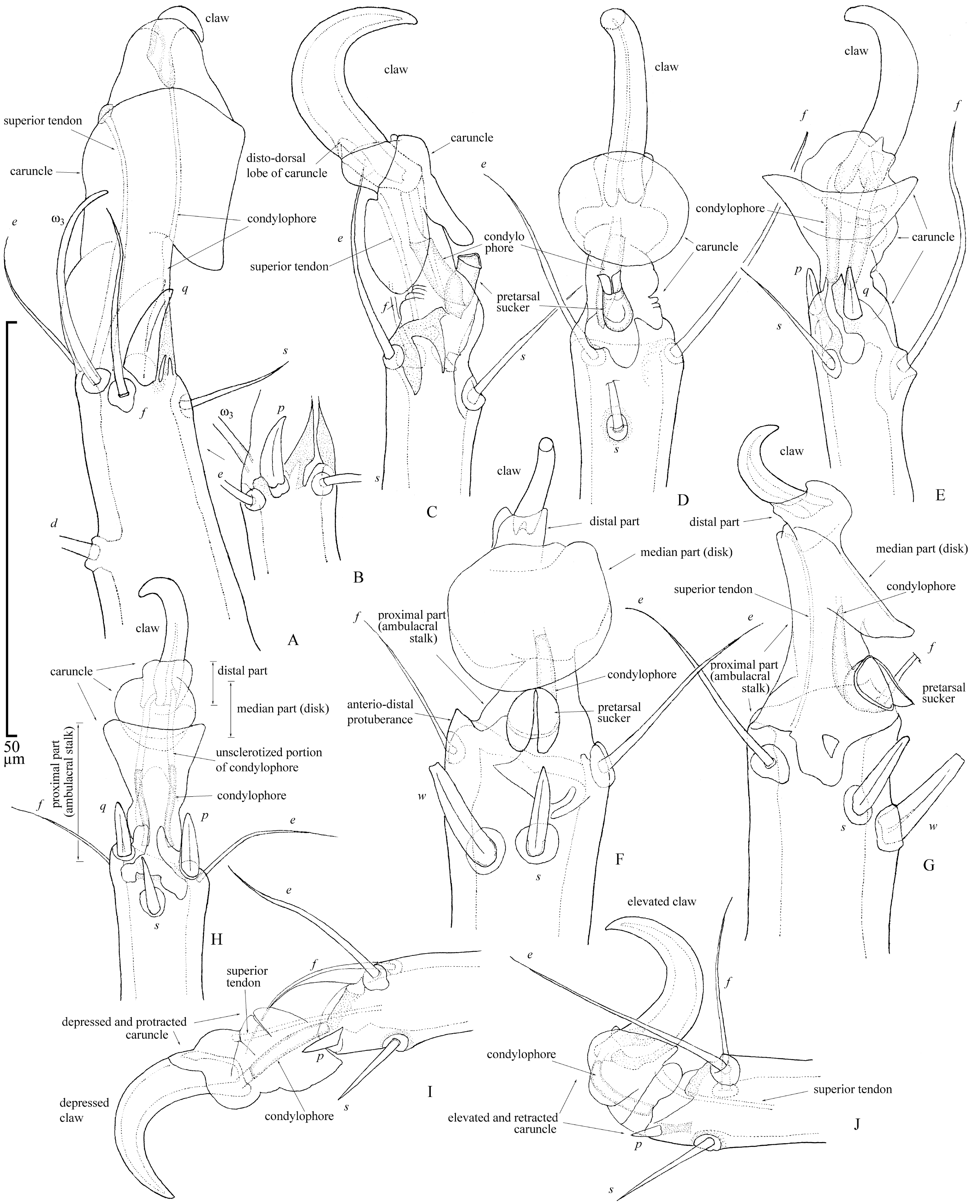

Fig. 16. Ambulacra of adult Chaetodactylidae. A, B - *Roubikia panamensis*; heteromorphic male (paratype); tarsus I; dorso-lateral and ventro-lateral view; C, D - *Sennertia* sp. 1 (BMOC 79-1125-001); male; tarsus IV; lateral and ventral view; E - *Sennertia* sp. 1; female; tarsus IV; ventro-lateral view; F, G - *Chaetodactylus krombeini*; male; ventral and lateral view; H - *Ch. krombeini* (BMOC 79-0312-001); female; ventral view; I, J - model of ambulacrum movements based on *Sennertia scutata* (BMOC 79-1125-005); depression of claw with concomitant depression/protraction of caruncle (I); elevation of claw concomitant with elevation/retraction of caruncle (J).

nostics. In some *Sennertia*, the pretarsal suckers IV are much smaller and have a vestigial ventral surface compared to those on legs I–III (Fig. 16 *C*,*D*). Condylophores of males of *Roubikia* are unique as their sclerotized portions are fused and incorporated into the disto-ventral sclerotized tarsal wall. The pretarsal suckers are not developed, but the condylophores still have long, elastic, transparent parts connected to the claw (Fig. 16 *A*). In females of *Roubikia*, the sclerotized condylophores are rather short and thin and have a distinct proximal unsclerotized part connected to the tarsus (Fig. 50*E*–*F*). The basilar piece in chaetodactylids is fused to the claw and represented by dorsal and ventral dark thickening that do not have distinct boundaries; because of this, in this work, we use the term claw as a synonym of the apotele of adult chaetodactylids. The claw is sickle-shaped in females and usually larger than in males.

As indicated above, claws of acariform mites are operated with two antagonistic muscles, levators (extensors) and depressors (flexors). In free-living Astigmata, such as *Acarus* or *Rhizoglyphus*, tendons of these muscles are visible inside the caruncle but their insertion points are not definitely established (Grandjean, 1943; pers. observation). Grandjean (1943) hypothesized that in *Acarus*, levators of claws insert via their narrow tendons on the dorsal caruncle near the claw, and the depressors similarly insert on the basilar piece fused to the claw. In chaetodactylids, we were able to observe tendons of the claw levator (superior tendons) indeed inserting on the caruncle (Fig. 16 *A*), but the insertion points of the depressor and even these tendons themselves were not seen. Probably, tendons of depressor muscles are present but much less developed than the corresponding levators, since there are two distinct but often entangled bundles of claw muscles originating in the tibia, and there are two closely situated tendons visible at the distal end of these muscles. However, even if the depressor of the claw is present, it may not be solely responsible for the claw depression. The pattern of the ambulacrum position in mounted specimens of *Sennertia scutata* suggests the possibility of two types of antagonistic movements of the claw *and* pretarsus: depression+protraction and elevation+retraction (Fig. 16 *I*–*J*). When the claw is depressed and protracted, the condylophores are straight and oriented ventrally at a small angle, and the caruncle is distinctly expanded distally (Fig. 16 *I*). When the claw is elevated and retracted, the condylophores are bent and directed dorsally, and the caruncle is greatly compressed (Fig. 16 *J*). The elevation/retraction movements are most probably accomplished by the claw levator whose well-developed tendon inserts on the dorsal caruncle. The depression/protraction probably occurs as the result of elastic energy of the bent condylophores and internal hydraulic pressure. Neither of these was assumed for the apotele of acariform mites previously. Podomeres of mites lacking extensors (tibia, genu, and tarsus) extend by hydraulic pressure (Evans, 1992). Antagonistic muscles presumably operate ambulacra, sometimes with a concomitant reduction or increase of hydraulic pressure when the ambulacrum is retracted or extended (Atyeo, 1979). Unlike hydraulic extension, elastic extension has not been documented for mites at all. Sensenig & Shultz (2003, 2004) described elastically deformable transarticular sclerites situated on synarthrodial membranes in different groups of arachnids other than Acari. Flexor muscles load these sclerites during flexion and energy from elastic recoil is used for extension. The latter may or may not be synergetic with internal fluid pressure. The authors also state that joints operated by antagonistic muscles lack apparent specializations for either elastic or hydraulic extension, suggesting that depressors (muscles with inferior tendons) of claws are probably absent in chaetodactylids.

Model of claw-pretarsus movements in adults

Based on the above data, we propose the following elastic-hydraulic model of the claw+pretarsus extension for chaetodactylids: the caruncle is an enclosed, folded, and expandable membrane connected to the leg cavity; the condylophores are elastic, especially at their proximal and distal portions; the muscle of the claw with an inferior tendon is underdeveloped or absent; when the superior muscle of the claw contracts, the caruncle folds and compresses, the condylophores bending upward, and the claw and pretarsus elevate (elevation+retraction) (Fig. 16 *J*); the claw+pretarsus extension (depression+protraction) (Fig. 16 *I*) occurs due to the synergetic forces of internal body pressure and recoiling energy of the bent condylophores. The broader implication of the model is that the ambulacral membrane probably represents a synarthrodial membrane, and the condylophores, at least in chaetodactylids, may be analogous to transarticular sclerites (Sensenig & Shultz, 2003).

Ambulacrum in heteromorphic deutonymphs

Functional ambulacra are present only on legs I–III in heteromorphic deutonymphs. *Roubikia* has a vestigial ambulacrum IV represented by a small, apical spine, probably homologous to the empodial claw (Fig. 51 *F*). In all other taxa, the ambulacrum is completely absent. In contrast to adults, the basilar piece develops as a horizontal sclerite distinguishable from the claw by its better sclerotization. The basilar piece has a complex three-dimensional structure (cf. Fig. 17 *E*,*F*), which is not yet fully understood. In all chaetodactylids, it includes two parts, dorsal and ventral, connected to each other by a cuticular bridge (Fig. 17 *B*). The bridge is thin in all genera but *Centriacarus*. The dorsal part is formed by a well-developed process, while the ventral part is weakly developed and represented by a small cuticular elevation at the base of the claw (Fig. 17 *B*). The empodial claw is claw-like, simple in *Centriacarus* (Fig. 17 *I*, *J*) or spirally twisted in all the other genera (Fig. 17 *A*–*H*). The latter is an apparent modification for clasping of the bee host's setae. Like in adults, the caruncle of heteromorphic deutonymphs is a transparent, deformable, closed membrane, with the proximal end connected to the internal tarsal cavity and the distal end bearing the empodial claw. The overall shape of the caruncle is, however, different. In *Chaeto-*

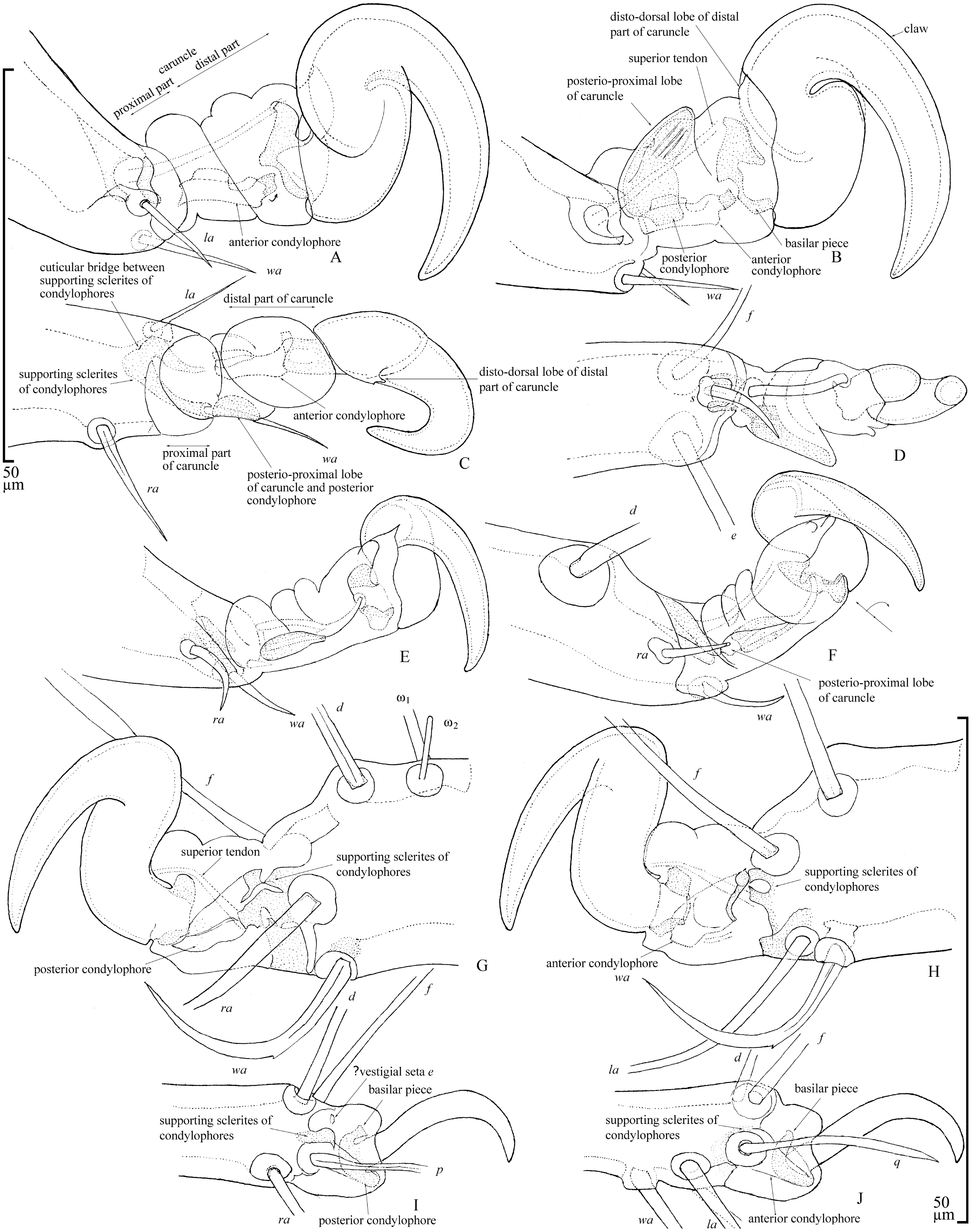

Fig. 17. Ambulacra of mobile heteromorphic deutonymphs of Chaetodactylidae. A–C - *Sennertia americana* (BMOC 04-0917-001), anterior and posterior lateral views, dorsal view, respectively; D–F - *Sennertia sodalis* (BMOC 03-1008-054), dorsal view and two lateral views with possible movements of the ambulacrum semidepressed and protracted (E) and elevated and retracted (F). Arrows show possible movements of the claw; G, H - *Roubikia panamensis* (paratype), posterior and anterior lateral views; I, J - *Centriacarus turbator* (Mexico). Scale bars: upper right corner (A–F), lower left corner (G–J).

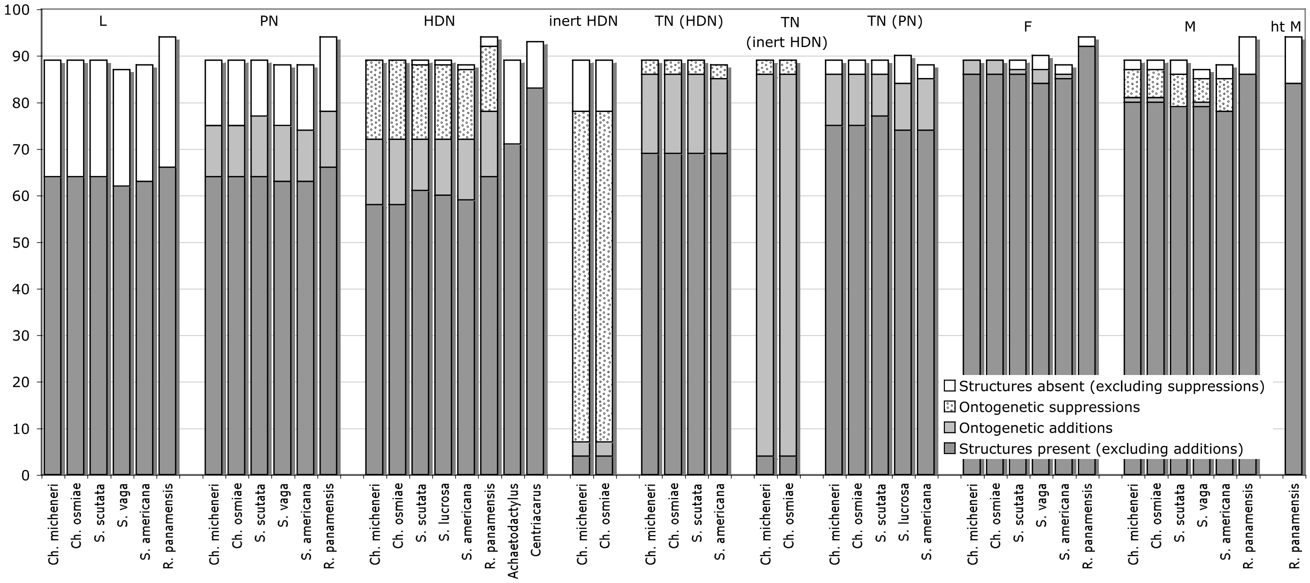

Fig. 18. Quantitative changes in the number of setae and solenidia in the postembryonic instars of chaetodactylids. Ontogenies of *Roubikia panamensis*, *Centriacarus*, and *Achaetodactylus* are incomplete. L = larva, PN = protonymph, HDN = phoretic heteromorphic deutonymph, inert HDN = inert heteromorphic deutonymph, TN (HDN, inert HDN, PN) = tritonymph resulted from the molts of corresponding instars, F = female, M = homeomorphic male, ht M = heteromorphic male.

dactylus, *Achaetodactylus*, and *Sennertia*, it has two distinct parts; the distal part is homologous to the corresponding part of the adults, while the proximal part is homologous to the median and proximal parts of adults. The dorsal portion of the distal parts forms a large asymmetrical cuticular fold, while the proximal part has 1–3 folds distinctly smaller than the distal one (*Achaetodactylus*, *Chaetodactylus*, *Sennertia*). The distal fold may also have secondary dorsal folds (*e.g.*, undescribed Neotropical *Sennertia* from the metasomal acarinarium of *Ceratina*). The geometry of the dorsal folds suggests that they may accumulate energy when the ambulacrum is elevated (folds are compressed), and release this energy contributing to the depression of the ambulacrum (Fig. 17 *E–F*). Like in adults of *Sennertia* and *Chaetodactylus*, the distal part of the caruncle has a disto-dorsal lobe that seems to be present only in the three derived genera; in deutonymphs the lobe is relatively better developed (Fig. 17 *B*). The ambulacra in *Roubikia* and *Centriacarus* are shorter (Fig. 17 *G–J*), with dorsal cuticular folds weakly developed in *Roubikia* (the distal fold is smaller than the single proximal one) or indistinct in *Centriacarus*. The proximal part also forms a lateral lobe (see below); in the *S. argentina* lineage, the distal part of the ambulacrum also forms a similar lateral lobe (Fig. 79 *A*). The ventral surface of the ambulacrum is almost straight in all chaetodactylid deutonymphs. Condylophores of deutonymphs, unlike adults, are more or less uniformly sclerotized and apparently lack long transparent extensions. Condylophores of the two early derivative genera are large, almost symmetrical, and probably fused to the lateral walls of the caruncle; they are weakly sclerotized and difficult to see from the lateral side but distinct in dorsal or ventral aspects. As in females, the tarsus-apotele joint is bicondylar in these two genera. Condylophores of *Chaetodactylus*, *Achaetodactylus*, and *Sennertia* are strongly modified (Fig. 17 *A–F*). Like in males, they are asymmetrical, with the anterior one unmodified and the posterior one incorporated into the subtriangular latero-proximal lobe (in males the anterior condylophore is unmodified and the posterior one is modified). The apotele-condylophore joint, thus, can be classified as monocondylar in the above three genera, since the posterior condylophore is not a functional part of the joint. The lobe is a composite structure that comprises the posterior condyle and the sclerotized and unsclerotized walls of the caruncle. The boundaries between the condyle and the sclerotized wall are indistinct, but the former can be recognized by the condylophore-resembling process at the base of the lobe and the latter because it forms a fold with the opening at the base of the lobe (*e.g.*, *Sennertia* (*Afrosennertia*)). The degree of development of the proximal pretarsal lobe and its elements varies substantially among different lineages of *Sennertia* (cf. Fig. 17 *B* and *D*) and can be used to distinguish between them (*e.g.*, *S.* (*Afrosennertia*)). On the whole, discrete states of this character cannot be unambiguously established. The shape of the anterior condylophore also strongly varies, representing a continuous interspecific variation. Generally, it can be described as consisting of a wide proximal part and a thin, elongated and often upwardly bent distal part. The crown of the former sometimes forms a lobe and the apical outlines of the latter sometimes are elaborated (Fig. 17 *B*). In *S. horrida* and the *S. argentina* lineage, the anterior condylophores are very thin and uniform in all their lengths, while the posterior ones are completely absent (the lateral lobe is, however, present without any sclerotization) (Fig. 79 *A*). At the point of origin of both condylophores, the tarsus is elaborated. In *Chaetodactylus*, *Achaetodactylus*, and *Sennertia*, there are corresponding sclerites, distinctly separated from the rest of the tarsus and connected dorsally by a cuticular bridge (Fig. 17 *C*). In dorsal or ventral aspects, these sclerites are parallel to each other. The dorsal bridge serves as a fulcrum for the superior tendon. In *Roubikia* and *Centriacarus*, the supporting sclerites are indistinctly separated from the tarsal apex and do not form a dorsal cuticular bridge. *Roubikia* is distinct in having the above sclerites irregularly-shaped and fragmented (Fig. 17 *G, H*). In *Centriacarus*, they are not separated from the tarsal apex and also do not form a dorsal bridge. The number of tendons operating the claw and the points of their insertion are difficult to see. In all species we were able to observe the superior tendon that, like in the adults, probably inserts on the dorsal caruncle, however, it could insert on the basilar piece. The inferior tendon was observed only in an undescribed species from the *Sennertia japonica*-group, although the unusual development of the ventral part of the basilar piece may suggest its presence in all chaetodactylids. Obviously, more sensitive methods should be used to address the issue.

Model of claw-pretarsus movements in heteromorphic deutonymphs

The movements of the ambulacrum of heteromorphic deutonymphs are difficult to reconstruct. Some preliminary conclusions below are based on a study of large series of mounted *Sennertia* and may be affected by artifacts of preparation. Our observations suggest that dorso-ventral bending of the ambulacrum occurs at its base (cf. Fig. 17 *E* and *F*). The empodial claw can also move in the vertical plane but these movements are probably very limited (cf. Fig. 17 *E* and *F*). Since the ambulacrum of the three derived genera is monocondylar, with only the anterior condylophore functional, the movements of the claw may be different from those typical for the vertical dicondylar joint. In mounted specimens we found postures suggesting simultaneous vertical and horizontal movements. When the claw is elevated, it probably also rotates so the apex of the claw is directed posteriorly (cf. Fig. 17 *E* and *F*), pressing the host's seta against the caruncle. To some extent, the horizontal component of these movements is probably restricted by the well developed disto-dorsal lobe of the distal part of the caruncle and the posterio-proximal lateral lobe. The latter is usually heavily sclerotized and may also provide additional support when the horizontally rotated claw presses the host's seta against the caruncle. The two folds may probably release the energy of compression, ensuring the reverse horizontal movement of the claw. The anterior condylophore probably prevents the claw from horizontal movements to the opposite side (anterior). Elevation of the ambulacrum also causes retraction of the caruncle and compression of its dorsal folds. The folds probably release the energy of compression, contributing to the depression/protraction of the ambulacrum also accomplished by the weakly developed depressor. Elevation/retraction is due to a single levator muscle that inserts on the dorsal caruncle. Our model of claw elevation and depression suggesting posterior claw bending in the vertical plane explains the positions of the claws grasping the host setae from above on SEM pictures (Okabe & Makino, 2002, Fig. 6), however it cannot explain the position of a single claw grasping the seta from below (Okabe & Makino, 2002, Fig. 6).

Sexual dimorphism and andropolymorphism

The most conspicuous differences in the legs between adult male and female chaetodactylids are displacement of solenidion ω_3 to the posterior part of the tarsus in the females (cf. Fig. 28 *A* and Fig. 30 *A*) and modifications of ambulacra in males. The medial parts of the ambulacral caruncles I–IV of chaetodactylid males are transformed into large suckers or disks (Fig. 16 *A,C,D,F,G*). The anterior condylophores I–IV in *Sennertia* and *Chaetodactylus* are modified into pretarsal suckers, and the sclerotized part of the posterior one is shortened and thickened, while in males of *Roubikia* all condylophores are vestigial (see section on Apotele, p. 43 for details). Some apical tarsal setae (*p*, *q*, *f*) are lacking in males compared to females and these differences are more conspicuous in *Sennertia* and *Chaetodactylus* (Table 4). In these genera, males lack setae *q* II, *p* and *q* III–IV, while *f* and *p* III–IV are absent in males of *Roubikia*. Seta *p* II is absent in males of *S. vaga*, but it is present in *Roubikia*, *Chaetodactylus*, and other *Sennertia* (Table 4). We found only one difference in proral setae on tarsus I: *q* I is absent in males of *S. scutata*. The tarsi of *Chaetodactylus* males are distinctly thicker than those of females (Fig. 16 *H,F*). For example, the height of tarsus III is 27% of the length of tarsus III in the female and 49% in the male in *Ch. micheneri*, 15 and 26% in *Ch. krombeini*, 17 and 25% in *Ch. osmiae*. In this genus, each tarsus has a distinct anterio-dorsal protuberance, the shape and proportions of which are good taxonomic characters (Fig. 16 *H,F*).

Male dimorphism has been recorded only for *Roubikia panamensis* (Baker *et al.*, 1987). It is expressed in the variable development of legs II. In the heteromorphic male, the trochanter-tarsus segments of legs II, and setae *s* and *p* are enlarged, setae *hT* are spiniform, and setae *q* and solenidion ω_2 are absent (Fig. 50 *A, B*). In the homeomorphic male and females, the podomeres of legs II, and setae *s* and *p* are not enlarged, setae *hT* are filiform, setae *q* and solenidion ω_2 are present. The presence/absence of seta *q* and solenidion ω_2 indicates that the variation between the two male morphs, known from one specimen each, is discrete rather than continuous. The biological basis for male dimorphism is unknown, but in other Astigmata it involves precopulatory antagonistic behavior by males. In heteromorphic males of a proconjugate species, *Histiostoma palustre* (Histiostomatidae), legs II are transformed into clasping organs used to hold rival males when fighting over the female tritonymph (Wirth, 2004). Since copulatory success of hetero- and homeomorphic males was nearly the same, modified legs II may also be used for a better hold during copulation (Wirth, 2004). In retroconjugate *Sancassania* and *Rhizoglyphus* (Acaridae), heteromorphic males use enlarged legs III to kill rival males (Timms *et al*., 1981; Radwan, 1995, 2000).

Joints

All articulations between the podomeres are eudesmatic. The coxa-trochanter and trochanter-femur articulations are pivot joints with antagonistic muscles. The former articulation and extrinsic muscles of the first two proximal podomeres were described in the section on Coxisternal region (p. 16). The trochanter-femur articulation is bicondylar, with the two condyles always well developed (Fig. 15). It is nearly vertical and perpendicular to the horizontal coxa-trochanter joint, allowing promotor-remotor movements. The femur-genu, genu-tibia, and tibia-tarsus articulations are dorsal hinge joints with flexors inserted on the ventro-proximal margin of the target podomere. This may be a succeeding podomere (genu and tarsus), next after succeeding (tibia and tarsus), or next after two podomeres (tarsus II). The nature of the tarsus-apotele articulation, which is usually transverse bicondylar in acariform mites (Hammen, 1989; Shulz, 1989), is unknown. It may be transverse bicondylar in females and probably males and monocondylar in heteromorphic deutonymphs (see section on Apotele). In the feeding instars of *Roubikia* and *Chaetodactylus*, the disto-dorsal surfaces of the tibia and often the genu have distinct, paired, subtriangular, condyle-like cuticular protuberances, probably restricting horizontal movements of the joints (Fig. 14 *A,D*). On tibia I–II, these protuberances may be asymmetrical, with the better developed one situated on the anterior (paraxial) side of the podomere (Fig. 14 *A*). This presumably allows some rocking of the tarsus. Similar paired tibal protuberances were described for the trombidiform genus *Anystis* (Anystidae) (Hammen, 1989). The author speculated that the extensor of the claw can also function as a levator of the tarsus, but the extent of the raising of the tarsus is limited by the dorso-proximal tibial tubercles. In *Roubikia*, the paired tibial protuberances are absent as distinct structures. Dorsal protuberances of the genu-tibia joint are usually weakly developed (Fig. 14 *A,C*), with the posterior (antiaxial) protuberance often lacking (Fig. 14 *C*). In *Chaetodactylus*, there is a thin, transverse sclerite lying under the arthrodial membrane between the dorsal surfaces of the genu and tibia. The sclerite may be heavily fragmented (Fig. 14 *C*). Further investigation is necessary to test whether it functions as the transarticular sclerites of other arachnids (Sensenig & Shultz, 2003, 2004). The femur has a transverse, band-like condylar plate articulated to the genu in *Sennertia* and *Chaetodactylus* (Fig. 14 *A,B*). In some species, this surface has a broad median concavity (Fig. 14 *B*). The femur of *Roubikia*, instead, has a small condylar posterio-lateral plate. Judging from the presence of the large areas of arthrodial cuticle flanking the femoral condylar surface, some rocking is possible at the femur-genu joint.

The joints of the femur-tarsus in the heteromorphic deutonymphs are similar to those of the feeding instars, but the cuticular protuberances are usually weakly developed. Dorsal condyles of trochanter-femur joints I–III are situated on sclerites separated from the dorsal sclerotized walls of trochanters I–II (*e.g.*, *Roubikia*, *Sennertia*, *Chaetodactylus*). *Centriacarus* and *Roubikia* are distinguished by the absence of characteristic dorsal condylar sclerites on femur-genu joints I–IV. Like in adults (Fig. 14 *A,B*), these sclerites are present in heteromorphic deutonymphs of *Achaetodactylus*, *Chaetodactylus* and *Sennertia* (Fig. 14 *G,F*), but unlike adults these sclerites are fused to the genu rather than to the femur. Distal tibial processes I–III are also well developed, and tarsus and tibia IV are fused dorsally but separated ventrally in the *S. horrida* group and *S.* af. *basilewskyi* (BMOC 90-1212-014). In some *Sennertia* (*e.g.*, *S. americana*), synarthrodial membranes of femur-tarsus joints have areas of weak sclerotization visible in the ventral aspect.

Musculature

The proximal borders of the trochanters serve for the attachment of well-developed protractors of the femur (Fig. 15). On legs I–II, these muscles attach to both the anterior dorsal and ventral parts of the trochanter, while on legs III–IV they attach to the dorsal part (except for a small posterior region). Retractors of femora I–IV attach to the corresponding anterior apodemes and insert on the posterior end of the femur (Fig. 7). A set of muscles originating on femora I–IV comprises flexors of the genu and tibia. Besides these two muscles, femur II also has flexors of the tarsus in *Roubikia* and *Chaetodactylus* but not *Sennertia*. This is probably the only difference in the leg musculature in chaetodactylids. Other flexors of the tarsus originate on the tibia and genu I–IV. Muscles operating the claw originate on the disto-ventral parts of tibiae I–IV. They form a single group of two, often difficult to see, bundles that may correspond to the levator (extensor, most distal and better developed) and flexor (depressors, proximal) of the claw. In previously studied astigmatid, oribatid, and prostigmatid mites, the points of origin of depressors and levators of the claw are closely associated, and the levators are distal to their depressors (Grandjean, 1941; Akimov & Yastrebtsov, 1989; Kuo & Nesbitt, 1970; Mitchell, 1962; Schulz, 1989). In *Cytodites nudus* (Cytoditidae), however, these muscles are separated and the levator is the most proximal and situated on the dorso-proximal part of the tibia (Atyeo, 1979). Insertion points of the claw muscles are discussed in section on Apotele above.

Transpodomeric muscles operating the femur, tibia, tarsus, and claw are described for free-living and parasitic Astigmata, oribatid and prostigmatid mites (Akimov & Yastrebtsov, 1989; Kuo & Nesbitt, 1970; Mitchell, 1962; Schultz, 1990; Wurst, 1993; Woodring & Carter, 1974). The so called transpatellar muscle, that was considered to be characteristic of arachnids and *Limulus* (Shulz, 1989), is identifiable in chaetodactylids as the flexors of the tarsus originating from the genu and also from femur II in *Roubikia* and *Chaetodactylus*. Kuo & Nesbitt (1970) documented transpodomeric muscles for all podomeres of adult *Sancassania*, including ones originating in the trochanter and inserting on the genu. Except for *Anystis* (Hammen, 1989), these muscles were not found in any other acariform mites, although muscles originating in the basifemur and inserting on the genu were described for the trombidiform genera *Blankaartia* (Trombiculidae) and *Dinothrombium* (Trombidiidae) (Mitchell, 1962; Shulz, 1989).

The above account of leg myology is based on a comparative study of adults of *Roubikia panamensis*, females of *Chaetodactylus micheneri* (BMOC 03-0310-001) and *Sennertia* sp. 1.

ONTOGENY AND REPRODUCTION

The life cycle of chaetodactylids includes five or six instars: prelarva, larva, protonymph, facultative heteromorphic deutonymph (phoretic or inert), tritonymph, and adults (females, homeomorphic and heteromorphic males). The prelarva and inert heteromorphic deutonymph are calyptostases (neither capable of locomotion nor feeding). The former is covered by the egg chorion and the latter usually does not emerge from the protonymphal cuticle (endostases). The phoretic heteromorphic deutonymph is an ellatostase (capable of locomotion, but not feeding). The larva, protonymph, tritonymph, and adults are feeding instars. The two types of heteromorphic deutonymphs are facultative instars, while the others are obligate instars. Inert deutonymphs are known only in the genus *Chaetodactylus*, heteromorphic males are known only in the genus *Roubikia*.

The presence of two facultative, dimorphic, heteromorphic deutonymphs in *Chaetodactylus* allows three different developmental pathways in the life cycle. The protonymph is able to molt directly to the tritonymph or to either the phoretic or inert heteromorphic deutonymph. These developmental pathways are adaptations for different survival strategies: to complete the development sooner by bypassing the heteromorphic instar in favorable conditions inside the host nest (protonymph-tritonymph molt), to disperse on the newly emerging bees and establish a new colony in the new host nest (phoretic heteromorphic deutonymph), or to remain in the nest cavity in adverse conditions, as a dormant stage, and infest a new generation of cells when the cavity is re-used (inert heteromorphic deutonymph). The three potential developmental pathways of the protonymph have also been documented for *Glycyphagus privatus*, *G. ornatus, Baloghella melis* (Glycyphagidae), *Alabidopus asiaticus* (Chortoglyphidae), and presumably *Hericia* sp. (Algophagidae) which also have dimorphic heteromorphic deutonymphs (Fashing, 1991; Knülle, 2003; Lukoschus *et al*., 1981; Wurst & Pfister, 1990). In two other astigmatid families with known inert deutonymphs, the life cycles have only two pathways, with the protonymph molting to either the phoretic or inert deutonymph (but not directly to the tritonymph) as in a histiostomatid *Tensiostoma veliaphilum* (Wurst & Kovac, 2003) or to either the inert deutonymph or the tritonymph as in an acarid *Acarus immobilis* (Griffiths, 1964). Feeding instars are usually similar to each other in their cuticular ornamentation and the shape and proportions of dorsal idiosomal setae. However, the morphology of a single protonymph that probably belongs to *Sennertia koptorthosomae*, suggests that substantial alterations in these characters may occur throughout ontogeny. All dorsal idiosomal setae of this protonymph have clavate papillae (serrate in adults); setae *se*, c_1, c_2, c_p, c_3, d_1, d_2, e_1, e_2, f_2, h_1 are large, flattened, foliate (short, lanceolate, slightly barbed or smooth in adults); c_2, d_2, e_2 and c_1, d_1, e_1 are situated in almost straight longitudinal rows (c_2-e_2 are not in horizontal rows in adults); and the dorsal cuticle is tuberculate, accompanied with numerous tiny mammillae (with conical mammillae, tiny secondary mammillae sparse and irregular in adults).

Trouessart (1904b) found that inert deutonymphs of *Chaetodactylus* always transform to females, while phoretic deutonymphs may transform to both sexes. He believed that inert deutonymphs, unlike phoretic ones, are females with distinct secondary sexual characters, including inseminatory apparatus and could be normally inseminated by males. After a long hibernation period inside the nest, these female deutonymphs would molt to tritonymphs and finally to females that could produce eggs developing into both males and females. We were unable to find any inseminatory apparatus in inert deutonymphs of *Ch. osmiae*, *Ch. claudus*, and *Ch. micheneri* and, unfortunately, Trouessart did not test experimentally whether the "female deutonymphs" were really inseminated or simply produced parthenogenetic females. Krombein (1962) cast doubt on the possibility of pre-adult insemination and hypothesized that inert deutonymphs transform into females each of which lays a single egg that develops very rapidly into an adult male. This male mates with its mother, or with another female that may be in the same cell, and the female then proceeds to lay fertilized eggs. A similar mode of parthenogenesis has been observed in species in the family Winterschmidtiidae that live in the nests of solitary wasps. In addition to 'small' males developing from unfertilized eggs, they also produce 'large' males developing directly from phoretic deutonymphs (Klompen *et al*., 1987). No other observations on this interesting issue have been made on chaetodactylids.

Mating is proconjugate (observed in *Chaetodactylus* (Chmielewski, 1993) and is suggested by the structure of the male genitalia in *Roubikia* and *Sennertia* (p. 26)).

Females of chaetodactylids deposit eggs in nests of their hymenopteran hosts. In *Chaetodactylus nipponicus*, the fecundity of the female resulting from direct protonymph-tritonymph molts is 243±28 eggs per female (24°C), and it decreases at lower (20°C) or higher (28°C) temperatures. Fecundity also differed for females that passed through the deutonymphal instar, averaging 213±25 eggs per female from phoretic deutonymphs and 45±11 from inert deutonymphs (Qu *et al*., 2003). The time of development from egg to adult ranges from about 10 to 40 days depending on the temperature (Table 6).

Table 6. Duration (days±SD) of *Chaetodactylus nipponicus* developmental instars at different temperatures (after Qu et al., 2003)

T (°C)	Egg	Larva	Protonymph	Tritonymph	Total	One generation
16	12.8±1.7	11.5±2.6	7.8±1.3	8.1±2.8	40.2±3.6	
20	6.6±0.7	4.9±1.3	3.3±0.7	4.0±1.1	18.7±2.5	53.2
24	4.9±0.5	3.5±0.8	2.3±0.6	3.1±0.8	13.7±1.7	50.4
28	3.4±0.5	2.0±0.6	2.1±0.6	2.1±0.6	9.5±1.1	44.8
32	3.2±0.4	4.5±0.8	3.2±1.6	2.8±1.0	13.7±5.6	

At optimal temperature and humidity and with the abundance of pollen and nectar, the life cycle of *Chaetodactylus osmiae* is short and can repeat itself as many as ten times in a single season without appearance of the deutonymphal instar. The number of cycles depends exclusively on these factors (Krunić *et al*., 2005).

Circumstantial evidence from preserved host specimens suggests reproduction may occur on the body of adult bees. All feeding instars of *Sennertia vaga*, including males, females and larvae, were found on four adult *Xylocopa tabaniformis orpifex*. Feeding instars of a similar species of *Sennertia* regularly occur on adult *Centris* (*e.g.*, *C. vittata*, *C. trigonoides*) in the Neotropical region. The presence of numerous protonymphs and larvae suggests that the mites possibly molt and reproduce on the host. No phoretic deutonymphs that could represent these species have been observed on these hosts. A similar phenomenon is known for *Aeroglyphus peregrinans* (Aeroglyphidae) occurring on *Xylocopa valga* and *X. violacea* in the western Palaearctic. The occurrence of feeding instars of mites on adult bees was also documented for *Sennertia cantabrica* (Zachvatkin, 1941). In all these cases it is unknown whether reproduction or molting occurred on live insects in nature or on the dead hosts following collection. The presence of feeding instars on adult bees could also be a result of natural contamination as newly emerged bees may break through cell partitions and/or enter adjacent nest tunnels looking for food (Nininger, 1916).

Post-embryonic development, or at least its main period, occurs outside the female's body, although we observed almost completely developed larvae inside females of *Sennertia* sp. (*vaga*-group) attached to the hairs of the propodeum of adult *Centris* (*e.g.*, *Sennertia* sp. 2 belonging to the *vaga*-group). Because astigmatid mites, including chaetodactylids, are relatively resistant to poisons used in insect killing jars, it is unknown whether the presence and reproduction of feeding instars on adult insects is typical for this species, or it resulted from a secondary development from deutonymphs on killed bee hosts. It is also not clear whether the female deposits eggs with almost developed larvae or hatching of the larvae occurs inside the female oviducts and, therefore, causes her death (aparity, see review in Evans, 1992).

The full or nearly full ontogeny has been described for species in three genera: *Roubikia*, *Chaetodactylus*, and *Sennertia* (Baker, 1962; Baker *et al*., 1987; Lombert *et al*., 1987; OConnor, 1993a; Van Asselt, 2000), and was used along with morphological characters for reconstruction of the phylogeny of the family (OConnor, 1993a).

In the different chaetodactylid instars, the number and position of setae and solenidia generally follow the general astigmatid pattern (OConnor, 1982), although there are several unique changes, most notably the absence or reduction to alveoli of the external vertical setae *ve* in all instars; the absence of tarsal setae *aa* I, *u* and *v* I–IV from all instars; the shift of solenidion ω_3 to the posterior side of tarsus I in the tritonymphs and females; the absence of setae *e* and *ba* I–II in the heteromorphic deutonymphs; the modifications of condylophores to pretarsal suckers in males of *Sennertia* and *Chaetodactylus*; the asymmetrical pretarsi and condylophores in heteromorphic deutonymphs of *Achaetodactylus*, *Chaetodactylus*, and *Sennertia*; the precocial development of setae *e* and *f* on tarsus IV in some *Sennertia* protonymphs; and the development of an additional solenidion on tarsus II in females and homeomorphic males in *Roubikia*. Below, we give a brief account of known developmental instars of chaetodactylids; the accounts include similarities and dissimilarities with the respective generalized astigmatid instar (Griffiths *et al*., 1990; OConnor, 1982) and characters variable within chaetodactylids. Characters that are invariable throughout postembryonic development (excluding the inert heteromorphic deutonymph) but different across taxa are not mentioned. Characters of presence/absence of setae are documented in Table 7.

Prelarva

The prelarva of known chaetodactylids is calyptostatic, as in all Astigmata, represented by an apoderma within the chorion. It consists of a thin membrane and two well sclerotized protuberances (egg bursters, after Evans, 1992) at the cephalic pole (Fain & Herin, 1979). The protuberances serve to rupture the chorion by the larva that develops inside the prelarval cuticle (Hughes, 1959). So far, we have observed this instar in species of *Chaetodactylus* and *Sennertia*. Its presence in the remaining taxa is assumed. Measurements of a single available prelarva of *Chaetodactylus micheneri* are as follows: length 222, width 153, distance between cephalic pole and protuberance 41, cuticular protuberance length 11, width 18. Measurements of two prelarvae of *Sennertia* sp. (BMOC 04-0508-223): length (173–176), width (100–117); cephalic pole-protuberance (32–47); cuticular protuberance length (5–5), width (6–8.5).

Larva

The larva (Fig. 19, Fig. 31, Fig. 32) is similar to the generalized astigmatid larva in the absence of dorsal hysterosomal setae f_2 and h_3, coxal setae *4a* and *4b*, genital setae *g*, progenital chamber, genitalia and genital papillae, legs IV and associated apodemes, all trochanteral setae, tarsal solenidia ω_2 and ω_3 and by the presence of Claparède's organs (absent in *Sennertia*). Several differences include reductions that also characterize all subsequent instars: supracoxal setae of subcapitulum and tarsal setae *aa* I, *v* and *u* I–IV are absent; setae *ve* are represented by alveoli and placed almost at the middle of prodorsal shield, or absent (some *Sennertia*).

In *Roubikia*, Claparède's organs are present, not constricted distally (Fig. 14 *J*); two distinct dorsal sejugal sclerites are present; c_3 are not enlarged (distinctly shorter than c_p), and placed at the level of cupules *ia*; the sternum (excluding adjacent sclerotized cuticle) is almost the same length as the free parts of anterior apodemes I; solenidion σ III is distinct, more than two times longer than its alveolus.

In *Chaetodactylus*, Claparède's organs are present, with a characteristic constriction at the tip (Fig. 14 *I*); distinct dorsal sejugal sclerites are absent; c_3 are not enlarged (distinctly shorter than c_p), and placed at the level of cupules *ia*; the sternum is several times shorter than free parts of apodemes I (*Ch. osmiae*) or almost of the same length (*Ch. micheneri*); solenidion σ III is minuscule, about two times longer than its alveolus.

In *Sennertia*, Claparède's organs are absent; distinct dorsal sejugal sclerites are absent; c_3 are enlarged (distinctly longer than c_p), and distinctly posterior to cupules *ia*; the sternum is several times shorter than free parts of apodemes I; solenidion σ III is distinct, more than two times longer than its alveolus. Distinct alveoli of *ve* are lacking in *S. americana*.

Protonymph

The protonymph (Fig. 20, Fig. 21, Fig. 33, Fig. 32) follows the generalized astigmatid pattern in adding two pairs of dorsal idiosomal setae (f_2 and h_3), genital and pseudanal setae (*g*, ps_1-ps_3), progenital chamber, one pair of genital papillae, solenidion ω_2 on tarsus I, apodemes and legs IV with the tarsus bearing setae *d*, *w*, *r* (*r* is present in *Roubikia*, absent in *Chaetodactylus* and *Sennertia*), *p* and *q*, with the other podomeres glabrous. Claparède'*s* organs are absent in the protonymph and all subsequent instars. Some *Sennertia* are unusual in adding tarsal setae *e* and *f* IV or only the latter (see below). These setae normally appear only in the subsequent instar in most other astigmatid mites.

Roubikia. Solenidion ω_2 is paramedial, proximal to the level of setae *d*; setae *ba* II is present, approximately as long as solenidion ω_1 II; setae *w* and *r* III–IV are present; solenidion σ III is long, much longer than its alveolus.

Chaetodactylus. Solenidion ω_2 is apical, between setae *d* and *e*; setae *ba* II is present, approximately as long as solenidion ω_1 II; setae *w* III and *r* III–IV are absent; solenidion σ III is long, much longer than its alveolus.

Sennertia. Solenidion ω_2 is apical, between setae *d* and *e*; setae *ba* II is absent (*S. americana*), or if present it is several times shorter than solenidion ω_1 II (two African species from *Ceratina* and *S. vaga*); *w* III and *r* III–IV are absent; solenidion σ III is long, much longer than its alveolus. The protonymph of *S. vaga* displays development of a bulge on genu I (Fig. 32 *O*), which is absent in all other instars. *Sennertia scutata* and *S. koptorthosomae* show a very unusual deviation from the ancestral pattern: they add setae *e* and *f* IV that normally appear only in the deutonymph. Compared to the development in the closest outgroup (*Chaetodactylus*), we can conclude that the onset of morphological development of *e* and *f* IV is initiated earlier in these two species. This is a pre-displacement according to the classification of heterochronic processes by Alberch (1980) and McNamara (1986). *Sennertia vaga* adds only setae *f* IV, but *e* IV is lacking as in the ancestral pattern.

Phoretic Heteromorphic Deutonymph

This instar (Fig. 22) undergoes drastic morphological changes associated with the phoretic mode of life. Like in other Astigmata, it is non-feeding and lacks a functional digestive system. The gnathosoma is vestigial and probably serves as a sensory organ (p. 2); the anus is also reduced. The body of the phoretic deutonymph is usually strongly sclerotized, with the dorsum covered by shields. The posterio-ventral opisthosoma bears an attachment organ serving for attachment to insect hosts. This is a complex structure including adanal and pseudanal setae or their alveoli modified as suckers and conoids (p. 21). Leg proportions, ambulacra, and coxisternal region, including coxal apodemes, change substantially compared to the feeding instars (p. 28). The changes, however, do not involve drastic alterations of the ground plan or development of new structures. Leg setae are variously modified, with some setae suppressed. Suppressions common for most other astigmatid deutonymphs include: σ'' I (present in some taxa, *e.g.*, *Schulzea*), *ba* I (present in some taxa, *e.g.*, *Cerophagus* and *Horstia*), *u* and *v* I–IV (in chaetodactylids these setae are absent from all instars). Leg modifications and setal suppressions specific to chaetodactylids are discussed in the section on Legs (p. 31). Common to the generalized astigmatid deutonymph, chaetodactylids add the second pair of genital papillae, coxal setae *4b* and *4a*, trochanteral setae *pR* I–II, *sR* III, and tarsal solenidion ω_3. Alveoli of *ve* are added in species where they were absent in the larva and protonymph (*e.g.*, *S. americana*, *S. leei*). Differences between genera of chaetodactylid heteromorphic deutonymphs are given in the key below (p. 99).

Inert Heteromorphic Deutonymph

In Chaetodactylidae, an inert heteromorphic deutonymph (Fig. 24) is found only in the genus *Chaetodactylus*. This form is a cyst-like, immobile instar that usually remains within the cuticle of the preceding instar (protonymph). The protonymph is different from that of any other molting instar in having a

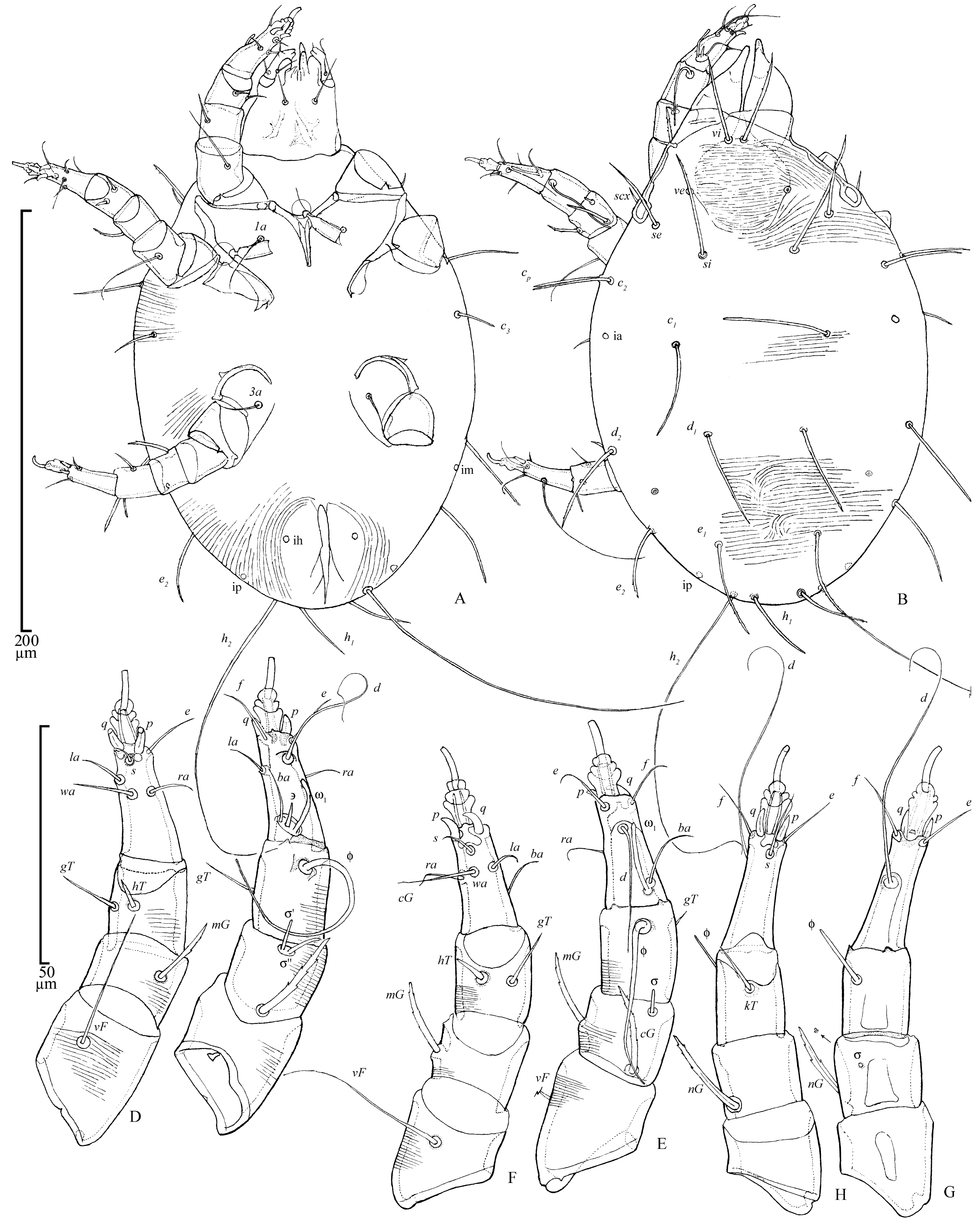

Fig. 19. *Chaetodactylus micheneri*, larva (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view; C, D - leg I, dorsal and ventral view; E, F - leg II, dorsal and ventral view; G, H - leg III, dorsal and ventral view.

Fig. 20. *Chaetodactylus micheneri*, protonymph (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view.

distinct network of dense substance in the epidermal layer under the protonymphal cuticle. The inert deutonymph is a highly regressive instar lacking functional mouthparts, legs, an attachment organ, and most of the setae. The body is rounded, with a distinct posterior projection in *Ch. ludwigi*. The gnathosoma is represented by two very small protuberances probably representing palpal solenidia. The dorsum has only supracoxal setae developed, the venter only pseudanal (ps_1-ps_2) and anal (ad_1-ad_3) setae forming vestigial conoids and suckers of the rudimentary attachment organ (Fig. 24). No apparent cupules are present. The progenital opening is comparatively well developed, with two pairs of large genital papillae. The coxal region is represented by the usual apodemes, but apodemes III and IV are often undeveloped. Posterior apodemes I are separate from anterior apodeme II and almost parallel to the midline. Posterior apodeme II is separate, with numerous muscles attached (Fig. 24 *A*). The legs are conical, without ambulacra, and with all podomeres fused; in *Ch. ludwigi*, the legs are elongated and subdivided into three articles (Trouessart, 1904a). The anterior pair of legs has a dorsal solenidion. All other legs are glabrous,

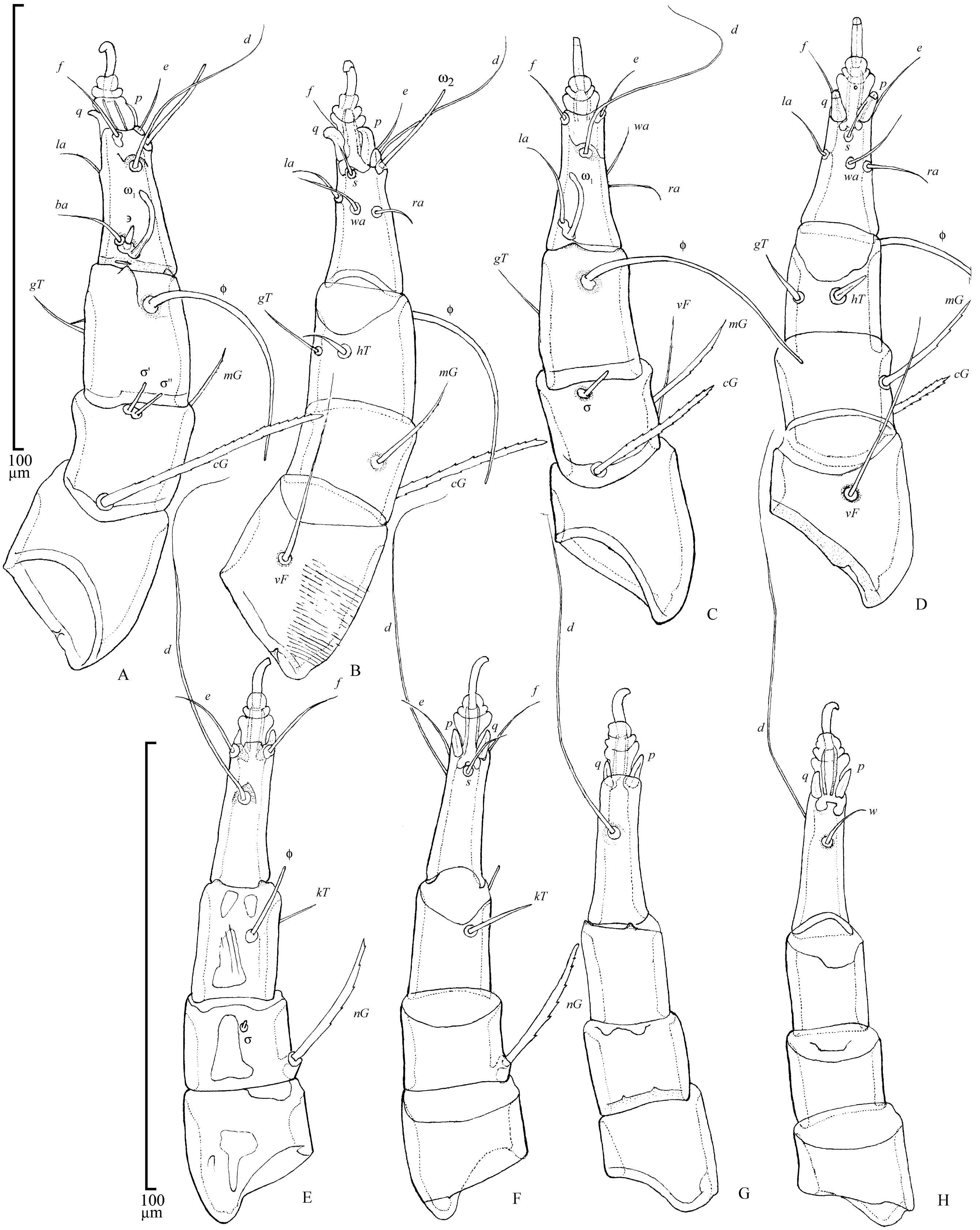

Fig. 21. *Chaetodactylus micheneri*, protonymph (form 3, BMOC 03-0310-001). A, B - leg I, dorsal and ventral view; C, D - leg II, dorsal and ventral view; E, F - leg III, dorsal and ventral view; G, H - leg IV, dorsal and ventral view.

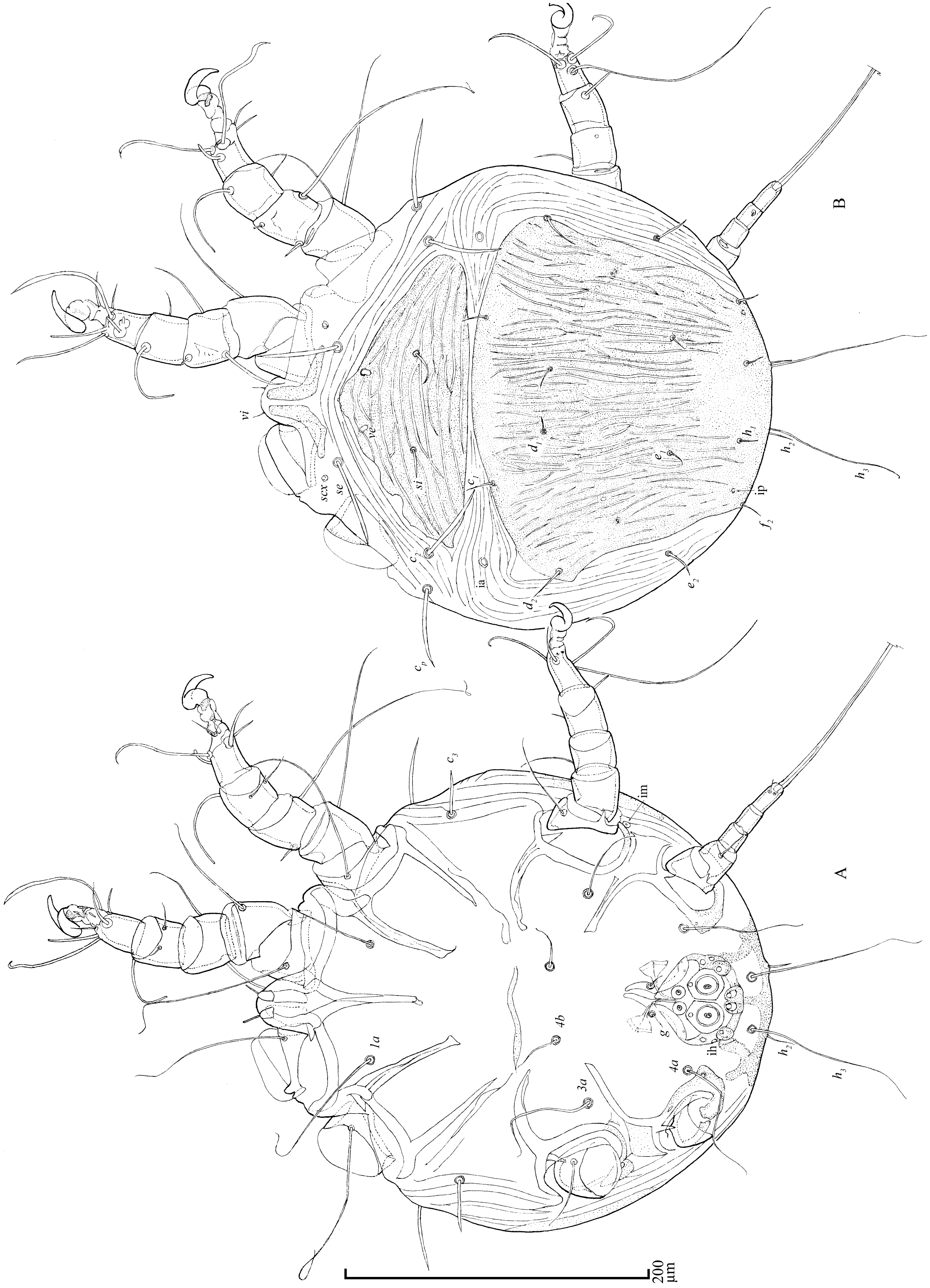

Fig. 22. *Chaetodactylus micheneri* sp. n., heteromorphic deutonymph, (form 1, BMOC 96-0510-127), holotype. A, B - ventral and dorsal view.

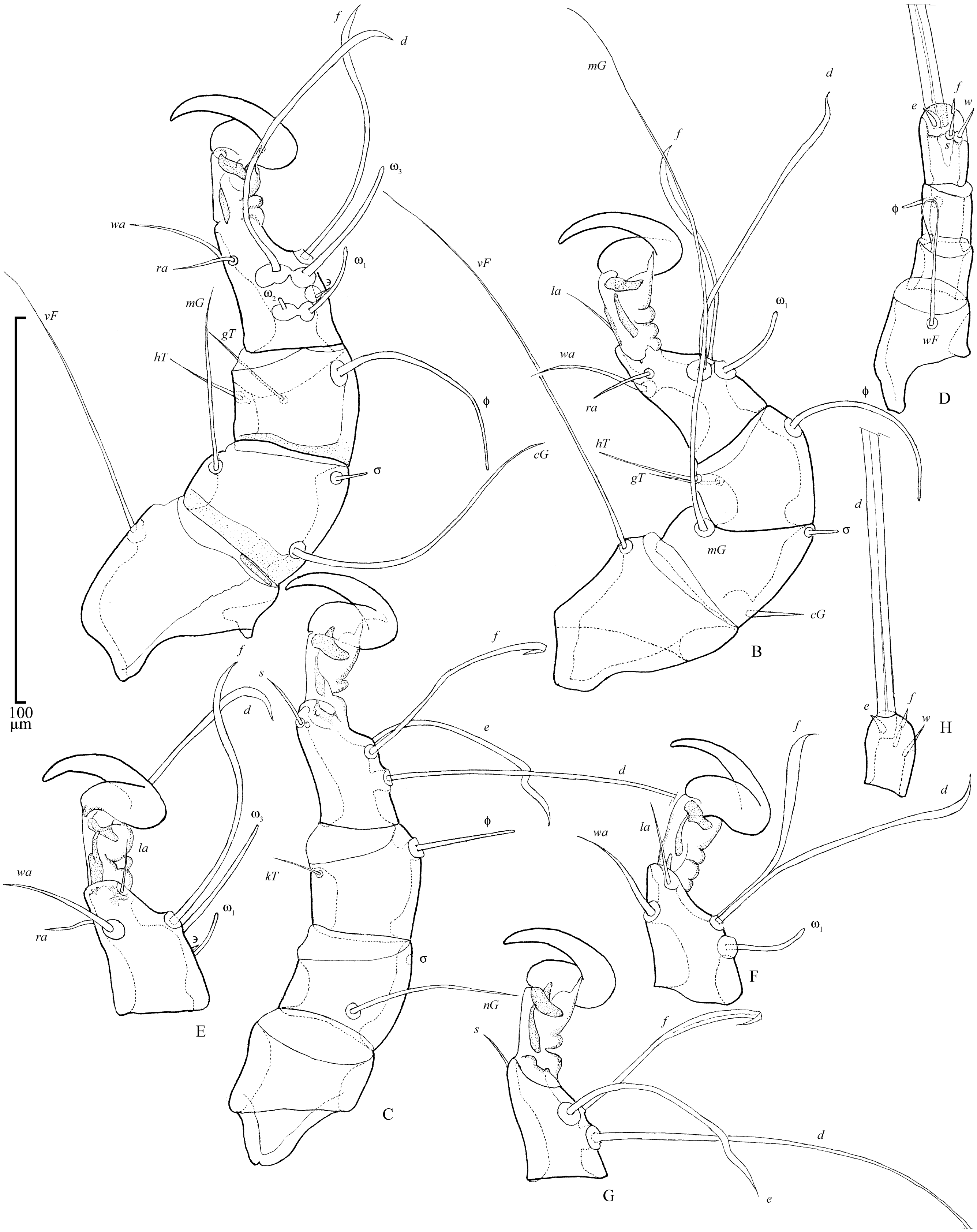

Fig. 23. *Chaetodactylus micheneri* sp. n., heteromorphic deutonymph, (form 1, BMOC 96-0510-127 (A, C-E, G-H), -128 (B, F)). A–D - legs I–IV, respectively; E–H - tarsi I–IV, respectively.

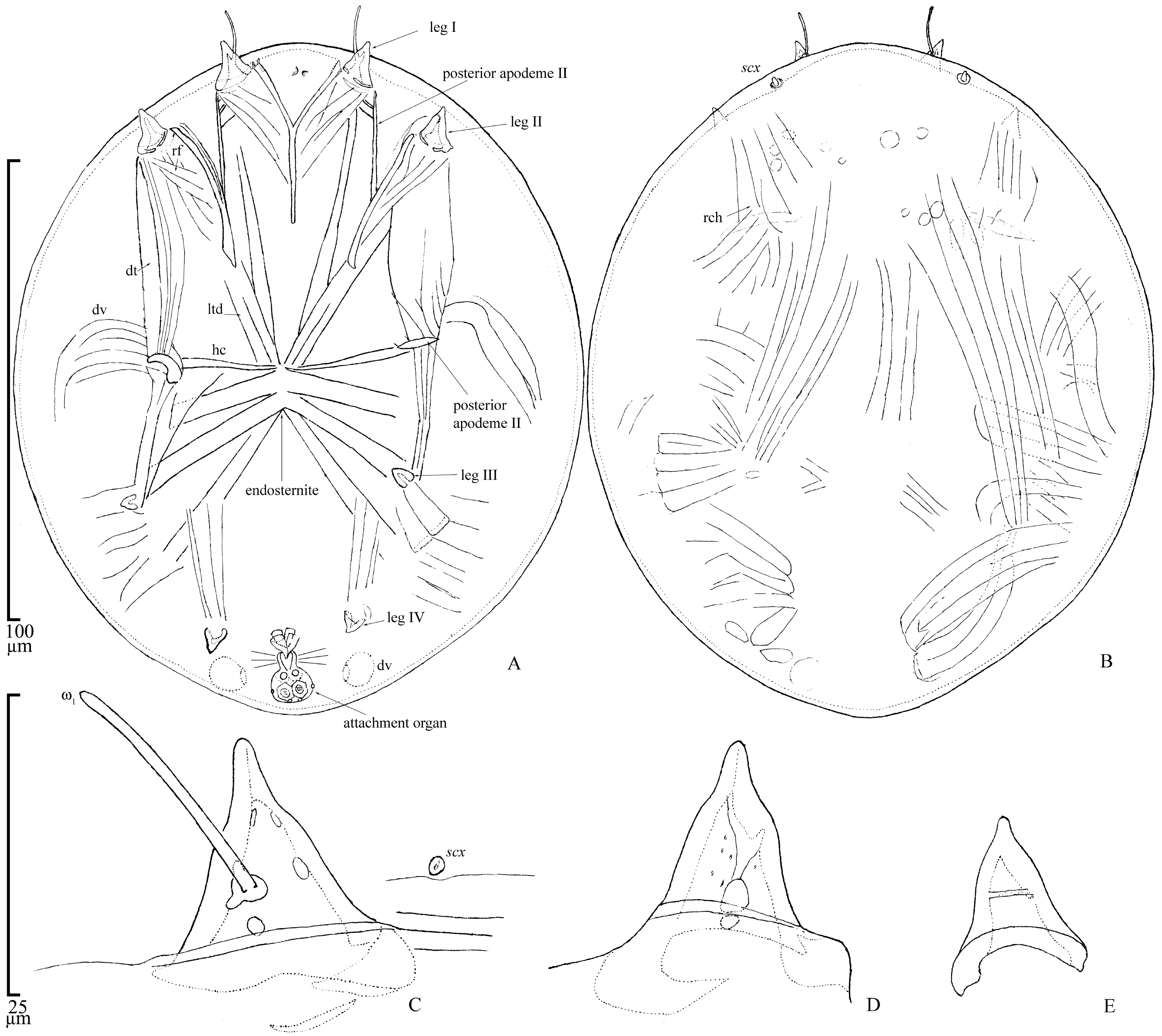

Fig. 24. *Chaetodactylus micheneri*, inert heteromorphic deutonymph (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view, C–E - legs I, II, and IV, respectively. **dt** - depressor of trochanter; **dv** - dorso-ventral muscle; **hc** - horizontal constrictor; **ltd** - dorsal part of trochanteral levator; **rch** - retractor of chelicera; **rf** - remotor of femur. Musculature is shown by solid lines, should not be used for reference.

although they may have unsclerotized cuticular fields probably corresponding to bases of setae. The identity of the single solenidion is not clear; it could be σ, ϕ or ω_1. Judging from the presence of its elaborate cuticular base and the rounded shape of its tip (Fig. 24 *B*), we believe that it is ω_1. Although external structures have undergone substantial regression, their extrinsic musculature seems to be affected to a much lesser extent. The existence of well-developed cheliceral retractors and an almost complete set of locomotory muscles of the coxisternal region and endosternite (Fig. 24 *B*) is difficult to explain because the chelicerae are completely absent and the legs not functional. The presence of well-developed dorso-ventral muscles that normally create hydrostatic pressure necessary for various needs, including locomotion, feeding, and mating, is also remarkable.

Tritonymph

The tritonymph (Fig. 25, Fig. 26, Fig. 34, Fig. 35) follows the generalized astigmatid pattern in not adding any new structures from the deutonymphal stage, but structures modified in

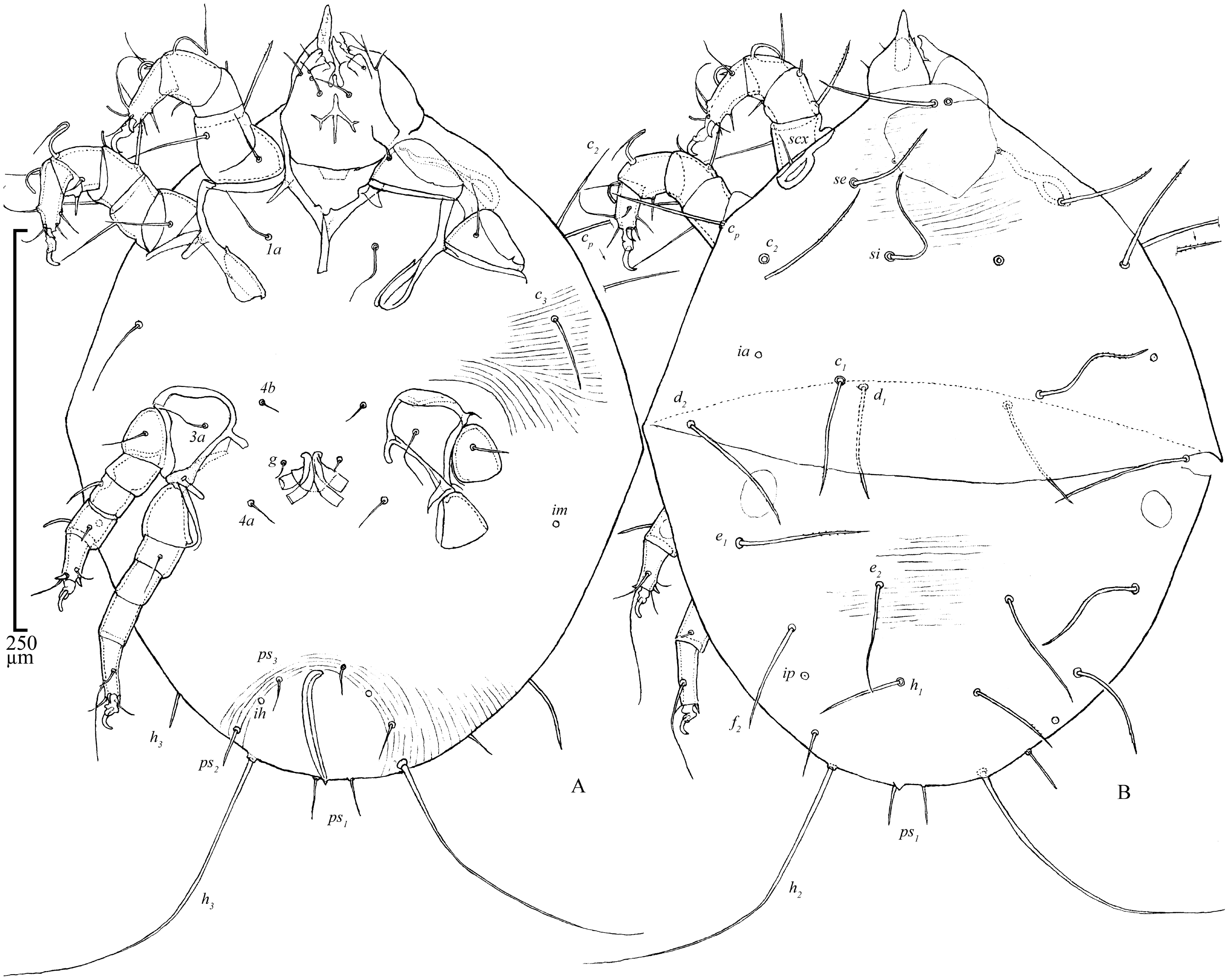

Fig. 25. *Chaetodactylus micheneri*, tritonymph (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view.

the heteromorphic deutonymph typically return to their protonymphal form.

Compared to the phoretic heteromorphic deutonymph (characters in parenthesis), setae ps_3 reappear (alveolus), setae ad_1-ad_3 are lacking or represented only by alveoli (modified into suckers of attachment organ), in *Chaetodactylus* and *Sennertia* solenidion ω_2 is apical, like in protonymphs (medial or subproximal), solenidion ω_3 is displaced to the posterior side of tarsus I (anterior side), setae *ba* I, *e* and *s* I–II, and solenidion σ'' I are present (absent); except for *S. americana*, setae *ba* II are present (absent); tarsal setae *p* I–II, *q* I–III are present (absent, except for *Centriacarus*); *p* and *q* IV are present (absent, except for *Centriacarus* and *Roubikia*); σ III is present (alveolus, but in *Sennertia* it is present, too); solenidion ϕ IV present (absent, except for *Chaetodactylus*). *S. americana* and *S. leei* have lost the alveoli of *ve* (present in phoretic deutonymphs). This loss resembles that of the protonymph.

Adults

Adults (Fig. 27, Fig. 28, Fig. 29, Fig. 30, Fig. 36, Fig. 37, Fig. 38, Fig. 39) are similar to the tritonymph but add genitalia and associated structures (p. 21) and sexually dimorphic changes. Compared to the tritonymph, they may add filiform adanal setae (see section on Hysterosomal setae on p. 11 and Table 7), setae ps_3 are displaced anteriorly; legs of the males have undergone several reductions in apical setae, modifications of the anterior condylophores to pretarsal suckers in *Chaetodactylus* and *Sennertia*, changing of the shape and proportions of the tarsi in *Chaetodactylus* or the legs themselves in the heteromorphic male of *Roubikia* (p. 41).

Ontogenetic Trends and Their Evolutionary Implications

All chaetodactylids share two basic ontogenetic pathways, differing in whether the phoretic deutonymph is formed or not

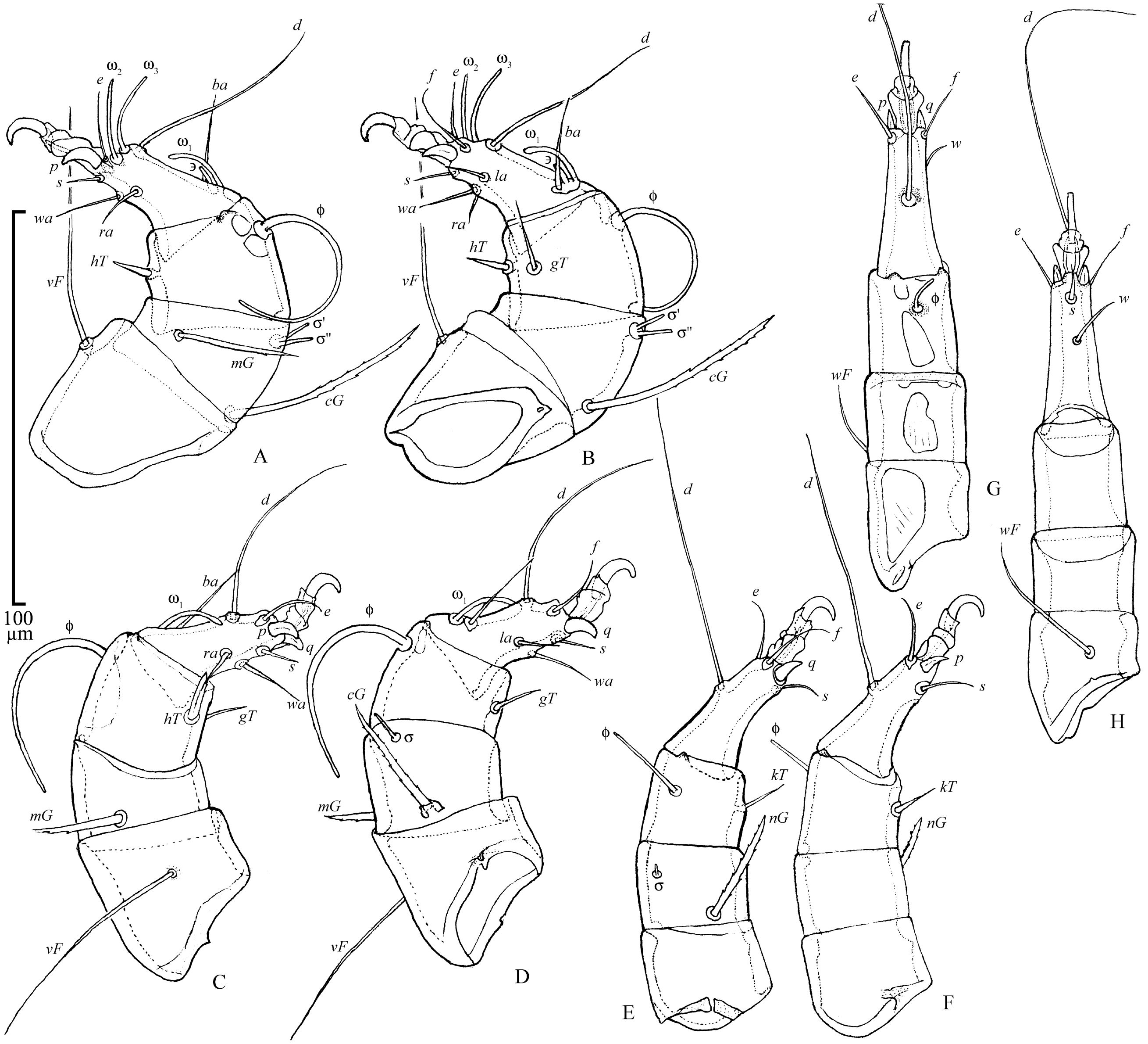

Fig. 26. *Chaetodactylus micheneri*, tritonymph (form 3, BMOC 03-0310-001). A; B - leg I; posterior and anterior view; C; D - leg II; posterior and anterior view; E; F - leg III; anterior and posterior view; G; H - leg IV; dorsal and ventral view.

in the middle of the life-cycle. *Roubikia* displays terminal modifications of these pathways resulting in alternative molts to either homeo- or heteromorphic male. *Chaetodactylus* shows alternative modification of the deutonymph to an inert instar. The expression of these ontogenetic patterns is adaptive and dependent largely on environmental factors.

The molt from larva to protonymph is common for all ontogenenetic pathways. It is accompanied by the most numerous and profound changes, namely the development of legs IV, several leg and hysterosomal setae and tarsal solenidion ω_2, and suppressions do not occur at this molt. With the notable exception of inert deutonymphs, the next molt, protonymph-(deutonymph, tritonymph) also involves adding new structures on the ventral hysterosoma and legs, although the changes are not so drastic. In contrast, the tritonymph-adult molt, also common for all ontogenies, is characterized by a few ontogenetic additions. It may add only adanal setae; if a female is produced then no suppressions occur, but they do occur if either male morph is produced. Quantitative changes in the number of setae and solenidia among ontogenetic stages (Table 7) are summarized on Fig. 18. The transitions between larva-protonymph, protonymph-tritonymph, phoretic and inert heteromorphic deutonymphs-tritonymph, and tritonymph-female display an increase in the number of setae and solenidia. A substantial amount of ontogenetic additions occurs following all these molts, except for the tritonymph-female molt, where only a few ada-

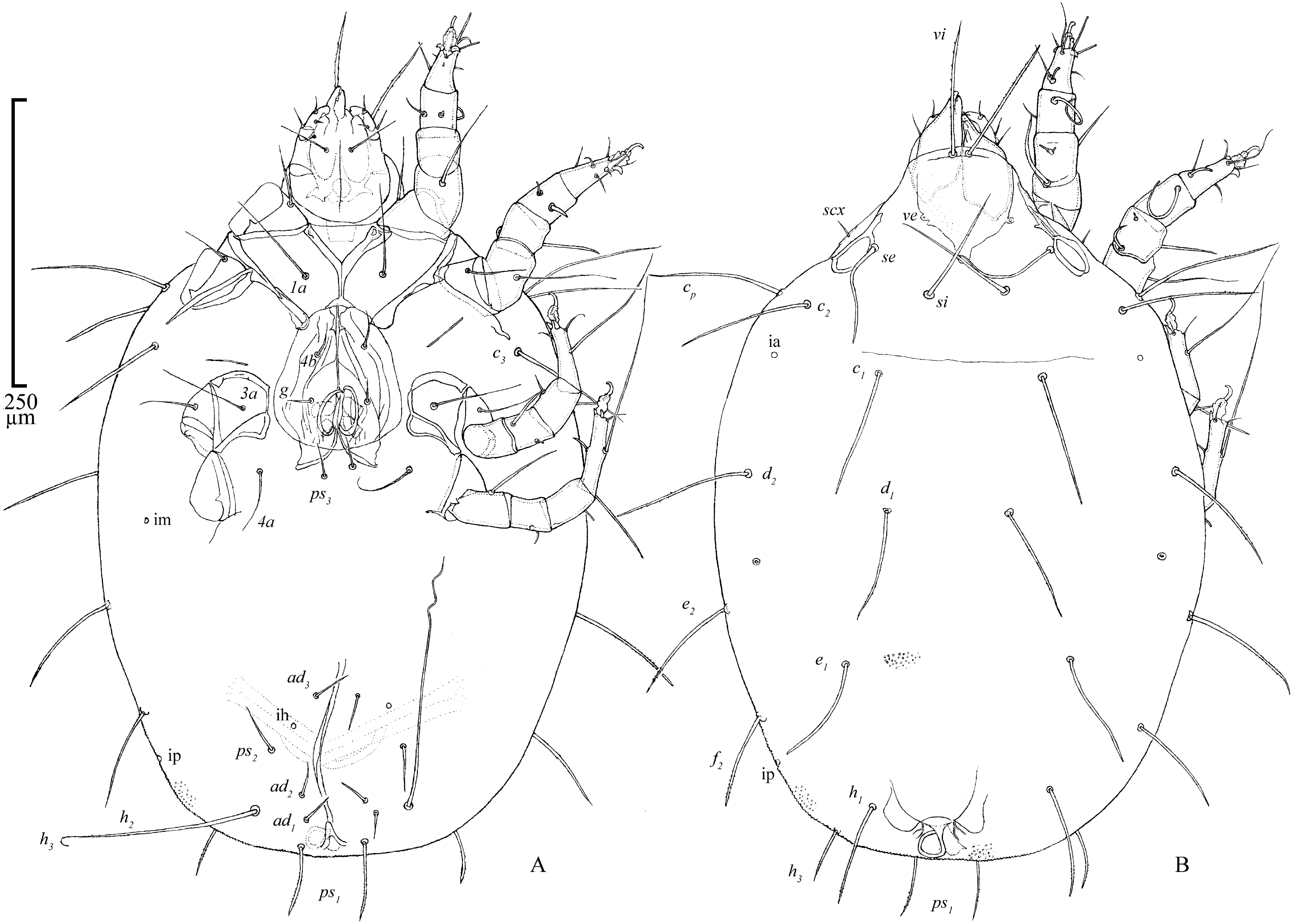

Fig. 27. *Chaetodactylus micheneri*, female (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view.

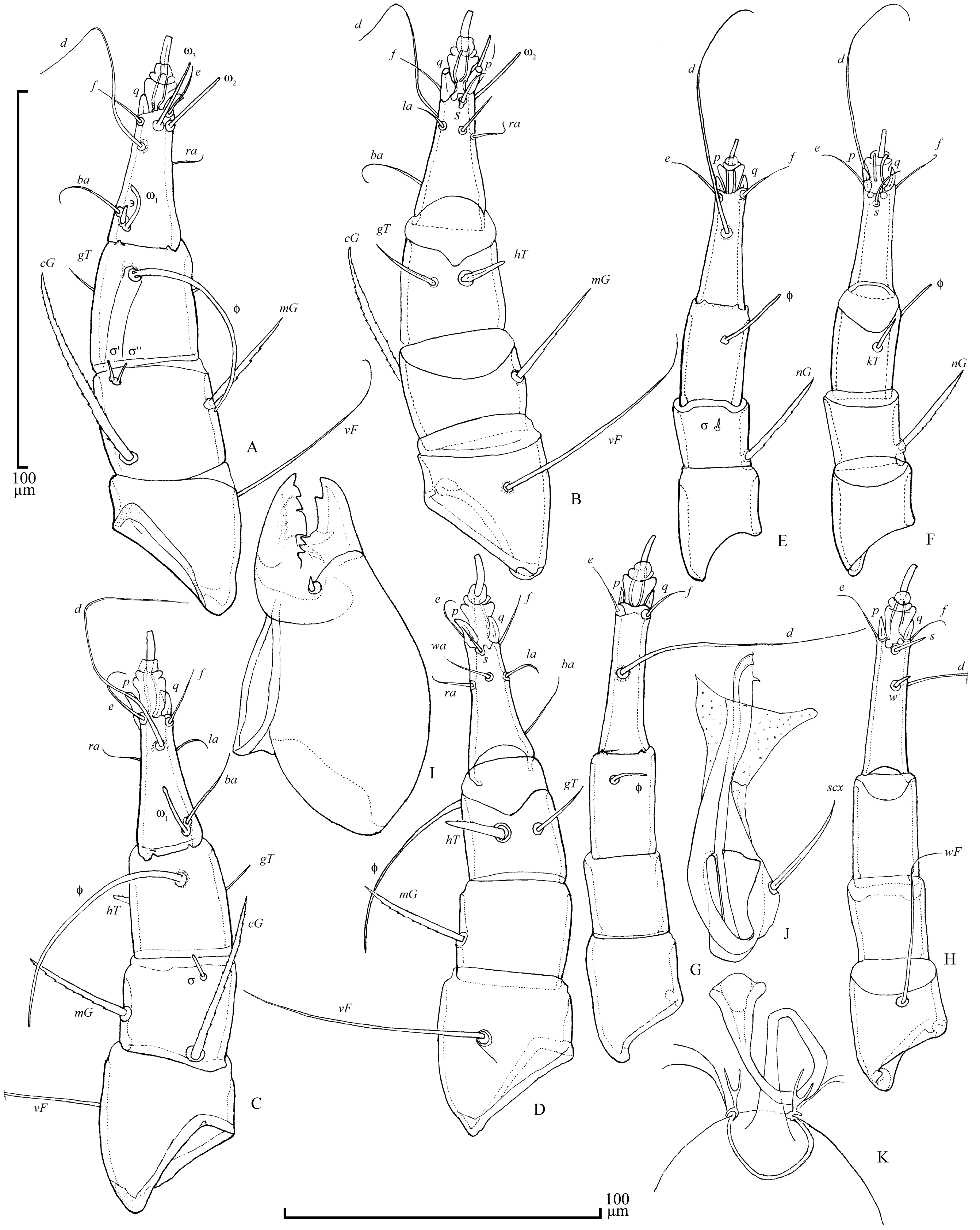

Fig. 28. *Chaetodactylus micheneri*, female (form 3, BMOC 03-0310-001). A, B - leg I, dorsal and ventral view; C, D - leg II, dorsal and ventral view; E, F - leg III, dorsal and ventral view; G, H - leg IV, dorsal and ventral view; I - Chelicera; J - supracoxal sclerite; K - spermatheca.

Fig. 29. *Chaetodactylus micheneri*, male (form 3, BMOC 03-0310-001). A, B - ventral and dorsal view.

nal setae may be added. The total number of leg setae and solenidia decreases following the molts from tritonymph-male, protonymph-phoretic deutonymph and especially, protonymph-inert deutonymph, and the reductions are mostly ontogenetic suppressions. Structural suppressions following the molts protonymph-phoretic deutonymph and inert deutonymph-tritonymph are concomitant with some ontogenetic additions. No suppressions occur following the molts larva-protonymph, protonymph-tritonymph, and tritonymph-female.

It is obvious from our cladogram (Fig. 40) that the origin of the three major groups in the family (*Roubikia*, *Centriacarus*, and the clade including *Achaetodactylus*, *Chaetodactylus* and *Sennertia*) has been associated with losses of different morphological structures. These non-ontogenetic structural reductions (Fig. 18) are probably evolutionarily irreversible, thus capable of channeling further pathways of morphological evolution. The large number of reductions is not surprising because feeding instars of the mites live in concealed cells of bee nests where physical and biological parameters are more or less constant.

The pattern of reductions and additions occurring in different instars suggests that the ontogeny of chaetodactylids is not just a way of successive "unfolding" of morphological structures, but a dynamic adaptive mechanism interlaced with an

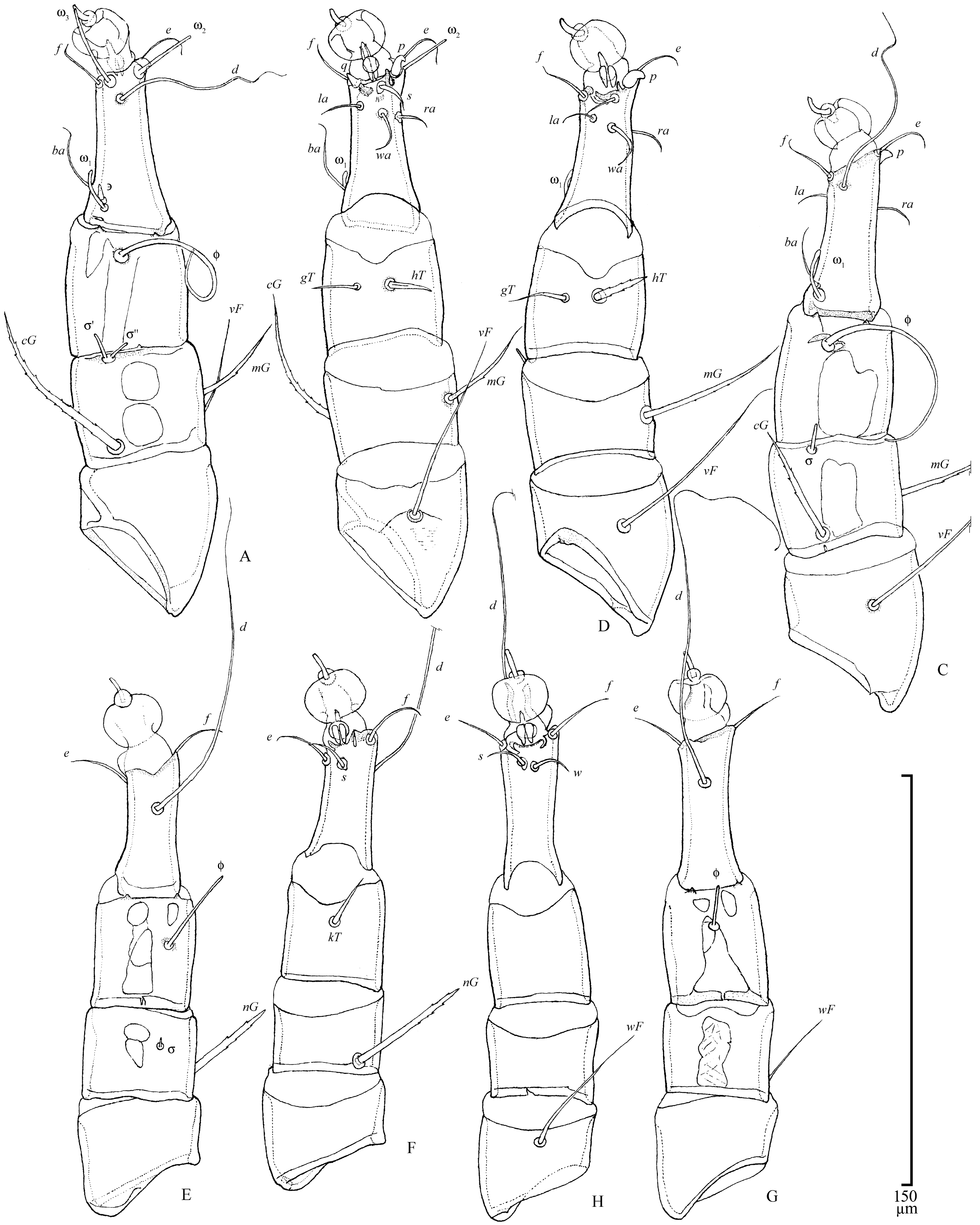

Fig. 30. *Chaetodactylus micheneri*, male (form 3, BMOC 03-0310-001). A, B - leg I, dorsal and ventral view; C, D - leg II, dorsal and ventral view; E, F - leg III, dorsal and ventral view; G, H - leg IV, dorsal and ventral view.

Table 7. Ontogenetic changes in chaeto- and solenidiotaxy in chaetodactylids.

	Structure	L^2	PN^2	HDN^3	TN^1	F^2	M^2	HT M^4
idiosoma	*ve*	aaa−−a	aaa−−a	aa−aaaa−	aaaa−	a	a	a
	f_2	−	+	+	+	+	+	+
	h_3	−	+	+	+	+	+	+
	ps_1	−	+	+	+	+	+	+
	ps_2	−	+	+	+	+	+	+
	ps_3	−	+	a	+	+	+	+
	ad_1	−	−	+	−−aaa	++−+−+	++−+−a	a
	ad_2	−	−	+	−−aaa	++−+−a	−	−
	ad_3	−	−	+	−−aaa	+++++a	−	−
	4b	−	−	+	+	+	+	+
	4a	−	−	+	+	+	+	+
	g	−	+	+	+	+	aa++aa	a
legs I	ω_2 I	−	+	+	+	+	+	+
	ω_3 I	−	−	+	+	+	+	+
	e I	+	+	−	+	+	+	+
	s I	+	+	−	+	+	+	+
	p I	+	+	−	+	+	+	+
	q I	+	+	−	+	+	++−+++	+
	ba I	+	+	−	+	+	+	+
	σ'' I	+	+	−	+	+	+	+
	pR I	−	−	+	+	+	+	+
leg II	ω_2 II	−	−	−	−	−−−−−+	−−−−−+	−
	e II	+	+	−	+	+	+	+
	s II	+	+	−	+	+	+	+
	p II	+	+	−	+	+	++−+−+	+
	q II	+	+	−	+	+	−−−−−+	−
	ra II	+++−++	+++−++	+	+++−+	+++−++	+++−++	+
	la II	+++−++	+++−++	+	+++−+	+++−++	+++−++	+
	ba II	++++−+	++++−+	−	++++−	++++−+	++++−+	+
	pR II	−	−	+	+	+	+	+
Leg III	*f* III	+	+	+	+	+	+++++−	−
	w III	−−−−−+	−−−−−+	−−−−−++−	−	−−−−−+	−−−−−+	+
	r III	−−−−−+	−−−−−+	−−−−−++−	−	−−−−−+	−−−−−+	+
	p III	+	+	−−−−−++−	+	+	−	−
	q III	+	+	−	+	+	−−−−−+	+
	σ III	+	+	aa+++aaa	+	+	+	+
	sR III	−	−	+	+	+	+	+
Leg IV	*e* IV	−	−−+−−−	+++++++−	+	+	+	+
	f IV	−	−−++−−	+	+	+	+++++−	−
	d IV	−	+	+	+	+	+	+
	w IV	−	+	+	+	+	+	+
	r IV	−	−−−−−+	−−−−−++−	−	−−−−−+	−−−−−+	+
	s IV	−	−	+	+	+	+	+
	p IV	−	+	−−−−−+++	+	+	−	−
	q IV	−	+	−−−−−++−	+	+	−−−−−+	+
	ϕ IV	−	−	++aaaaaa	+	+	+	+
	kT IV	−	−	−−−−−++−	−	−−−−−+	−−−−−+	+
	wF IV	−	−	+	+	+	+	+

Note: Constant characters present in all instars but the inert heteromorphic deutonymph are omitted: *vi*, *si*, *se*, *scx*, c_1, c_2, c_3, c_p, d_1, d_2, e_1, e_2, *1a*, *3b*, ω_1 I, *f* I, *d* I, *wa* I, *ra* I, *la* I, famulus ε I, ϕ I, *gT* I, *hT* I, σ' I, *cG* I, *mG* I, *vF* I, ω_1 II, *f* II, *d* II, *wa* II, ϕ II, *gT* II, *hT* II, σ II, *cG* II, *mG* II, *vF* II, *e* III, *d* III, *s* III, ϕ III, *kT* III, *nG* III. If the inert heteromorphic deutonymph were included, constant characters would be only *scx*, and ω_1 I. Complete ontogenies were studied for four species: *Chaetodactylus micheneri, Ch. osmiae, Sennertia scutata*, and *S. americana*. The tritonymph of *Roubikia panamensis* is unknown; the heteromorphic deutonymph of *S. vaga* is unknown, in *A. leleupi* and *C. turbator*, only heteromorphic deutonymphs are known. Immobile heteromorphic deutonymphs known only for *Chaetodactylus* are not included because of the difficulties in interpretation of setal homologies. + = presence; − = absence; a = alveolus; L = larva; PN = protonymph; HDN = heteromorphic deutonymph; TN = tritonymph; F = female; M = homeomorphic male; HT M = heteromorphic male. If a character is variable within an instar, a sequence of corresponding states is given. The sequences can be identified by the superscript in the first row: **1** = *Ch. micheneri, Ch. osmiae, S. scutata, S. vaga, S. americana*; **2** = 1+ *R. panamensis*; **3** = 2+ *A. leleupi, C. turbator*; or **4**=*R. panamensis*.

Fig. 31. *Sennertia vaga*, larva (BMOC 04-1122-025), A, B - dorsal and ventral view.

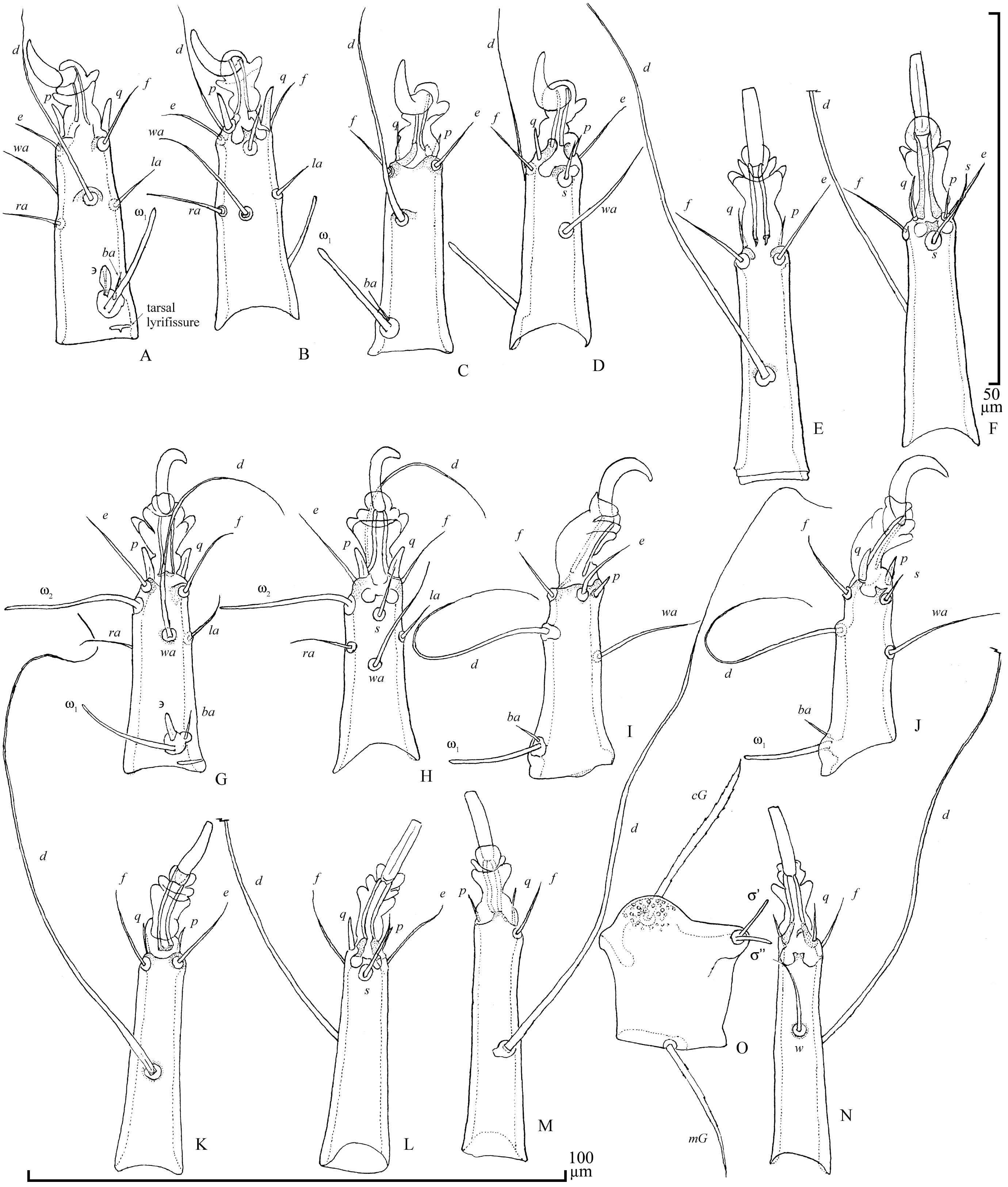

Fig. 32. *Sennertia vaga* (BMOC 04-1122-025), larva (A–F) and protonymph (G–O). A, B - tarsus I, dorsal and ventral view; C, D - tarsus II, dorsal and ventral view; E, F - tarsus III, dorsal and ventral view; G, H - tarsus I, dorsal and ventral view; I, J - tarsus II, anterior and posterior sides; K, L - tarsus III, dorsal and ventral view; M, N - tarsus IV, dorsal and ventral view; O - genu I, posterior side. Scale bars: A–F - 50 µm, G–O - 100 µm.

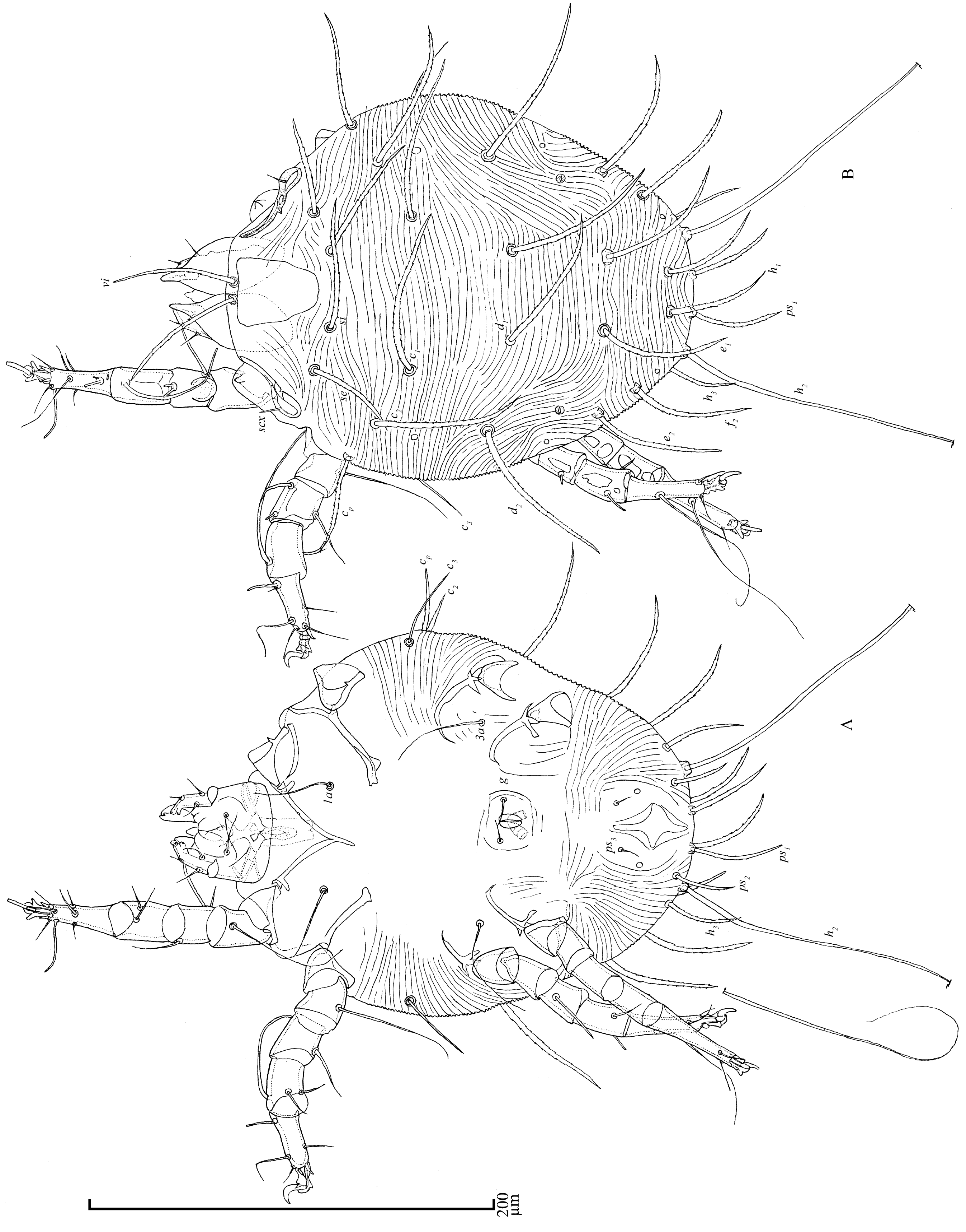

Fig. 33. *Sennertia vaga*, protonymph (BMOC 04-1122-025). A, B - ventral and dorsal view.

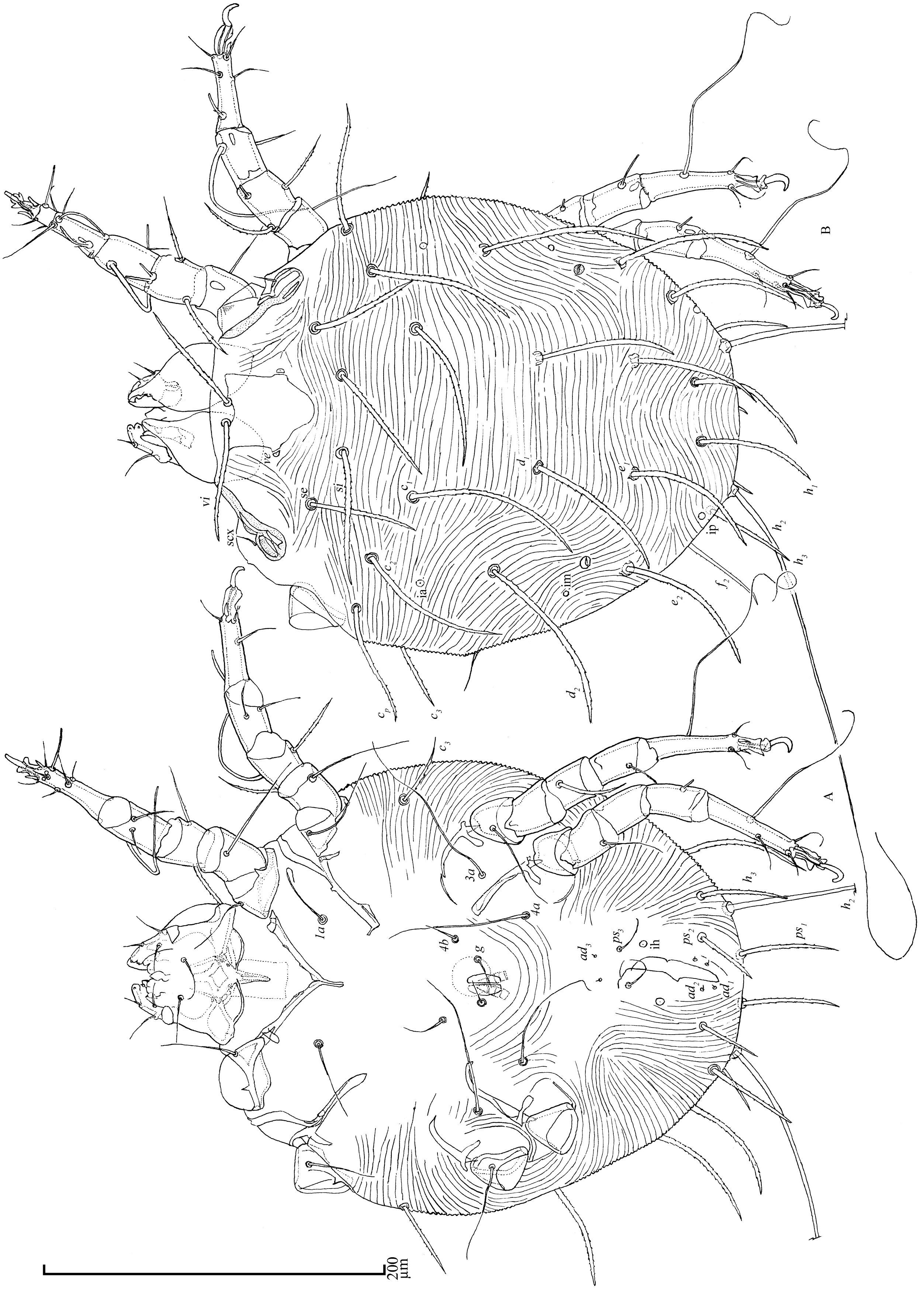

Fig. 34. *Sennertia vaga*, tritonymph (BMOC 04-1122-025). A, B - ventral and dorsal view.

ontogenetic pattern. This could be generalized to all Astigmata, which probably have evolved as a result of a drastic modification of the ancestral ontogeny, namely the development of the heteromorphic deutonymph and paedomorphosis, concomitant with the appearance of derived mating systems and direct sperm transfer. It is interesting to note that in chaetodactylids these two very different instars (phoretic deutonymphs and males) share several character states: closer position of progenital and anal openings, modification of ad_1 to suckers; retention of solenidion ω_3 on the anterior side of the tarsus I (shifted to the posterior side in females and tritonymphs of Chaetodactylidae), suppression of setae *p* and *q* III–IV, *q* II and often *p* I (*Chaetodactylus* and *Sennertia*, Table 7), and the asymmetry of the condylophores. Given that many of above mentioned shared characters do not occur in early derivative groups, it is very speculative to suggest that they have the same underlying nature. These characters might have evolved "independently" from each other due to similar biological constraints.

The large number of setal suppressions and changes in the position of setae occurring in the heteromorphic deutonymphs and males (Table 7, Fig. 18) may create polymorphisms in these characters when they are considered as independent ontogenetic transformations (*e.g.*, Grandjean, 1957a; André, 1988) rather than discrete characters (de Queiroz, 1985) in phylogenetic analyses. Except when the changes in different instars are correlated, such characters are traditionally considered independent from each other (*e.g.*, separately coded for different instars). Because these characters are homologous, their states cannot be entirely independent in different instars. Resulting from the fact that the information on multiple character states is retained in the genotype, potential dependency of the ontogenetic characters may create substantial difficulties in interpreting their derived and ancestral conditions in any particular instar. Changes in such characters may occur as alterations of their expression mechanisms and may better be described as a network rather than a hierarchical branching pattern (*e.g.*, "disharmonic" evolution, see André, 1988). A large amount of homoplasy, therefore, could be expected. It is worth noting that since genetic information for amphistatic suppressions is not lost, these characters retain evolutionary potential and then could be adapted to new functions.

Although most researchers now agree that the sequence of ontogenetic transformations is usually uninformative about inferring phylogenetic character polarities (de Queiroz, 1985), there are some discrepancies in how to code them for phylogenetic analyses. Klompen & OConnor (1989) argued that characters should be coded as 'ontogenetic patterns' in place of the 'instar by instar' approach, while André & Fain (2000) thought that the reverse is preferable. Despite the fact that the 'instar by instar' coding by definition contains all possible information that can be derived for the 'ontogenetic pattern' coding, Klompen and OConnor (1989) suggested that the use of the latter coding increases the information content of the dataset. From the informational point of view, both these methods are equal, but the ontogenetic pattern coding is more likely to introduce errors or biases associated with interpretations of the patterns (*e.g.*, the case presented on p. 97 of Klompen & OConnor (1989) resulted from incorrect coding of character 25 where neither of its states is applicable to *Chirnyssoides surinamensis*). Parsimony analyses based on both coding methods should produce the same results, although some parameters (*e.g.*, consistency or homoplasy indices) will be different due to the different number of characters.

BIOLOGY AND HOST ASSOCIATIONS

Host Associations

Chaetodactylid mites are associated with solitary or facultatively social bees of the families Megachilidae and Apidae. *Centriacarus* and *Roubikia*, early derivative genera restricted to South and Central America (Plate 2), are associated with apid bees. *Achaetodactylus* occurs in Sub-Saharan Africa on *Ceratina* (Apidae), while its sister clade, comprising *Chaetodactylus* and *Sennertia*, is cosmopolitan and is associated with both megachilid and apid bees (Plates 1–4). Table 8 summarizes information about host and geographic distributions of both mites and their insect hosts at the generic level.

Feeding instars of mites usually occur in the nests of their host, while the adult insects are used as transport by the phoretic deutonymphs. The *Sennertia vaga*-group probably does not form the deutonymphal instar and disperses as feeding instars on adults bees evidenced by their non-random distribution on the host. Because the proportion of different instars is often similar to that of a normally reproducing colony, we suspect that feeding and reproduction may occur while dispersing. Inert heteromorphic deutonymphs of *Chaetodactylus* may infest new bee nests constructed in old nest cavities. Below we consider the conspecific transfer of mites from parents to offspring (vertical transfer), the transfer between different host species (horizontal transfer), accidental phoretic associations, and interactions of the mites with their hosts inside nests.

Vertical Transfer

Although only female bees can establish new nests, chaetodactylids usually occur on both male and female hosts. Mites phoretic on males will fail to start a new colony unless they migrate to a female. As was demonstrated for *Parasitellus* (Parasitidae) mites and their *Bombus* hosts, mites may move from a male or worker to a queen but never from a queen to either of these casts (Huck *et al.*, 1998). Venereal transmission of the winterschmidtiid mite, *Kennethiella trisetosa*, from male to female of the wasp *Ancistrocerus antilope* was documented by Cooper (1954) and assumed for *Ensliniella parasitica* associated with *Allodynerus delphinalis* (Vitzthum, 1925). Okabe & Makinio (2002) found some *Sennertia* in the genital chamber of female *Xylocopa circumvolans* and hypothesized mite transfer from male to female during copulation. Abrahamovich and

Table 8. Host associations and distribution of chaetodactylids. Aust = Australian region, Orient = Oriental region, Madag = Madagascar, Afr = Afrotropical region, Palear = Palearctic region, Near = Nearctic Region, Antill = the Greater and Lesser Antilles, excluding Trinidad, Arauc = Araucanian region (after Michener, 2000). Unusual finding of chaetodactylids on *Andrena*, *Halictus*, *Anthophora*, *Apis*, *Bombus*, *Vespula*, Passalidae (Chmielewski, 1993; Haitlinger, 1999; Zachvatkin, 1941; our data) are omitted. Cleptoparasites of the principal hosts (parenthesis) that may transfer chaetodactylids are also not included: apid *Coelioxoides* (*Tetrapedia*), *Stelis* (*Osmia*), sapygids *Polochrum* (*Xylocopa*) and *Sapyga* (*Chelostoma*) (Samšiňák, 1973; Zachvatkin, 1941; our data). See discussion about phoresy of adult *Sennertia* on Neotropical *Centris* in the text.

Bee taxon	**Mite taxon**	**Aust**	**Orient**	**Madag**	**Afr**	**Palear**	**Near**	**Neotr**	**Antill**	**Arauc**
Megachilidae										
Lithurgini										
Lithurgus	*Chaetodactylus*	+	+	+	+	+	+	+	+	+
Trichothurgus	*Chaetodactylus*									+
Microthurge	*Chaetodactylus*							+		
Osmiini										
Osmia	*Chaetodactylus*					+	+			
Hoplitis	*Chaetodactylus*						+			
Chelostoma	*Chaetodactylus*					+				
Anthidiini										
Rhodanthidium	*Chaetodactylus*					+				
Anthidium	*Chaetodactylus*									+
Megachilini										
Megachile	*Chaetodactylus*					+				
Apidae, **Xylocopinae**										
Xylocopini										
Xylocopa	*Sennertia*	+	+	+	+	+	+	+	+	+
Ceratinini										
Ceratina	*Sennertia*		+		+	+	+	+		
Ceratina	*Achaetodactylus*				+					
Apidae, **Apinae**										
Tapinotaspidini										
Chalepogenus	*Chaetodactylus*									+
Tetrapediini										
Tetrapedia	*Roubikia*						+	+		+
Emphorini										
Melitoma	*Chaetodactylus*						+			
Diadasia	*Chaetodactylus*						+			+
Ptilothrix	*Chaetodactylus*									+
Ancyloscelis	*Chaetodactylus*							+		
Centridini										
Centris	*Centriacarus*						+	+		

Alzuet (1990) came to the same conclusion for *X. splendidula*. Vicidomini (1996) reported mite transfer during copulation of *X. violacea*, without mentioning the direction and whether the mites were migrating to the genital chamber. Mites of the *Sennertia argentina* group distributed in the New World are known to be phoretic inside the genital systems of females and males of large carpenter bees of the subgenus *Neoxylocopa* (Vinson, pers. comm.; our data), suggesting that venereal transmission is likely in these species.

As mites from a single bee are usually descendants of the same colony originating from the parental nest, their possible transfer from males to females may alleviate the risk of inbreeding depression. We have observed higher abundance of *Sennertia* on males of large Neotropical *Xylocopa* (*Neoxylocopa*) than on females. This may be circumstantial evidence supporting this hypothesis although other explanations are possible (a quantitative analysis of this phenomenon has not yet been conducted). Krombein (1962) attributed higher infestation rates of *Chaetodactylus krombeini* on the males of *Osmia lignaria* to the skewed sex ratio and the prior emergence of males in the spring. However, xylocopine bees usually have a female-biased sex-ratio (Vicidomini, 1998). Direct observations or a thorough statistical analysis taking into account the infestation rate as well other factors that could influence it may reveal whether the mites can distinguish between different hosts sexes.

Some bee species of the Asian subgenus *Xylocopa* (*Zonohirsuta*) display remarkably strong gender differences in the location of phoretic *Sennertia lauta* and *S. ratiocinator*. In the female, the mites are situated in a groove between the scutellum and metanotum, forming a concave line outlining the posterior borders of the scutellum (Plate 4). In the male, large

PLATE 1

Above. *Lithurgus echinocacti* from Arizona with phoretic mites *Chaetodactylus abditus*; **Middle.** *Osmia lignaria* from Michigan with phoretic mites *Chaetodactylus krombeini*; **Below.** *Xylocopa californica arizonensis* from Arizona with phoretic mites *Sennertia lucrosa*

PLATE 2

Top left. *Ceratina amabilis* from Belize with phoretic mites *Sennertia recondita*; **Top right.** *Xylocoipa californica* from Arizona with phoretic mites *Sennertia segnis*; **Bottom left.** *Tetrapedia sp.* from Argentina with phoretic mites *Roubikia imberba*; **Bottom right.** *Centris* sp. from Venezuela with phoretic mites *Centriacarus guahibo*.

PLATE 3

Top left. *Coelioxoides waltheriae* (cleptoparasite) from Bolivia with phoretic mites *Roubikia panamensis*; **Top right.** *Stelis montana* (cleptoparasite) from Washington with phoretic mites *Chaetodactylus krombeini*; **Bottom left.** *Anthidium funereum* from Peru with phoretic mites *Chaetodactylus* sp.; **Bottom right.** *Chelostoma rapunculi* from Europe with phoretic mites *Chaetodactylus birulai*

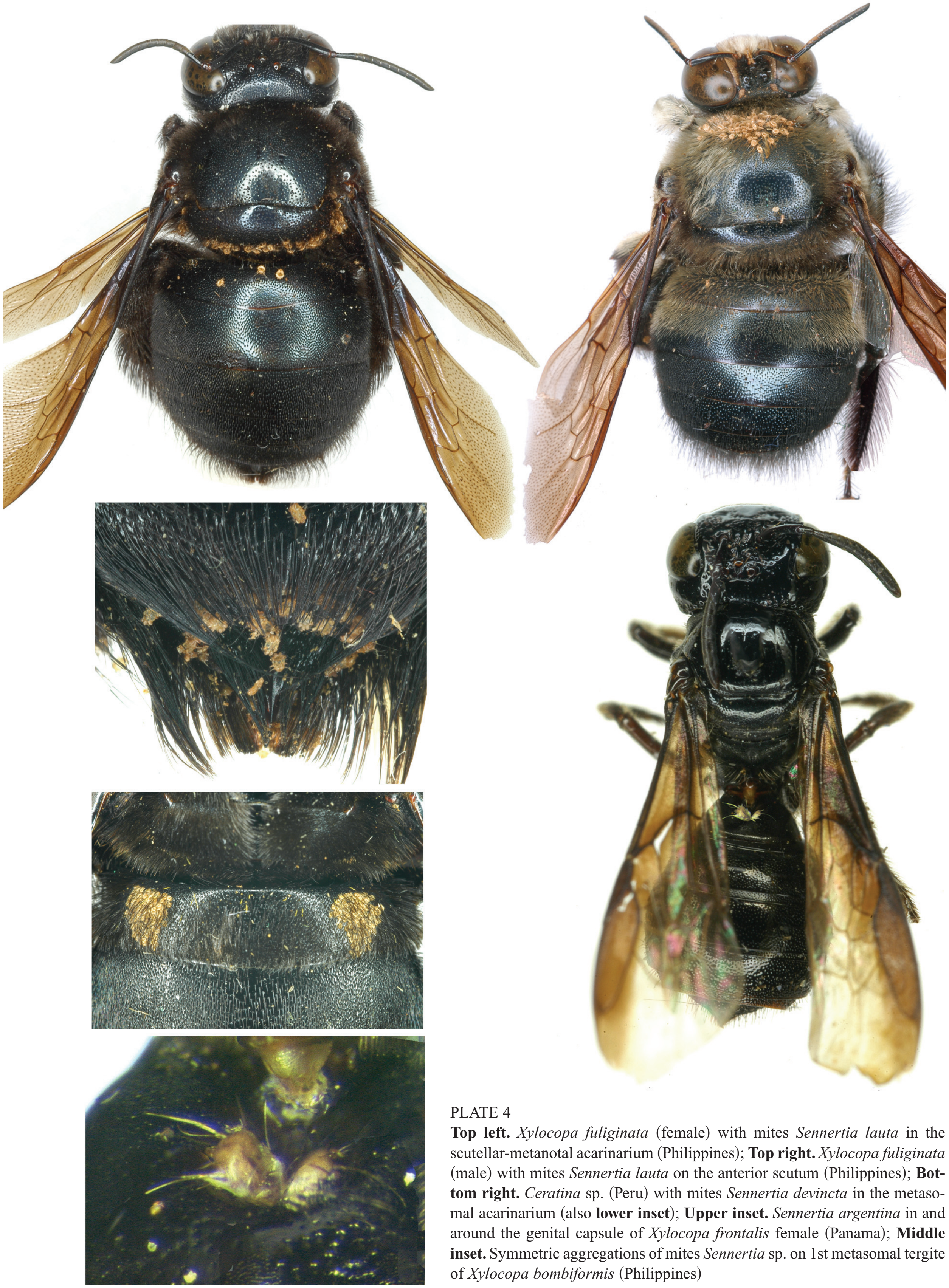

PLATE 4

Top left. *Xylocopa fuliginata* (female) with mites *Sennertia lauta* in the scutellar-metanotal acarinarium (Philippines); **Top right.** *Xylocopa fuliginata* (male) with mites *Sennertia lauta* on the anterior scutum (Philippines); **Bottom right.** *Ceratina* sp. (Peru) with mites *Sennertia devincta* in the metasomal acarinarium (also **lower inset**); **Upper inset.** *Sennertia argentina* in and around the genital capsule of *Xylocopa frontalis* female (Panama); **Middle inset.** Symmetric aggregations of mites *Sennertia* sp. on 1st metasomal tergite of *Xylocopa bombiformis* (Philippines)

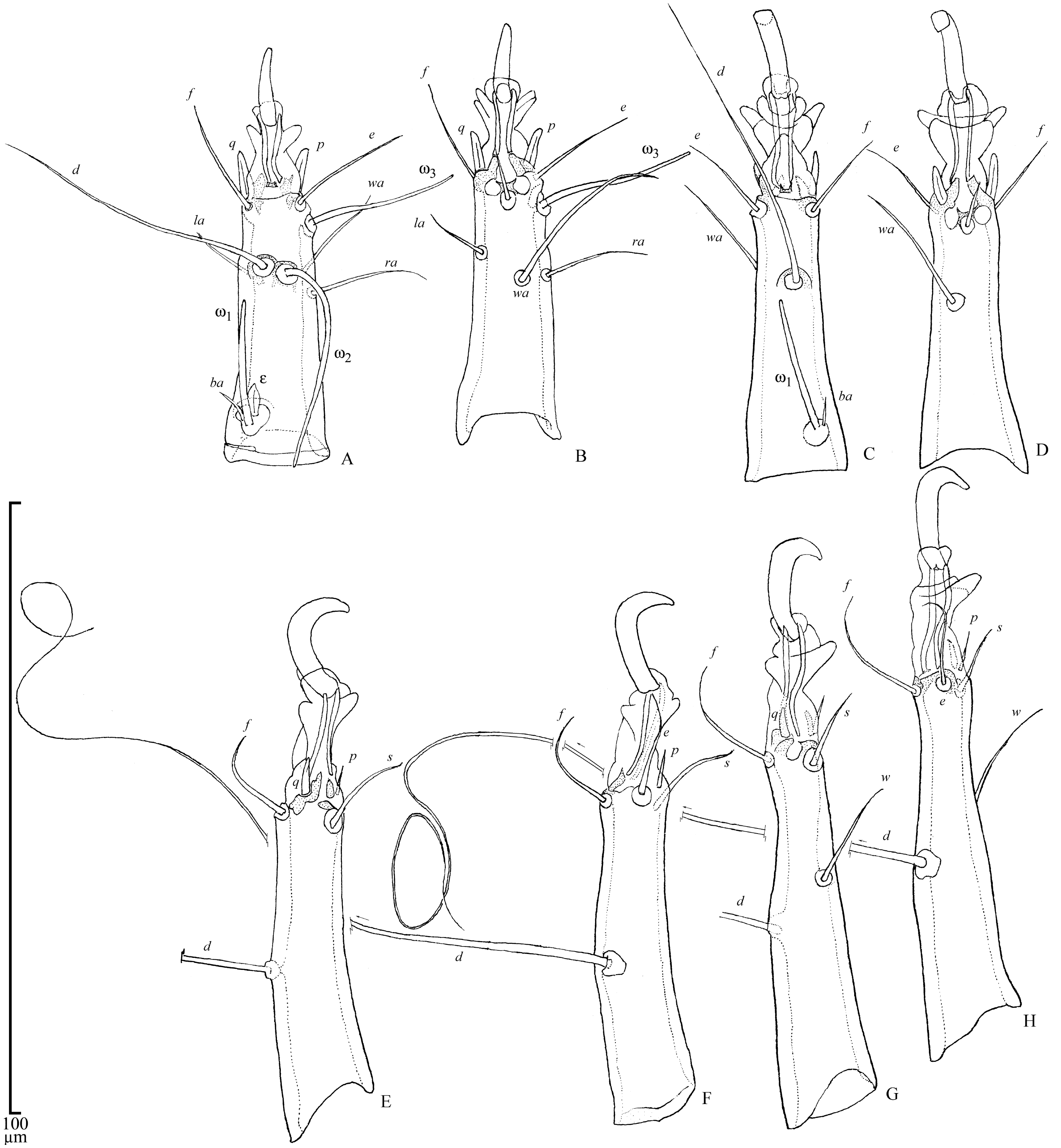

Fig. 35. *Sennertia vaga*, tritonymph. A, B - tarsus I, dorsal and ventral view; C, D - tarsus II, dorsal and ventral view; E, F - tarsus III, dorsal and ventral view; G, H - tarsus IV, dorsal and ventral view.

groups of mites can be found on the anterior scutum and adjacent pronotum (Plate 4). These differences cannot be explained so far, but probably they suggest the ability of the phoretic deutonymph to discriminate between different host sexes and, therefore, maintain the proper balance between the female-offspring and male-female transfers.

Some behavioral features of bees that may affect both vertical and horizontal mite transfer are discussed in the next section.

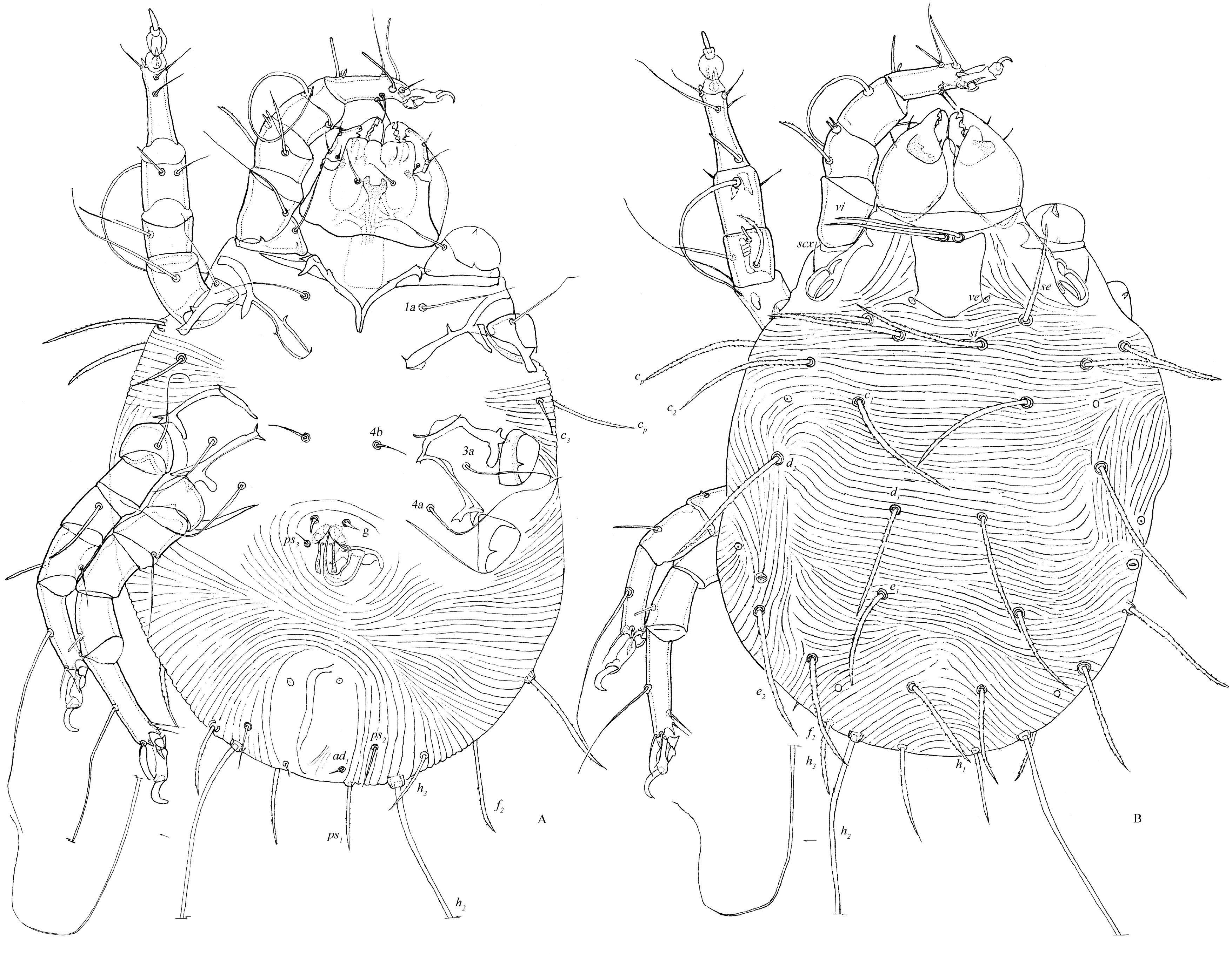

Fig. 36. *Sennertia vaga*, male (BMOC 04-1122-025). A, B - ventral and dorsal view.

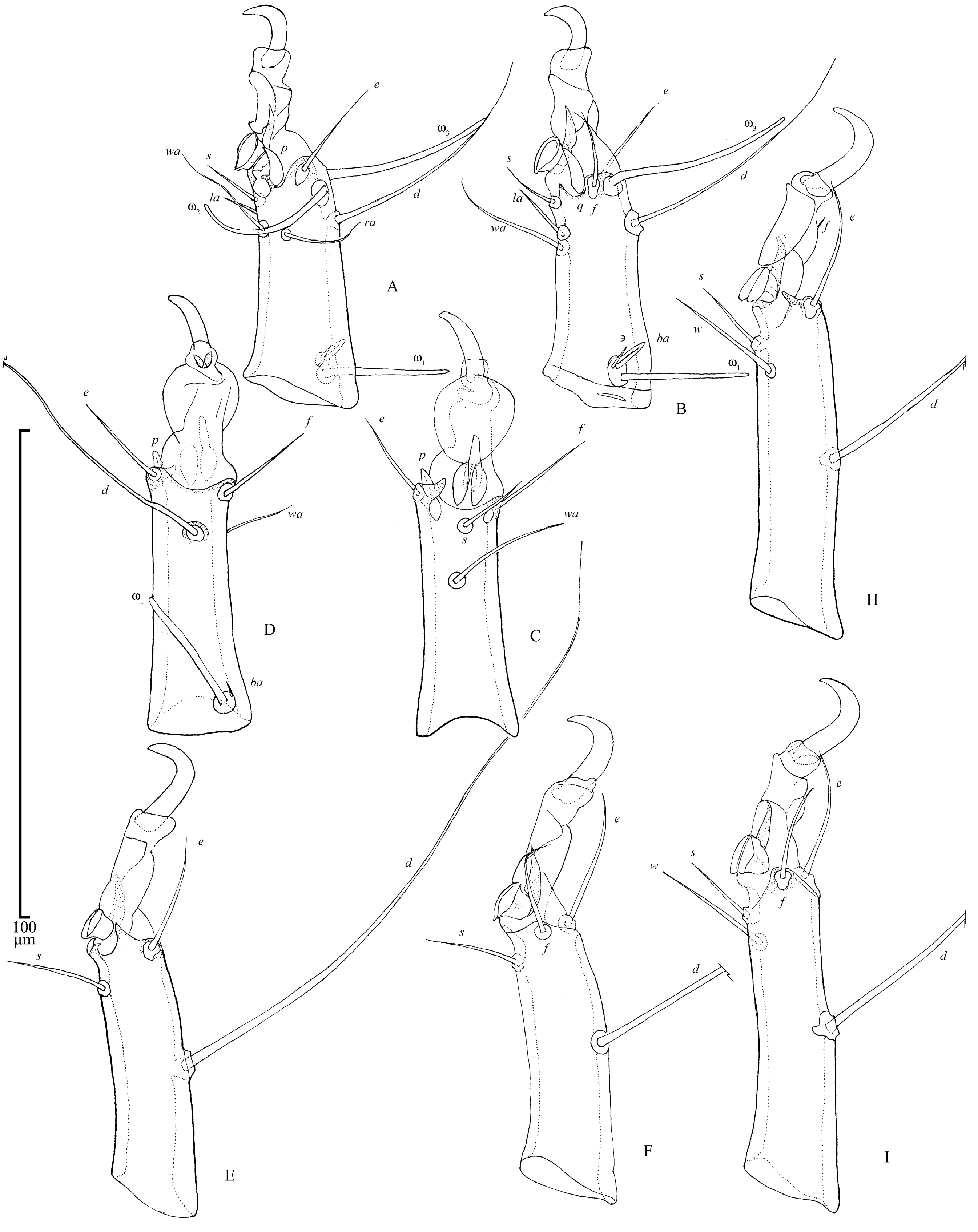

Fig. 37. *Sennertia vaga*, male (BMOC 04-1122-025). A, B - tarsus I, ventral and dorsal view; C, D - tarsus II, ventral and dorsal view; E, F - tarsus III, posterior and anterior view; H, I - tarsus IV, posterior and anterior view.

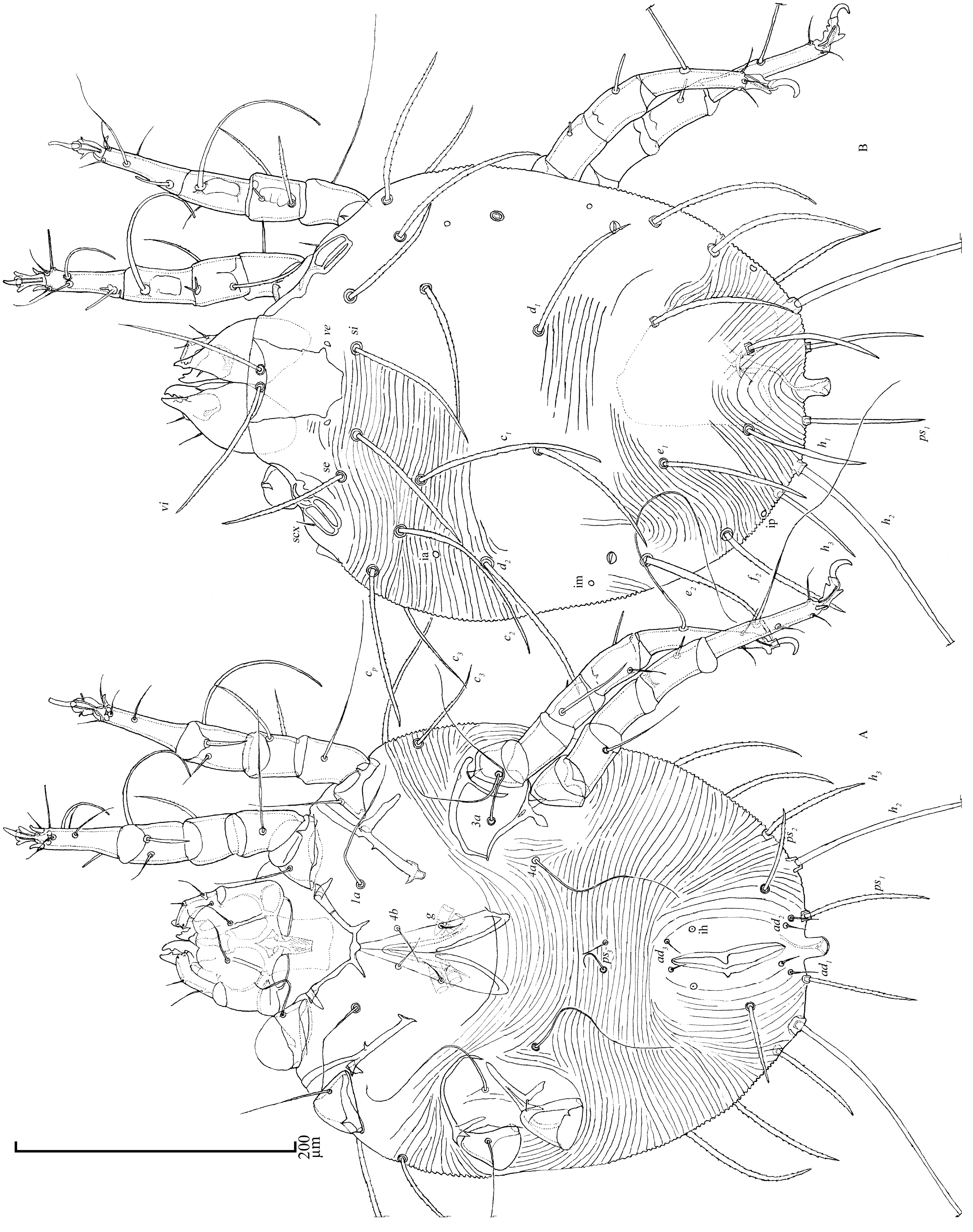

Fig. 38. *Sennertia vaga*, female (BMOC 04-1122-025). A, B - ventral and dorsal view.

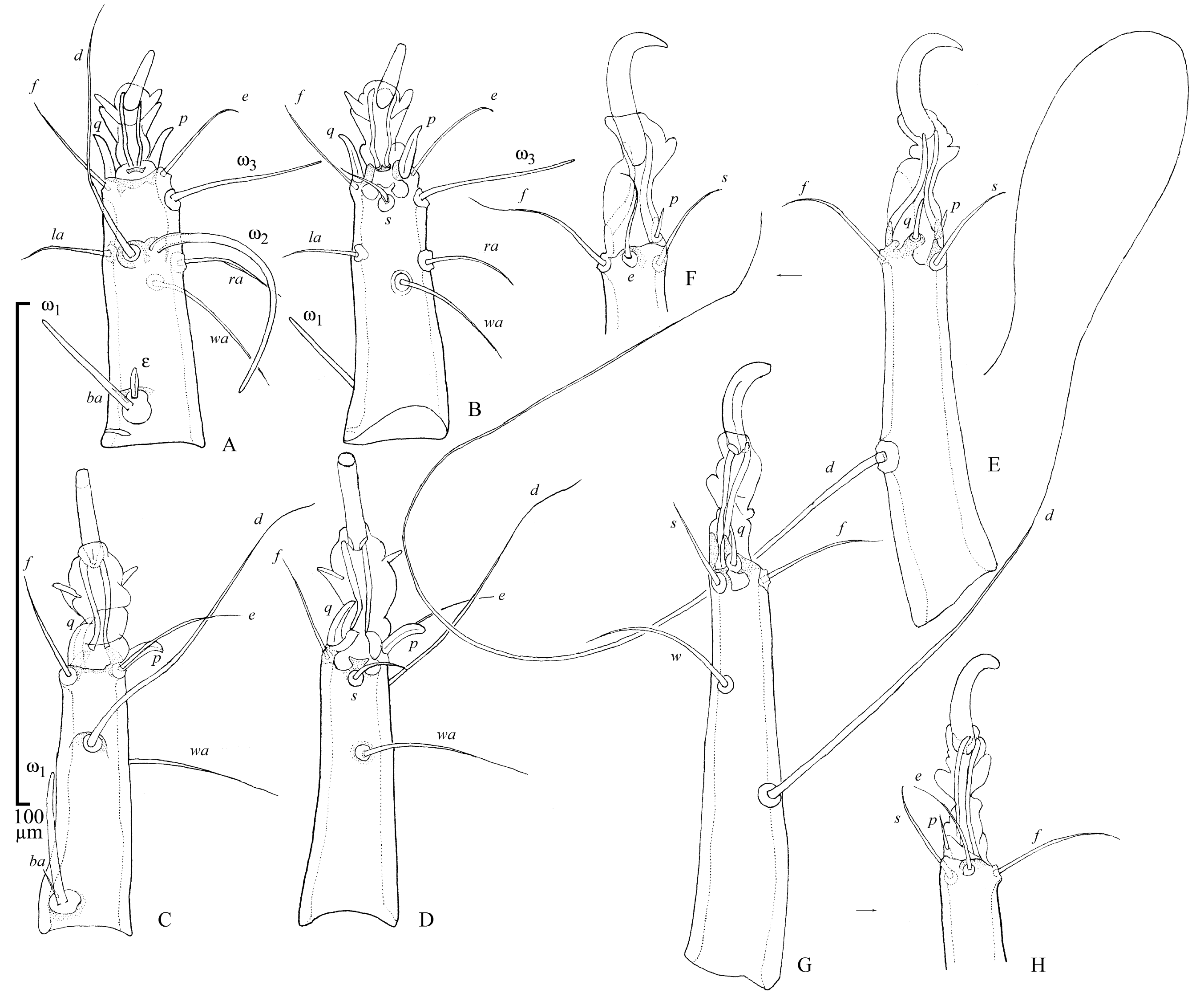

Fig. 39. *Sennertia vaga*, female (BMOC 04-1122-025). A, B - tarsus I, dorsal and ventral view; C, D - tarsus II, dorsal and ventral view; E - tarsus III, anterior side; F - apex of tarsus III, posterior view; G - tarsus IV, anterior side; H - apex of tarsus IV, posterior side.

Horizontal Transfer

Dispersal to new nests and horizontal host transfer may be accomplished by hymenopteran cleptoparasites that utilize a range of related hosts and provide a means for gene exchange between populations of mites associated with different host species. This phenomenon was suggested by OConnor & Eickwort (1988) to explain the host ranges of mites of the genus *Vidia* on their *Megachile* hosts, and by Richards & Richards (1976) for *Parasitellus* spp. associated with bumblebees. The above examples represent commensal or mutualistic associations.

Although no cases of infestation of chaetodactylids introduced by cleptoparasites have yet been documented, they are highly probable, as cleptoparasitic bees regularly carry a number of mites normally infesting their hosts. Sapygid wasps in the genera *Polochrum* and *Sapyga* may play a substantial role in mite dispersal, as they can deposit their eggs prior to construction of a cell closure by *Xylocopa* and megachilid bees, respectively (Munster-Swendsen & Calabuig, 2000; Samšiňák, 1973; Zachvatkin, 1941). Similarly, deutonymphs of *Chaetodactylus krombeini* were found to be phoretic on an oligoxenous cleptoparasite, *Stelis montana* (Megachilidae) (Plate 3), that introduces its eggs while the nest is provisioned by the host or after it is provisioned but not yet closed (Torchio, 1989). Although the host ranges of *S. montana* and 2–3 species of *Chaetodactylus* associated with its hosts do not necessary overlap, cross-infestation by the cleptoparasite may allow gene flow between two incipient *Chaetodactylus* species (our data). Similarly, *Chaetodactylus reaumuri* attacking several European species of *Osmia* was found on the cleptoparasite bee *Stelis murina* (Türk & Türk, 1957). Apid bees of the genus *Coelioxoides*, cleptoparasites of *Tetrapedia* (Alvez-dos-Santos *et al*., 2002), often carry numerous *Roubikia* (Plate 3).

Another potential source of horizontal mite transfer involves the biology of both bees and mites. Bees of the genus *Lithurgus* typically excavate their own burrows in rotten wood (Michener, 2000). They also can construct cells in old burrows or use nest debris from old burrows (Parker & Potter, 1973), facilitating mite exchange between different bee species or between different generations of the same bee species. *Chaetodactylus* is well-adapted to such behavior by forming highly regressive, non-phoretic deutonymphs that can survive for a long time without the presence of the host. Other wood-nesting bees, such as *Osmia*, *Hoplitis*, and *Megachile* may reuse old *Lithurgus* burrows for their nests (Rust *et al*., 2004); at least two host shifts with subsequent speciation are suspected to have followed this route (the ancestor of the *osmiae*-group to *Osmia* and *Ch. dementjevi* to *Megachile* (*Eumegachile*) *bombycina*).

Host shifts can be facilitated by nest supersedure, the taking over of a nest partly provisioned by one individual by another individual of the same or different species (Krombein, 1967). Interspecific supersedure has been described for several species of *Osmia*, *Xylocopa*, and *Megachile* (Bohart, 1955; Hogendoorn, 1996; Maeta, 1969; McCorquodale & Owen, 1994; Rust, 1974), and chaetodactylid species associated with these genera are known to occur on multiple sympatric host species.

In *Xylocopa caffra*, female cells are usually constructed at the bottom and the male cells closer to the entrance of the nest. The first adult to emerge in the nest, usually the occupant of the bottom cell and the oldest member of the family, does not remain dormant in her cell until those in front of her emerge. She breaks down the partitions between her cell and adjoining cells, clearing the way to the entrance of the nest. Her brothers and sisters in the pupal stage are left lying among debris of the broken partitions and excrement. The female does not leave the nest but rests near the entrance. She and other emerging adults may remain more or less quiescent for a week or longer in the nest allowing for cross-infestations by *Sennertia caffra* originating from different cells (Skaife, 1952). Associations of mother bees and their dependent adult offspring has been documented for neotropical *Xylocopa* as well (Camillo & Garofalo, 1982, 1989).

The following behavioral features of bees may also aid horizontal mite transfer: the use of a common surface entrance for several intraspecific or interspecific nest tunnels (*Xylocopa tabaniformis orpifex* and *X. varipuncta*; *Hoplitis albifrons* and *H. spoliata*; *Melitoma segmentaria* and *M. marginella* and *Centris "lanipes"*[5] and *Ancyloscelis apiformis*), nest reuse, consuming provision from adjoining nests by newly emerging bees, aggressive behavior of males of different species attempting to grasp counterparts in a copulatory position (*X. t. orpifex*), and hibernating aggregations (*Xylocopa*) (Cruden, 1966; Fye, 1965; Gerling *et al*., 1989; Linsley *et al*., 1980; Nininger, 1916; Sakagami & Laroca, 1971; Vicidomini, 1996).

Roubik (1987) suggested the possibility of horizontal transfer outside parental nests. Mites of the genus *Roubikia* apparently leave the nest with emerging *Tetrapedia* and may disembark or be dislodged from them within small areas in which female bees collect loose dirt for their nests. The mites either actively look for a new host bee or are passively transferred with the soil by the bees. Although *Roubikia* is known to be restricted to *Tetrapedia*, transfer by other bees visiting the same sites (*Centris*) is also possible. Vicidomini (1996) reported colonization of *Xylocopa violacea* by deutonymphs of *S. cerambycina* on flowers.

Accidental Phoretic Associations

Accidental phoretic associations may occur as a result of physical contact between mites and organisms other than their hosts or their cleptoparasites. Normally developing mites live exclusively in concealed cells or, if cell partitions are not constructed, in isolated nest tunnels (*Lithurgus*). As host nests restrict access of any intruders, mites have a limited opportunity to contact the outside world until the nest cells are opened by newly emerged bees, parasites, or predators. At this point, the heteromorphic deutonymphs may attach themselves to unrelated "hosts", decreasing the chances of successful dispersal and establishing a new colony. The junior author observed 494 individuals of *Chaetodactylus hopliti* on a single sphecid wasp, *Isodontia mexicana*, emerging from a nest tunnel constructed in proximity to a nest of *Hoplitis* sp. (Megachilidae), the principal host of the mite. We have occasionally observed adult *Sennertia* on *Centris* probably as a result of the same phenomenon, although the absence of phoretic nymphs may indicate that their host nests were broken prior to the completion of the host bee development. In literature, there are many records of chaetodactylids from atypical hosts such as *Andrena*, *Halictus*, *Anthophora*, *Apis*, *Bombus*, or even from the non-apoid hosts: *Vespula* and Passalidae (Abou Senna, 1997; Chmielewski, 1993; Haitlinger, 1999, 2000; Zachvatkin, 1941; our data) that are attributable to the same biological traits or collecting artifacts.

Host Specificity and Possible Isolation Mechanisms

The broad range of opportunities for horizontal mite transfer outlined above suggests that many chaetodactylids have adapted to multiple hosts rather than a single host species. Utilizing multiple hosts is more advantageous because it allows maintenance of a large population size, expanded geographic range, and it minimizes the risk of extinction when a natural population bottleneck occurs in one or several host species. As a rule, widely distributed species of chaetodactylids are associated with several bee species, although some host preferences are apparent. For example, *Ch. osmiae* is predominantly associated with *Osmia rufa*, *Ch. krombeini* with *O. lignaria*,

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[5] Probably this record belong to *Centris* (*Heterocentris*) *trigonoides* but it could possibly be another species such as *Centris tarsata* (J. Ascher, pers. comm.).

Ch. micheneri s. str. with *O. subaustralis*, and *Sennertia cerambycina* with *Xylocopa violacea* (see host ranges of these species in the systematic part). Neotropical *Sennertia* belonging to the *argentina* group display no host preference within a group of closely related species of the subgenus *Neoxylocopa*. As they are usually phoretic inside the genital chambers of both sexes and probably migrate from male to female during copulation, they must have alternative ways of dispersal on different host species or merely represent an ancestral association with this group of bees. Three species of *Chaetodactylus* associated with bees of the genus *Lithurgus* in the United States present a well-documented case: one mite species may have multiple hosts, and mite speciation probably was influenced by temporal and geographic factors rather than isolation due to different hosts (Klimov & OConnor, 2004). *Chaetodactylus abditus* and *Ch. lithurgi* are sibling species occurring on different, partially sympatric hosts. *Chaetodactylus lithurgi* is associated with bees flying predominantly in the spring: *L. apicalis*, *L. littoralis*, and western *L. gibbosus*. *Chaetodactylus abditus* occurs exclusively on fall-flying *Lithurgus echinocacti* and *L. planifrons* in the northern part of their range. Compared to the above two species, *Ch. gibbosi* is allopatric and associated with a single bee species (*L. gibbosus*). Another example also suggests that both geographic isolation and isolation due to different hosts might play an important role in the incipient speciation of *Chaetodactylus* associated with several species of mason bees of the subgenus *Osmia* (*Cephalosmia*) in North America.

Occurrences of multiple species of mites on a single host are not rare. As many as five species of *Chaetodactylus* (*Ch. claviger*, *Ch. osmiae*, *Ch. zachvatkini*, *Ch. reaumuri*, and *Ch.* sp.) can be found in different parts of the range of *Osmia tricornis*. Some of these species are sympatric or partially sympatric and may occur together on a single bee. Similarly, *Sennertia frontalis* and *S. argentina* are phoretic on *X. frontalis*, *S. tanythrix* and *S.* aff. *basilewskyi* phoretic on *X. torrida*, *S. koptorthosomae* and *S. hipposideros* phoretic on *Xylocopa latipes*, and *S. horrida*, *S. dissimilis*, and *S. oudemansi* phoretic on *X. nasalis* (OConnor, 1993b; Zachvatkin, 1941; our data). In the two former cases, the phoretic deutonymphs were spatially isolated on the host (see below).

In contrast, *Sennertia americana* was found in association with a single species, *Xylocopa virginica*, throughout its broad geographic range. *Chaetodactylus anthidii* is also associated with a single host, *Rhodanthidium sticticum*, but only a few records of this species are available.

An annotated list of chaetodactylid hosts can be found in the systematic section for North American species and for other regions in Appendix 7 (p. 98).

Interactions of Mites and Bees Inside Nests

Different species of chaetodactylids may act as commensals feeding on provisioned pollen and cell materials without causing any damage to the developing larva (*Roubikia*), as parasitoids killing the eggs or the larva and then feeding on provisioned pollen (*Chaetodactylus*), or both (*Sennertia*).

In *Roubikia*, the mites presumably feed on materials in the cells, and possibly on the fatty acids from floral oils mixed with some of the fill dirt. Individuals of *R. panamensis* were much more numerous in nests from which bees had emerged than in the nest containing young larvae, which suggests that they reproduce there (Roubik, 1987).

Observations on *Chaetodactylus* species unequivocally suggest that these mites, when possible, kill the bee egg or larva in its early developmental instars and then feed on the provisioned food inside the cell. This has been documented for *Ch. krombeini* attacking *Osmia lignaria* (Krombein, 1962), *Ch. hirashimai* attacking *Osmia excavata* (Hirashima, 1957), *Ch. nipponicus* attacking *O. cornifrons* (Qu *et al*., 2002), *Ch. osmiae* attacking *O. rufa* (Fain, 1966), and *Ch. birulai* attacking *Chelostoma florisomne* (Lith, 1957). In the latter case, the author observed a mite eating the tissue of the larva through a wound in its cuticle; artificial contamination of a healthy larva also resulted in the death of the latter. Other observations suggest that *Ch. osmiae* can live either as a parasitoid or as commensal, feeding on pollen without any damage to the larva (Popovici-Baznosanu, 1913). Qu *et al*. (2002) estimated that more than 50 adult *Ch. nipponicus* are needed to kill an egg of the host. Thus, killing the host larva is not a necessary prerequisite for mite development, which is also evident from rearing experiments on a pollen diet only (Chmielewski, 1993).

Mites of the genus *Sennertia* feed on provisioned pollen inside the nests of their hosts. *Sennertia splendidulae* and *S. augustii* do not cause any damage to their hosts, *Xylocopa splendidula* and *X. augusti*, respectively, since the mites are strictly dependent on their host in terms of food, habitat, and dispersal (Abrahamovich, Alzuet, 1990; Alzuet, Abrahamovich, 1990). These observations are very different from those of Vicidomini (1996), who recorded dead eggs and larvae of *X. violacea* in cells with *S. cerambycina*, but could not determine whether the ultimate cause of the death was direct parasitism or cleptoparasitism. He also noted that the nest infestation was low (about 3% of all cells of 5% of all nests), despite that 74% of female bees were infested with mite deutonymphs. Similarly, Nininger (1916) reported what was probably *S. lucrosa* destroying a small percentage of *X. tabaniformis orpifex* and *X. varipuncta* larvae in their nests. Skaife (1952) observed *Sennertia caffra* feeding on the nectar and pollen and competing with the bee larva in the nests of *Xylocopa caffra*. The host larva always outperformed the mite, but in the cells where the egg or larva failed to develop, the mites multiplied in great numbers. *Sennertia alfkeni* associated with *Xylocopa circumvolans* feeds on the pollen loaves and fecal pellets of developing larvae (Okabe, Makino & Endo, 2005, pers. comm.).

Formation of phoretic heteromorphic deutonymphs is assumed to be synchronized with the period of emergence of the host, which usually coincides with the depletion of the food supply in the nest. Qu *et al*. (2003) directly linked the appearance of deutonymphs of *Chaetodactylus nipponicus* to the low amount of residual pollen, and stated that if the protonymph ate much pollen it transformed to phoretic forms, if not to inert ones. Similarly, Krombein (1962) and Popovici-Baznosanu (1913) noted that heteromorphic deutonymphs of *Chaetodactylus* start to appear in the fall and become abundant in the winter when the pollen or nectar is almost entirely consumed. Qu *et al*. (2003) consider them as diapausing instars, although feeding instars remained in the cells throughout the winter as well. Fain (1966) believed that excessive desiccation and overcrowding may also contribute to the formation of the heteromorphic deutonymphs of *Chaetodactylus*. The appearance of phoretic deutonymphs of *Sennertia splendidulae* in the nest of *Xylocopa splendidula* is caused by stimuli of the adult bee and cell environment, such us the lack of food or the accumulation of excrement of the bee larva (Abrahamovich & Alzuet, 1990).

Deutonymph-tritonymph molt. The molt of the inert heteromorphic deutonymph is induced by the scent of the host bee in *Ch. nipponicus* (Qu *et al*., 2002) and by higher humidity in *Ch. osmiae* (Fain, 1966).

Analysis of Bee Traits Influencing Coevolutionary Associations

Four aspects of bee biology that may affect the suitability of a particular bee taxon as a chaetodactylid-host were considered: nest construction site, the arrangement of cells within a nest, the provisioning of cells, and the degree of sociality characterizing the bee taxa. Data for these traits in each bee taxon were primarily from Michener (2000), references cited therein, and more recent publications (Table 9). In a few cases, data were extrapolated from other species when the a trait appeared to be similar across the genus.

Logistic regression was used to investigate how these traits predict whether a bee taxon will (or will not) be associated with chaetodactylids. The fit of the data to the model was evaluated using a likelihood-ratio test to assess statistical significance. The predictive power of the model (i.e., the contribution of host biological traits to the observed pattern of bee-mite associations) was evaluated with the program SPSS ver. 11.0.4 (SPSS Inc., Chicago IL) by calculating the posterior probabilities for each bee taxon and estimating the percentage of correctly predicted associations.

There is a great diversity in the nesting behavior, nest site preference, and in the construction materials used by the hosts of chaetodactylids, and sometime these attributes may vary within a bee genus. Certain nest types are obviously more favorable for the mites and some are not. The former include nests built in cavities in wood or, to a lesser extent, burrows in the ground. Nests built in hollow stems, snail shells (especially nests with a single cell), in cracks in rocks, or exposed nests, seem less preferable, and some bee lineages with such nests are entirely lacking an associated chaetodactylid fauna. Examples include *Hoplitis* (*Monumetha*), making nests in wood holes versus other *Hoplitis* constructing their nests in pithy stems, *Osmia* (subgenera *Osmia*, *Cephalosmia*, *Helicosmia*) nesting in cavities in wood versus those with exposed nests or nests constructed in snail shells, and *Centris* (*Heterocentris*) nesting in cavities in wood versus ground-nesting *Centris*. Other attributes, for example, the presence or absence of cell partitions, primary nest material, overwintering stage, time of egg laying, and texture of the pollen provisions, probably have no or little effect on chaetodactylid distribution. It should be noted that nest sites and architecture are not the only factors influencing the presence of chaetodactylids. Several groups of bees, such as Manueliini and Allodapini, related to the chaetodactylid-rich Xylocopini and Ceratinini and constructing similar nests, entirely lack chaetodactylids.

Nests constructed in preexisting cavities or holes in wood were probably the ancestral habitats for chaetodactylids. Species of *Centris* (*Heterocentris*) and *Tetrapedia*, harboring the earliest derivative chaetodactylids (*Centriacarus* and *Roubikia*), utilize such nesting sites (Jesus & Garófalo, 2000; Roubik, 1987; Pereira *et al*., 1999). Many other chaetodactylid hosts nest in similar situations: they use burrows constructed by other insects (Osmiini, Anthidiini, Megachilini), excavate their own tunnels (Lithurgini, most Xylocopini, Ceratinini), or both. In contrast, chaetodactylids associated with bees having underground nests (Emphorini, Tapinotaspidini, and *Xylocopa* (*Proxylocopa*)) are less diverse.

Many bee hosts of chaetodactylid mites construct their nests as linear series of cells separated by cell partitions with a closing plug at the cavity entrance. In such nests (*Osmia*, *Xylocopa*, *Ceratina*), bees developing in the innermost cells chew their way out of the nest, and phoretic deutonymphs from the opened cells may attach to them. If mites in the innermost cell kill the developing larva (*Osmia*), they would possibly also die because of their inability to break through the partition (Krombein, 1962). Despite this, *Ch. nipponicus* infests mainly the innermost cells, killing less than one third of the eggs or young bees (Qu *et al*., 2002). Irrespective whether mites kill or live together with the developing larva, arrangement of cells in a linear series seems an important factor affecting dispersing success of chaetodactylids. In a linear nest, early developing bees may break through cell partitions, facilitating cross-contamination of the entire brood by the mites.

Logistic regression analysis indicated a significant relationship between the four bee traits considered (i.e., nesting site, cell arrangement, cell provisioning, and sociality; Table 9) and whether a specific bee taxon was associated with chaetodactylid mites; the overall model test, -2 Log Likelihood, is highly significant ($p = 0.024$). The overall classification accuracy for the model is 82.1%, indicating that these bee traits play an important role in structuring the bee-mite associations (Table 8). Any combination of models with one or more variables removed resulted in a decrease of the explanatory power, suggesting that all four factors affect the mite presence.

Distribution of Phoretic Deutonymphs on the Host Body

The distribution of phoretic deutonymphs on the host body depends on the presence of suitable areas for attachment, accessibility of these areas for grooming by the host, the number of mites, the host sex, the size of mites, and, possibly, the initial region of their attachment. Combinations of these factors create different patterns of mite distributions on the host body. These patterns were studied for *Sennertia splendidulae* (Abra-

Table 9. Aspects of host biology, and in particular nest architecture, considered to investigate the factors influencing associations between the chaetodactylid mites and their bee-hosts. The variable "cell construction material" was not included in the analysis because of difficulties with uniform coding. Cleptoparasitic bees were also not included because they do not have chaetodactylids by definition.

Bee taxon	Chaetodactylid present[a]	Nesting site[b]	Cell arrangement[c]	Cell construction material[d]	Provisioning[e]	Sociality[f]
Fideliini	0	1	4	3	1	1
Pararhophitini	0	1	4	3	1	1
Lithurgini	1	2	3	4	1	1
Anthidiini (*Trachusa perdita*)	0	1	1	8	1	1
Anthidiini (*Dianthidium concinuum*)	0	5	5	7	1	1
Anthidiini (*Rhodanthidium sticticum*)	1	4	1	9	1	1
Osmiini (*Heriades* (*Heriades*))	0*	2	1	1	1	1
Osmiini (*Chelostoma florisomne*)	1	2	1	12	1	1
Osmiini (*Osmia lignaria*)	1	2	1	3	1	1
Osmiini (*Osmia aurulenta*)	1	4	1	6	1	1
Osmiini (*Osmia nigrobarbata*)[g]	0	1	2	6	1	1
Megachilini (*Megachile apicalis* 1)	0	1	1	6	1	1
Megachilini (*Megachile apicalis* 2)	0*	2	1	6	1	1
Xylocopini (*Xylocopa virginica*)[g]	1	2	2	5	1	3
Xylocopini (*Proxylocopa*)	1	1	7	3	1	1
Manueliini (*Manuelia gayi*)	0	2	2	5	1	2
Ceratinini (*Ceratina mexicana currani*)	1	2	1	5	1	1
Ceratinini (*Ceratina japonica*)	1	2	1	5	1	3
Allodapini (*Braunsapis sauteriella*)	0	2	3	4	2	3
Ctenoplectrini (*Ctenoplectra vagans*, *C. armata*)[g]	0*	2	1	3	1	1
Tapinotaspidini (*Chalepogenus* 1)	1*	1	4	3	1	1
Tapinotaspidini (*Chalepogenus* 2)	1	1	5	3	1	1
Emphorini (*Melitoma marginella*, *Ancyloscelis apiformis*)	1*	1	2	3	1	1
Emphorini (*Diadasia afflicta*)	0	1	4	3	1	1
Emphorini (*Ptilothrix sumichrasti*)	1*	1	1	3	1	1
Exomalopsini (*Exomalopsis sidae*)	0	1	4	3	1	2
Eucerini	0	1	4	3	1	1
Tetrapediini (*Tetrapedia diversipes*)	1	2	1	13	1	1
Centridini (*Centris* (*Centris*)) *segregata*	0	1	2	10	1	1
Centridini (*Centris* (*Heterocentris*))	1	2	1	10	1	1
Anthophorini (*Anthophora urbana*)	0	1	2	10	1	1
Anthophorini (*Anthophora* (*Clisodon*))	0*	2	1	7	1	1
Euglossini (*Euglossa* 1)[h]	0	2	5	1	1	2
Euglossini (*Euglossa* 2)	0	3	5	1	1	2
Euglossini (*Eulaema*)	0	3	5	11	1	2
Bombini	0	3	6	2	2	3
Apini (*Apis florea*)	0	5	6	2	2	4
Apini (*Apis cerana*)	0	3	6	2	2	4
Meliponini (*Melipona*, *Plebeia* (*Schwarziana*))	0	3	6	2	1	4

For Ancylini and *Anthidium espinosai* nests are unknown. Nests of Teratognathini are known for one species; based on unpublished description (Rozen, 2006, pers. comm.), our model correctly predicts the absence of associated chaetodactylids.

*misclassified by the logistic regression analysis.

[a] chaetodactylid present: 0) no, 1) yes.

[b] Nesting site: 1 = soil, 2 = wood, stems or twigs, 3 = preexisting cavities (except for snail shells), 4 = preexisting cavities (snail shells), 5 = exposed. Categories 3 and 4 can be combined without any changes in prediction accuracy of the model.

[c] Cell arrangement: 1) sequential (linear sequences), 2) sequential (in branching tunnels), 3) linear nest with no cell partitions, 4) isolated cells in laterals of branching nest, 5) clusters, 6) combs (=clusters in regular layer), 7) sessile in branching nest.

[d] Cell construction material: 1) resin, 2) wax+other material, 3) mud, soil, 4) none, 5) sawdust, 6) leaves, 7) pebbles glued by resin, 8) resin+leaves, 9) mud, plant material, animal fragments, 10) soil+resin+oil, 11) mud+resin, 12) saliva+nectar+soil, 13) soil+oil.

[e] Provisioning: 1) mass, 2) progressive.

[f] Sociality: 1) solitary, 2) communal, 3) primitively eusocial, 4) highly eusocial.

[g] may occasionally use pre-existing cavities.

[h] several species (*e.g.*, *Euglossa cordata* and *E. variabilis*) are solitary (Bennett, 1966).

hamovich & Alzuet, 1989), *S. alfkeni* (Okabe & Makino, 2002) and *Chaetodactylus nipponicus* (Qu *et al*., 2003), although with different sampling methodologies and definitions of areas of mite attachments.

Attachment of chaetodactylid deutonymphs is accomplished by the ventral attachment organ and/or spirally twisted claws. The attachment organ functions by creating low pressure with its suckers and probably by using the adhesive forces of its cuticular "suckers" (Woodring & Carter, 1974). The claws are used to grasp the host setae. It is noteworthy that in deutonymphs phoretic on relatively "hairless" bees, such as *Tetrapedia* and *Ceratina*, the attachment organ is relatively larger and the claws are smaller (*Roubikia*, *Achaetodactylus*, *Sennertia surinamensis*-group). The reverse is true for *Chaetodactylus* and *Sennertia* associated with "hairy" hosts, *Lithurgus*, *Osmia*, and *Xylocopa*.

Xylocopine carpenter bees are large insects offering a diversity of attachment sites: areas covered with setae on the pronotum, metanotum, propodeum, and first metasomal tergite; glabrous sites such as the petiolar area of the propodeum and first metasomal tergite, axillar areas, and wings; and various cavities and grooves, most notably, the cavities under the tegulae, mesosomal and metasomal acarinaria, as well as the genital chamber. In smaller bees, the propodeum and adjacent areas, and the first metasomal tergite and, to a lesser extent, the pronotum, forewings, and occiput are usually the most attractive places for chaetodactylid attachment.

A thorough study of mite localization requires an analysis of large samples instantly preserved in liquid nitrogen to avoid artifacts in the original mite location due to movement after host death (Okabe & Makino, 2002), and experiments with live mites and hosts to standardize various factors affecting mite distribution (Qu *et al*., 2003). Because this study is beyond the scope of the present work, below we will only briefly describe the most remarkable attachment sites of chaetodactylids, including the acarinaria.

Metasomal acarinaria

Structures termed acarinaria that function to carry phoretic mites are found on the metasoma of various bees and wasps. In eumenine Vespidae, *Allodynerus*, *Parancistrocerus*, *Pseudonortonia*, and *Acarepipona*, the metasomal acarinarium is a specialized cavity at the base of the second metasomal tergite (Makino & Okabe, 2003; OConnor & Klompen, 1999). In the bee genera *Lasioglossum*, *Thectochlora*, and *Augochlora* (Halictidae), it is a gently concave area bordered by long, plumose setae and situated on the lower third of the anterior-facing surface of the first metasomal tergite of females (McGinley, 1986; Fain *et al*., 1999). In *Ctenocolletes* (Stenotritidae), it is represented by pouches under the ventrolateral edges of the third and fourth tergites of the female (Houston, 1987). OConnor & Klompen (1999) suggested that the structures in *Ctenocolletes* might actually be induced by the presence of the mites as they move under the metasomal tergites of the teneral bee immediately after its eclosure. A similar unpaired area or "pouch" is developed between sternites 3 and 4 in males of some Australian *Lasioglossum*. The mites attach their suckers along the entire length of sternite 4, most of which is overlain by sternite 3. The mites are aligned longitudinally with their legs directed posteriorly, and during mating, the location of the mites on the ventral surface of the metasoma aligns closely with the metasomal acarinarium of the female (Walter *et al*., 2002). In *Xylocopa* (Apidae), the metasomal acarinarium is a vertical groove (males and females) or large invagination on the anterior side of the 1st metasomal tergite of the female (Eardley, 1983; Madel, 1975; OConnor, 1993b; Okabe & Makino, 2002). We also found a similar acarinarium in *Ceratina* sp. from Peru (Plate 4) and *Tetrapedia* sp. from Peru. The above pattern of acarinarium distribution across taxa suggests that acarinaria have evolved in response to the presence of mites, rather than as structures sharing common evolutionary histories. OConnor & Klompen (1999) showed that some acarinaria in eumenine wasps appeared independently, and some unrelated hosts might have similar acarinaria carrying related mites.

As indicated above, the metasomal acarinaria of large carpenter bees (*Xylocopa*) include two major types. One is typical for *Xylocopa* (*Alloxylocopa*) *circumvolans*, and the other one is found in two other subgenera of Old World *Xylocopa*, *Koptortosoma* (*s. l.*) and *Mesotrichia* (*s. l.*).

The *Alloxylocopa*-type metasomal acarinarium is a well-developed medial groove on the anterior side of the first metasomal tergite. Okabe & Makino (2002) described this structure in males and females of *Xylocopa circumvolans*. Minckley (1998) also reported this structure in *Xylocopa* (*Mesotrichia*) (including *Platynopoda*, *Hoplitocopa*, and *Hoploxylocopa*), and *X.* (*Koptortosoma*) (including *Afroxylocopa*, *Oxyxylocopa*, *Cyaneoderes*, and *Cyphoxylocopa*). Unfortunately, he noted this structure only for females and did not mention the presence of mites.

In *X. circumvolans*, the metasomal acarinarium harbors *Sennertia japonica* and *Horstia helenae* (Oudemans) (Acaridae). Larger deutonymphs of *Sennertia japonica* attach to the dorsal setae of the mesosoma. They cannot fit inside the acarinaria because of the large body size, and, judging from its large claws, it is adapted to cling to the mesosomal hairs of the host (Okabe & Makino, 2002).

The *Koptortosoma*+*Mesotrichia*-type metasomal acarinarium is a large invagination of the anterior surface of the first mesosomal tergite open to the outside by a small orifice. It primarily serves for the transfer of laelapid mites of the genus *Dinogamasus* (Lindqvist, 1998), but other mites can be found in the cavity as well. The examples include *S. morstatti*, *Horstia glabra* (Vitzthum) (Acaridae), and *Histiostoma conclavicola* (Oudemans) (Histiostomatidae) on *X. nigrita*, *S. koptorthosomae*, *S. hipposideros*, *Horstia helenae* (Oudemans) (Acaridae), and *Stigmatolaelaps greeni* (Oudemans) (Laelapidae) on *X. latipes* (Krantz, 1998; OConnor, 1993b; our data). This type of acarinarium occurs in *Koptortosoma* (including *Afroxylocopa*, and *Cyaneoderes*) and *Mesotrichia* (including *Hoplitocopa*, *Hoploxylocopa*, and *Platynopoda*) (Minckley, 1998).

The metasomal acarinarium of female *Ceratina nigriceps* from Africa (Fain & Pauly, 2001) and *Ceratina* sp. (BMOC 03-0604-016) from Peru is probably similar to the *Koptortosoma*+*Mesotrichia*-type. In the former species it harbors *Achaetodactylus leleupi*; in the latter species, we were able to observe only its entrance situated on the first metasomal tergite (Plate 4). This acarinarium harbors *Sennertia devincta*. *Tetrapedia* sp. from Peru also has a metasomal acarinarium harboring *Roubikia latebrosa*.

Mesosomal acarinaria

Mesosomal acarinaria, like metasomal acarinaria, are diverse and originated independently in different groups of aculeate Hymenoptera. Eumenine wasps may have two mesosomal acarinaria: propodeal and scutellar (see review in OConnor & Klompen, 1999; Makino & Okabe, 2003). Chaetodactylids also disperse in two different mesosomal acarinaria of large carpenter bees, axillar and scutellar-metanotal.

In *Xylocopa*, axillar (=thoracic, mesosomal) acarinaria are known as paired longitudinal cavities situated dorsolaterally on the axillae of the mesosoma. Despite the potential usefulness of the character for the systematics of *Xylocopa*, its presence has been overlooked in major taxonomic revisions of the genus (Hurd & Moure, 1963; Minckley, 1998). OConnor (1993b) described this acarinarium for the subgenera *Koptortosoma* (including *Afroxylocopa*) and *Mesotrichia* (including *Platynopoda*) as harboring predacious mites of the genus *Cheletophyes* (Cheyletidae). It was hypothesized that *Cheletophyes* controls small cleptoparasites, and the bees have developed the mesosomal acarinaria to transfer the acarine mutualists to new nests. He also mentioned a similar, but much less developed acarinarium, in the subgenera *Alloxylocopa* and *Oxyxylocopa* (now part of *Koptortosoma*) harboring *Sennertia*. The acarinaria housing *Sennertia* and *Cheletophyes* are homologous, as they occupy the same position on the axillae. We propose to call them axillar acarinaria to avoid confusion with another previously undescribed acarinarium of several *Xylocopa* (see below). Axillar acarinaria and their mite fauna were recently described for *X.* (*Alloxylocopa*) *circumvolans* (Okabe & Makino, 2002). Like the *Alloxylocopa*-type metasomal acarinarium recorded for this species, it occurs in both males and females and houses predominantly *Sennertia japonica*.

Xylocopa (*Zonohirsuta*) *fuliginata* and *X.* (*Z.*) *dejeanii* from the Philippines and Malaysia display remarkably strong and non-random sexual differences in the location of phoretic *Sennertia lauta*. In all females of *X. fuliginata* (12.5% from a total of 96 examined specimens), mites were situated in the groove between the sclerotized plates of the scutellum and metanotum (Plate 4), while in all males, the mites were attached to the setae of the anterior scutum (50.9% from a total of examined 55 specimens) (Plate 4). The same pattern of non-random distribution among different sexes was observed in other species of *Xylocopa* (*Zonohirsuta*) harboring *Sennertia ratiocinator*: *X. bhowara* and *X. dejeanii*. The groove between the scutellum and metanotum in the above bees can be called an acarinarium because it is well-defined morphologically and is a preferred place for mite phoresy. The actual function of this structure is, however, unknown. As there is no obvious acarinarium in the male, the non-random distribution of mites in the female may present only circumstantial evidence for its function.

Genital acarinaria

Genital acarinaria were first described in the eumenine wasp, *Ancistrocerus antilope* (Hymenoptera: Eumeninae) (Cooper, 1954). In this species, the mite, *Kennethiella trisetosa* (Cooreman) migrates from the propodeal acarinaria of the male to the genital chambers of both sexes during copulation. Cooper (1954) did not detect any noticeable morphological modifications in the genital chamber to carry the mites. Based on the occurrence of *Sennertia* in the female genital chamber, venereal transmission was suspected to occur in *Xylocopa circumvolans* (Okabe & Makinio, 2002). Mites of the *Sennertia argentina* group distributed in the New World are known to be phoretic most often inside the genital systems of females and males of large carpenter bees of the subgenus *Neoxylocopa*, suggesting that venereal transmission is likely in these species. Numerous individuals of *Sennertia argentina* were found in a special pouch of the female genital system of *Xylocopa fimbriata* (Vinson, pers. comm.) and in the male genital chamber in this and other species of *Xylocopa* (*Neoxylocopa*) (our data; Plate 4). *Neoxylocopa* also harbors species of the *Sennertia frontalis* group that are usually phoretic dorsally on the posterior mesosoma and anterior metasoma.

Other attachment sites

Attachment sites other than presumed acarinaria do not have any obvious morphological adaptations for mite transfer, and mites usually do not form large aggregations in these areas. Mites seem to prefer these sites because they are unreachable for grooming by the host, suitable for the attachment organs of mites, and fit their body size. As in the acarinaria, there is some spatial segregation of different mite species that may be phoretic on a single host individual.

Abrahamovich & Alzuet (1989) identified three areas of mite aggregation on the body of museum specimens of *Xylocopa splendidula*: propodeum+petiole+1st metasomal tergite, mesosoma around the wing bases, and posterior head+pronotum. In both females and males, the first was the area most frequently occupied by the mite, *Sennertia splendidulae*. Probably as a result of collection artifacts, 67 and 44% of the mites were attached outside of any of these areas.

Qu *et al.* (2003) exposed females of the bee *Osmia cornifrons* to the mites *Chaetodactylus nipponicus* that are normally associated with this host. Results from twenty observations in the laboratory suggested that the forewing area was the most preferred attachment site. The other sites, ordered by mite preference, were as follows: first metasomal tergite, propodeum, occiput, and under the tegulae. None of these areas was occupied by more than 12% of the mites. A substantially smaller species of suidasiid mite, *Tortonia* sp., also associated with this bee, did not prefer any of these areas, although a significantly large number of specimens was found in the cavities under tegulae that are probably too small for *Chaetodactylus*.

The suitability of an area for attachment is not the only factor influencing the distribution pattern of chaetodactylids. *Sennertia* sp. may form symmetrical aggregations on the body of *Xylocopa bombiformis*, and these clusters do not correspond to any morphologically distinct areas of the host (Plate 4).

EVOLUTION

Phylogenetic Relationships among Chaetodactylid Genera

A data matrix containing 51 characters of chaetodactylid heteromorphic deutonymphs (Appendix 2) was subjected to parsimony analyses with equal character weights (standard parsimony) and with characters weighted according to the degree of homoplasy using Goloboff's (1993) concave weighting function with the constant of concavity (k) set to 2 (implied weights parsimony). A bootstrap majority rule consensus tree was calculated using the branch-and-bound algorithm with and the number of bootstrap replicates set to 10,000. Taxa with more than one character state were interpreted as "variable". Parsimony analyses were conducted using PAUP* 4.0b10 (Swofford, 2002). Bremer branch support or decay indices were calculated using PAUP* with a command file generated in TreeRot.v2 (Sorenson 1999). Characters were optimized using the accelerated transformation method (ACCTRAN).

We also conducted a Bayesian analysis with MrBayes ver. 3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) because it usually provides a less biased estimation of phylogenetic accuracy (Alfaro *et al*., 2003). The matrix was treated as the standard data type. Two independent simultaneous MCMC analyses with four chains (three hot, one cold) each were used with 5×10^6 of generations and a sampling frequency of 100. For each run, the burn-in values were determined by examining the average standard deviation of split frequencies. Five independent analyses were conducted (burn-in values range from 1100 to 2590), all of which gave similar output, suggesting that the most optimal topology was found.

We selected a distant outgroup, *Megacanestrinia*, because Chaetodactylidae may be the earliest derivative member of Hemisarcoptoidea, representatives of which were used as outgroups in previous studies (OConnor, 1993a). The influence of outgroup choice on the phylogeny and position of the root was thoroughly investigated and the topology of the tree was robust to different potential outgroups. Taxa for the analyses were selected to reflect the diversity of the family at the generic and subgeneric levels, including one new genus associated with *Centris*. The genus *Chaetodactylus* was sampled more intensively than *Sennertia* because of its potential paraphyly. Some subgenera or species-groups (*e.g.*, *Spinosennertia*, *Asiosennertia*, *Afrosennertia*, and the *Chaetodactylus claviger*-group, *Sennertia horrida* and *S. japonica*-groups) are treated as part of the corresponding inclusive groups because of the lack of variation in the selected characters.

Both parsimony and Bayesian analyses resulted in the same topology, except for unresolved relationships in the genus *Achaetodactylus* in the two parsimony analyses (Fig. 40). The analyses confirmed the monophyly of and the relationships among previously recognized taxa (OConnor, 1993a). Three basal clades were identified: *Centriacarus*, *Roubikia*, and a clade including *Achaetodactylus*, *Chaetodactylus*, and *Sennertia*. *Centriacarus* can be easily recognized among chaetodactylids by the retention of a number of plesiomorphic character states, but it is supported in the analysis by only two autapomorphic characters (some other apomorphies are not included). The discovery of this interesting taxon suggests that all six previ-

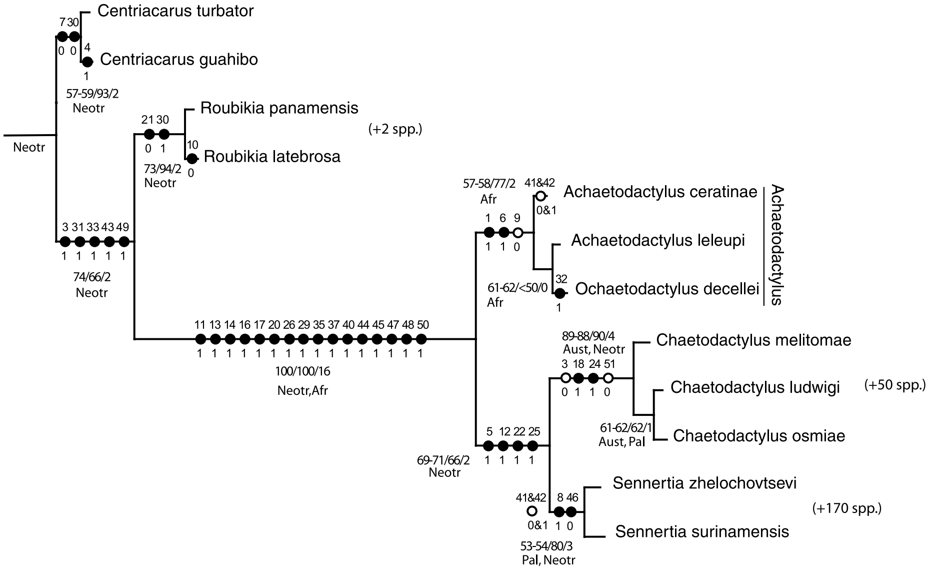

Fig. 40. Phylogenetic relationships within the family Chaetodactylidae (heteromorphic deutonymphs) based on a Bayesian analysis. Posterior probabilities, bootstrap values, and Bremer indices are shown. Bootstrap and Bremer support values were derived from a single most parsimonious tree (length = 75, CI = 0.747, RI = 0.873, HI = 0.264, RC = 0.652) found in the 51 character bootstrap analysis. Ancestral states and character changes are inferred using parsimony (only unambiguous apomorphies). The character list is given in Appendix 2. Ancestral area reconstructions (DIVA 1-1a, *maxareas* = 3) are indicated near each node: Afr = Afrotropical region, Aust = Australian region, Orient = Oriental region, Pal = Palearctic region, Near = Nearctic, Neotr = Neotropical region.

ously proposed apomorphies of the *Roubikia* deutonymph (OConnor, 1993a) are, in fact, plesiomorphies. *Roubikia*, however, is supported by two "autapomorphies" (Fig. 40) that may actually be homoplasies if a more extensive set of outgroup taxa were employed. The sister-group relationship of *Roubikia* and the *Chaetodactylus* (*s.l.*)+*Sennertia* clade (OConnor, 1993a) holds up, with the highest support by all estimators, 100% for the bootstrap and posterior probability values (Fig. 40).

The genus *Chaetodactylus* (*s.l.*) was suspected to be paraphyletic with respect to its previously recognized subgenera, *Achaetodactylus* and *Ochaetodactylus* (OConnor, 1993a). In our analyses, the two latter subgenera form a single clade, which forms a lineage sister to the remaining *Chaetodactylus* and *Sennertia*. Both *Achaetodactylus* and *Chaetodactylus* (*s. str.*) (including *Spinodactylus*) are well-supported lineages, characterized by three and four apomorphic character states, respectively (Fig. 40). In order to preserve the monophyly of the genus *Chaetodactylus*, the rank of the *Achaetodactylus*+*Ochaetodactylus* clade should be elevated to a genus, for which we choose the name *Achaetodactylus* Fain, 1981, **stat. n.** (=*Ochaetodactylus* Fain, 1981, **syn. n.**).

The *Chaetodactylus* (*s. str.*) and *Sennertia* clades are sister-groups characterized by two unambiguous apomorphies and two homoplasies (Fig. 40).

In the above discussion we relied on a parsimony character mapping. Branch length shown on phylogram resulting from the Bayesian analysis clearly illustrate the differences between the two methods. Parsimony analysis considers character states 41.0 and 42.1 as evolving independently (given that the opposite would require one additional step), while Bayesian analysis assumes that they could be present in the common ancestor of the two groups.

Historical Biogeography

Biogeographic history of the mites was reconstructed using dispersal-vicariance analysis (DIVA 1–1a, Ronquist, 1996, 1997). This method is based on a vicariance model and allows dispersals and extinctions. DIVA does not enforce area relationships to conform to a hierarchical "area cladogram" so it can be used to reconstruct "reticulate" biogeographic scenarios. Twelve taxa representing five chaetodactylid genera, the set of unit areas (Table 8), and the Bayesian phylogenetic tree were analyzed. DIVA optimal reconstructions with an unconstrained number of unit areas did not produce any plausible explanation of the distribution pattern of early derivative chaetodactylids. The ancestor of the entire family as well as the common ancestors of the recent mite groups could be distributed in any geographic region. We suspect that the lack of resolution results from the heavy weighting of the present distribution of *Chaetodactylus* associated with some hosts capable of distant intercontinental dispersals. One of the early derivative lineages, the *Chaetodactylus ludwigi* species-group, is an example. This group has the broadest distribution among any group of chaetodactylids below the generic level: South America, Africa, India, Oceania, Australia, and the eastern Palaearctic (southern Japan) (our data). Close morphological similarities among its species suggest that this distribution is a consequence of transoceanic migrations as nests of their hosts may disperse in drifting wood (Michener, 2000). Therefore, according to the ranges of the early derivative chaetodactylids (Table 8), we restricted the number of ancestral distribution areas to three.

The combination of geographic distribution and host range of recent chaetodactylid mites creates a very peculiar pattern: three early derivative genera are restricted to South America (*Centriacarus*, *Roubikia*) or Africa (*Achaetodactylus*), while two more recently derived sister-taxa, *Chaetodactylus* and *Sennertia*, are worldwide in distribution. The broad ranges of *Chaetodactylus* and *Sennertia* reflect the present distribution of their principal hosts (Table 8). The restricted ranges of *Centriacarus* and *Roubikia* can also be explained by their host distribution. However, *Achaetodactylus*, despite the broad range of its hosts of the genus *Ceratina*, is known exclusively from Africa. The DIVA analysis produced a single optimal hypothesis for ancestral distribution of early derivative lineages (Fig. 40), which identified the Neotropics as the center of origin for the family.

Chaetodactylidae are associated with the phylogenetically basal lineages of the families Megachilidae (Lithurgini) and Apidae (Xylocopini), suggesting that they may be as old as the split between the two families that took place in the Late Cretaceous, about 90 to 95 Mya (Engel, 2001a, 2001b). An alternative explanation is that chaetodactylids originated substantially later, in the Eocene, and have experienced several host shifts concomitant with intercontinental dispersals. The former scenario involves a Gondwanan distribution of chaetodactylids, while the latter a post-Gondwanan. Interestingly, different lineages of long-tongued bees also display both distributional patterns, which are largely not correlated with their supposed phylogeny. The tribes Fideliini (South Africa and the Araucanian region), Meliponini (pantropical), Lithurgini, Anthidiini, Ceratinini, and Xylocopini (worldwide) probably have a Gondwanan origin (Engel, 2001a, 2001b). The former two tribes lack associated chaetodactylid fauna, while the others are attacked by chaetodactylids. Leys *et al*. (2002) argued that the distribution patterns of at least Xylocopinae and Meliponini were shaped by historical migrations across continental bridges or island chains, and they are, in fact, post-Gondwanan. Similarly, many lineages of long-tongued bees show a post-Gondwanan distribution. Roig-Alsina & Michener (1993) indicated 14 tribes of bees, including the chaetodactylid hosts Tetrapediini and Centridini, that are endemic to the Neotropics and do not have immediate relatives in Africa, and which therefore are believed to have appeared after the full separation of the two continents (Roig-Alsina & Michener, 1993). Below we consider the two biogeographic scenarios in detail.

Hypothesis 1. A Neotropical origin of chaetodactylids during the early stages of the break-up of West Gondwanaland in the Late Cretaceous requires host shifts in two early derivative lineages of mites (*Centriacarus* and *Roubikia*). Their present hosts, bees of the genera *Tetrapedia* and *Centris*, are autochthonous Neotropical lineages that originated after the full separation of the South American and African continents. This hypothesis also requires an intercontinental dispersal from South America to Africa of the ancestor of *Achaetodactylus* roughly coincident with the separation of these two continents in the Late Cretaceous. By that time, West Gondwanaland was already separated into African and South American continents, although the distances were likely not substantial (Smith *et al*., 1994), allowing for occasional dispersal events.

Hypothesis 2. A Neotropical origin of chaetodactylids after the break-up of West Gondwanaland explains the occurrence of the early derivative chaetodactylids (*Centriacarus* and *Roubikia*) on endemic Neotropical bees. However, this hypothesis requires an intercontinental dispersal and, possibly, a host shift in *Achaetodactylus*, since the South American continent was fully separated from the North American and African continents from the Late Cretaceous. According to Leys *et al*. (2002) *Xylocopa* migrated to Africa only in the early Miocene, about 20 Mya, well after the migration to North America in the late Eocene before 34 Mya. Judging from the monophyly of *Sennertia* lineages associated with the New World carpenter bees, the mites migrated with their hosts to North America, and therefore, were already present at least 34 Mya. In our phylogenetic reconstruction, *Sennertia* originated from an *Achaetodactylus*-like ancestor (Fig. 40). Thus, the origin of *Achaetodactylus* should be dated earlier than the late Eocene, before the divergence of the Old and New World large carpenter bees.

The above facts do not allow a definitive answer regarding the timing of chaetodactylid origin. Like the biogeographic past of their hosts, there are several mutually contradictory distribution patterns, suggesting different biogeographic scenarios. Host shifts and intercontinental dispersals of early derivative groups should be involved to explain the present distribution and host associations of chaetodactylids. Irrespective of which hypothesis is preferred, the Neotropical region is identified as the center of origin of chaetodactylid mites.

Analysis of Host Associations

A global test for the presence of codivergence was conducted in ParaFit (Legendre *et al*., 2002). TreeFitter (Ronquist, 1995, 2003) was used to detect evolutionarily conserved patterns in coevolutionary histories of the mites and bees through exploration of event cost space (Ronquist, 2003). Reconstructions of historical associations of chaetodactylids and their bee hosts were performed in TreeMap 2.0.2β (Page & Charleston, 1998).

The ParaFit test (Legendre *et al*., 2002) assesses the fit between host and parasite phylogenetic distance matrices mediated by the matrix of host-parasite links (incidence matrix). Unlike TreeFitter or TreeMap, ParaFit is not affected by polytomies in the tree and, like TreeFitter, it can be used with any number of hosts per parasite or parasites per host. Host and symbiont phylogenies are converted to patristic distance matrices that allow their full representation, including branch length. The two patristic matrices are then transformed to principal coordinates. From the incidence matrix and two principal coordinate matrices, ParaFit computes a fourth-corner matrix, which is used to test the hypothesis of cospeciation through a permutation procedure in which the matrix of links is randomized. The program implements a global test as well as tests of individual links between the host and symbiont phylogenies estimated by the ParaFitLink1 and ParaFitLink2 statistics (Legendre *et al*., 2002). A correction for multiple testing was applied (Wright, 1992) when some individual H-P links are significant but the global ParaFit statistic is not. We derived the incidence matrix from Table 8. Patristic distance matrices for mite (Fig. 40, excluding the outgroup) and host (Roig-Alsina & Michener, 1993, analysis C; Engel, 2001a) trees were calculated in PAUP* 4.0b10. Because our reconstructions of host phylogeny using the same search parameters and datamatrix were different than originally published (Roig-Alsina and Michener 1993, analysis C) we used the majority rule consensus tree of 155 shortest trees. The relationships between chaetodactylid hosts and major lineages of bees were the same. The program DistPCoA (Legendre & Anderson, 1999) was used to transform patristic matrices to principal coordinates. The probabilities of correctly detected coevolutionary links were computed after 9999 random permutations.

TreeFitter (Ronquist, 1995) performs parsimony tree fitting based on the four-event model and allows association of each of these events with a cost inversely related to the likelihood of the event. The four events are: codivergence, duplication, sorting, and partial switching. TreeFitter performs general cost optimization by incrementally varying the cost of any event within a specified range and recording *P* values of the randomization test. The distribution of *P* values in parameter space gives insight on historically constrained association patterns present in the data set (Ronquist, 2003). For this test, the same data as above were used, except for the host tree, which was derived from the tribal-level cladogram of Engel (2001a). The lower-bound algorithm was employed to fit the bee and mite trees. TreeFitter randomization tests were conducted with 10,000 permutations of both H- and P-tree terminals to statistically test the overall cost and contribution of each type of event. The results were compatible with other randomization strategies (*e.g.*, involving P-terminals, P-trees, and H- and P-trees), but not H-terminals or H-trees. The latter two techniques are more suitable for testing cases when historical relationships are solely determined by host phylogeny (Ronquist, 2003). Cost event space was explored to find possible phylogenetically conserved event patterns.

TreeMap 2.0.2β performs cophylogeny mapping from a dependent phylogenetic tree (parasites) onto an independent one (their hosts) in order to recover the best possible coevolutionary explanation for the relationship between the two (Page & Charleston, 1998). The program computes all optimal solutions by exhaustive search, represented by Jungles (Charleston, 1998). TreeMap maximizes codivergence, and it is never considered as having a cost compared to other events. The program does not allow setting any other costs to zero. We used the same data set as for the TreeFitter analyses with the exception that only seven host taxa were retained because TreeMap cannot analyze data sets with hosts lacking parasites. The significance of each value was obtained through randomization tests, building 1000 randomly resampled jungles and randomizing the associate tree only. The null hypothesis that the level of similarity is due to chance alone was tested at the 0.05 level.

The phylogeny of major lineages of chaetodactylids superimposed on the phylogeny of their hosts (Roig-Alsina & Michener, 1993; Engel, 2001a) suggests the absence of any cophylogenetic pattern. Moreover, it appears to be non-randomly ‘descending’ from the most derived to early derivative groups (Centridini to Xylocopini), creating an unprecedented case of a reverse ‘codivergence’ (Fig. 41 *A*). Because the probability of a random appearance of this pattern is low, some underlining factors must contribute to such a bizarre distribution, for example, historical ecology. It is possible that chaetodactylids have been tracking a host resource (Kethley & Johnston, 1975), as there are some trends in the host nest architecture preference. Although a cophylogenetic pattern is not evident from extant host associations, it may be hidden by restricted host switches to ecologically similar hosts, duplications, and numerous extinctions. Based on relatively high correspondence between corresponding bee and mite lineages, we suspect past congruence of mite and host phylogenies in several deep nodes, especially those that gave rise to the *Sennertia*-Xylocopinae.

Comparison of the phylogenies of the chaetodactylids and bees failed to detect a significant coevolutionary convergence between the two (Table 10) however, this result reflects the restricted conditions required to reject a random pattern of association by the program PARAFIT (Legendre *et al*., 2002)—namely, co-divergence that is temporally correlated. In fact,

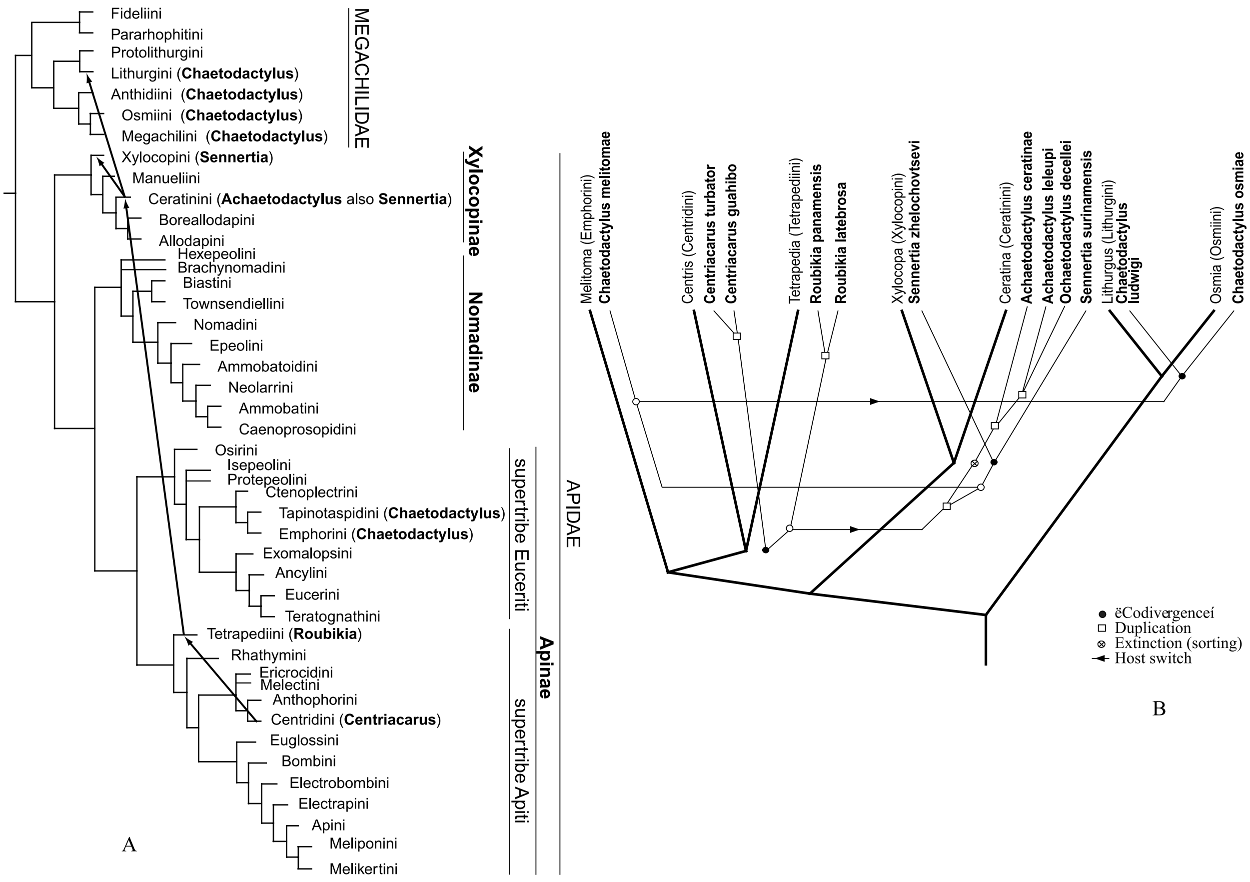

Fig. 41. A - Phylogeny of the family Chaetodactylidae superimposed on the phylogeny of long-tongued bees (Engel, 2001a; Roig-Alsina & Michener, 1993). Some host associations of *Chaetodactylus* are not resolved. B, C - TreeMap 2 suboptimal reconciliations of the two phylogenies (see also Table 12, set 2).

when the root of the mite tree is inverted, a significant ($P = 0.029$) correlation between the two phylogenies is clearly identified (Table 10). Not only does this analysis demonstrate that associations between mites and bee-hosts depart significantly from random expectations, but it also indicates that the host-symbiont phylogenies are indeed inversely correlated—that is, recently derived mites are not associated with recently derived bee taxa, but instead the converse is observed (i.e., recently derived mites are associated with basal bee taxa, and *vice versa*).

In order to find the most optimal coevolutionary explanation in this system characterized by the unprecedented pattern of 'reverse codivergence', we analyzed phylogenetically conserved association patterns through the exploration of cost space of four coevolutionary events (TreeFitter). Detection of optimal coevolutionary scenarios requires finding optimal event costs. This can be done based on *a priori* knowledge of certain biological features of the associated organisms, but in most cases, it is difficult to justify. Ronquist (2003) presented a method that handles all possible coevolutionary scenarios involving all combinations of one constrained (codivergence, duplications) and one unconstrained process: pure cospeciation, duplication-switching, cospeciation-duplication, cospeciation-sorting, cospeciation-switching, and patterns mixing more than two types of events. This method does not rely on arbitrary *ad hoc* hypotheses, but estimates them from P values obtained from the randomization tests of a continuum of event cost sets where duplications and cospeciation events usually have a low cost.

Optimization of different historical events across a broad range of costs for each event (Fig. 42*A*) using TreeFitter identified a variety of scenarios that would explain the observed correlation between mite and bee-host phylogenies. Even when the costs of particular events are allowed to vary, several significant historical scenarios (*i.e.*, those that differed significantly from random expectations) were identified (Fig. 42*B*) that differed with respect to (a) the total number of events required to produce the observed association between mite and bee phylogenies, as well as, (b) the number (and costs) of specific events for any given scenario (*e.g*, a history involving only speciation within a lineage and host switching—model 1, versus cospeciation, speciation within a lineage, extinction and host switching—models 2–5) (Table 11). Of the six significant models identified (Fig. 42*B*, Table 11), the absence of host shifts postulated by model 6 can be rejected as unlikely because it involves an excessive number of events (*i.e.*, 35 extinctions) and the highest total costs (lower, right corner of Fig. 42*B*, Table 11). Joint consideration of the total costs with the num-

Table 10. ParaFit test for codivergence between chaetodactylid mites and long tongued bees. The null hypothesis of the global test of significance for coevolution is that the evolution of the two groups, as revealed by the two phylogenetic trees and the set of association links, has occurred independently. The 42-host analyses consider only binary host (Engel, 2001a) and symbiont (Fig. 40 excluding the outgroup) trees, while the 83-host analysis considers both topology and branch length of host (Roig-Alsina & Michener, 1993, analysis C) and symbiont (Fig. 40) trees. In order to show the presence of negative codivergence, a second 42-host analysis was conducted with the mite tree inverted. To overcome the ParaFit format (f8.5) that does not allow printing large values, the values of patristic distance matrices were divided by 10 (42-host analyses) or by 100 (83-host analysis). The probabilities were computed after 9999 random permutations.

			(mite tree inverted)			
	42 hosts		**42 hosts**		**83 hosts**	
Mite taxon	**F**	**P**	**F**	**P**	**F**	**P**
Centriacarus turbator	0.859	0.015*	0.607	0.012	0.002	0.897
Centriacarus guahibo	0.859	0.014*	0.607	0.012	0.002	0.915
Roubikia panamensis	0.104	0.601	0.277	0.183	0.015	0.058
Roubikia latebrosa	0.013	0.814	0.277	0.192	0.015	0.059
Achaetodactylus ceratinae	0.308	0.171	0.290	0.042	0.001	0.869
Achaetodactylus leleupi	0.308	0.175	0.452	0.057	0.001	0.750
Ochaetodactylus decellei	−0.071	0.922	0.452	0.058	0.001	0.838
Chaetodactylus melitomae	0.207	0.467	0.078	0.546	0.001	0.678
Chaetodactylus ludwigi	0.300	0.285	0.438	0.102	0.009	0.092
Chaetodactylus osmiae	0.287	0.104	0.475	0.085	0.009	0.120
Sennertia zhelochovtsevi	0.134	0.454	0.215	0.433	0.003	0.790
Sennertia surinamensis	−0.186	0.992	0.052	0.864	−0.010	0.994
Global test for codivergence	2.484	0.146	2.996	0.029	0.053	0.677

F = ParaFitLink1 statistic, P—significance, *non-significant after correction for multiple testing (Wright, 1992)

ber of individual events required to produce the pattern of host-symbiont assemblages suggests that a model of speciation within hosts and host switching (model 1) is more parsimonious than other scenarios; a difference of 11 total events (model 1) versus 14, 18, 25, 37, and 46 events for models 2, 3, 4, 5, and 6, respectively.

TreeMap yielded 11 optimal reconciliations (Table 12). As in the previous analysis, three major hypotheses were recov-

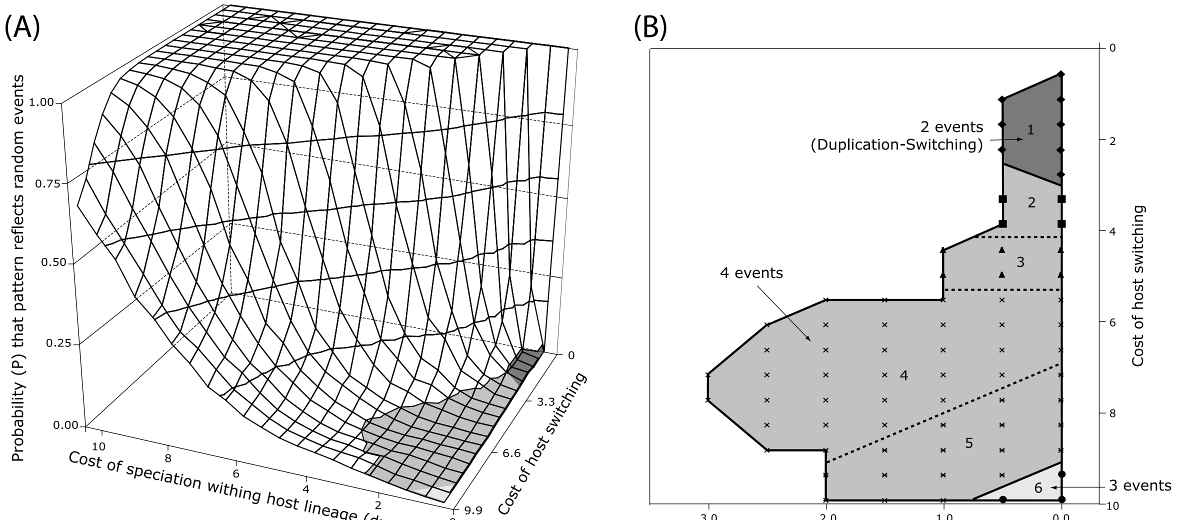

Fig. 42. Exploration of the cost space of coevolutionary associations of chaetodactylid and bees: (a) *P*-values were estimated from 10,000 random permutations of both host and symbiont terminals with a codivergence and extinction cost of 0 and 1, respectively; significant values ($P < 0.05$) are shaded and shown in detail (b), where the six different models and associated event-costs are shown. Information on the specific historical events and varying number of events specified under the six significant models are given in Table 11, along with range of cost-values encompassed by the models (after Klimov *et al.*, 2007).

Table 11. Significant models (Fig. 42*B*) characterized by different types of historical events and varying number of events specified under a particular model[a] (identified using event cost-optimization in TreeFitter). These significant models each encompass a range of cost values[b] such that the historical models differ with respect to the amount of cost-space consistent with each model (see Fig. 42*A*)

#	Events[a]	Total cost (all events)[b]	Duplication cost[b]	Switching cost[b]
1	0,5,0,6	3.3–16.5	0–0.5	0.55–2.75
2	1,5,3,5	19.5–24.75	0–0.5	3.3–3.85
3	2,5,7,4	24.6–31.8	0–1	4.4–4.95
4	3,5,12,3	28.5–50.9	0–3	5.5–8.8
5	3,7,26,1	33.15–49.9	0–2	7.15–9.9
6	3,8,35,0	35–39	0–0.5	9.35–9.9

[a] Number of events for codivergence, speciation within host (duplication), extinction (sorting), and switching, respectively.

[b] Total costs as indicated as ranges within corresponding sets of events (column 2).

ered: chaetodactylids originated on the common ancestor of the families Megachilidae and Apidae (Table 12, reconstruction 11), the family Apidae (7–10), or the supertribe Apitini (1–6). Direct comparison of these results with those obtained by TreeFitter is difficult because TreeMap restricts the set of host taxa to only terminals that are involved in present-day coevolutionary interactions. Although, for this reason, estimates of codivergence events may be positively biased, the proportion of the two unconstrained events (sorting, switching) and pulled constrained events (codivergence+duplication) is compatible with the TreeFitter results. Reconstructions 1–6, assuming no or only small scale extinctions, correspond to the duplication-switching model (set 1); reconstructions 7–10, considering duplications and the two unconstrained events, correspond to the four-event model (sets 2–5); and reconstruction 11, assuming no host switches, is equivalent to the reconciliation three-event model (set 6) (cf. Table 12 and Table 11).

If origin of chaetodactylids on the common ancestor of megachilid and apid bees or on early derivative lineages of the family Apidae is assumed (sets 7–11, Table 12), this would predict a Gondwanan distribution of all recent genera. This is in agreement with the sister-group relationships and present distributions of *Roubikia* and the *Achaetodactylus* (*Chaetodactylus*, *Sennertia*) clade, but requires a host shift in *Roubikia* and *Centriacarus* and extinction of South American *Achaetodactylus*. A Gondwanan distribution of *Xylocopa*, the host of most *Sennertia*, and the early derivative groups of the lineage including *Ceratina* (host of *Achaetodactylus* and *Sennertia*), was presumed by Engel (2001b) but contested by Leys *et al*. (2002). Because no chaetodactylid species or species group are known to have a Gondwanan distribution (see the section on Historical biogeography, p. 77), we refrain from assuming that the early evolution of the mites was associated with the early evolution of apid and megachilid bees or only the former. In contrast, the hypotheses of a post-Gondwanan origin of chaetodactylids (1–6, Table 12) require a smaller number of events to predict the observed cophylogenetic pattern, and the randomization test renders them as highly significant (Table 12). Host shifts and some *ad hoc* hypothesis explaining the present host associations and distribution of *Achaetodactylus* must still be introduced to account for all observed host-associations and biogeographic phenomena. According to the hypothesis of a post-Gondwanan origin of chaetodactylids (p. 77), the mites first originated in South America, probably in the Eocene, when the two continents were separated. This would explain the association of the early derivative genera, *Roubikia* and *Centriacarus*, with endemic South American bees, but makes it very difficult to explain the presence of *Achaetodactylus* only in

Table 12. TreeMap 2.0.2β optimal reconciliations of the phylogenies of chaetodactylid mites and their hosts.

Events[a]							Ancestral hosts[b]			
#	Co	Du	Lo	Sw	Cost	*P*	Chaetodactylidae	*Roubikia*	*Achaetodactylus* (*Chaetodactylus*, *Sennertia*)	(*Chaetodactylus*, *Sennertia*)
1	6	16	0	4	20	0.005	Apiti	Apiti	Tetrapediini → Euceriti	Euceriti
2	6	16	1	3	20	0.002	Apiti	Apiti	Tetrapediini → Xylocopinae	Xylocopinae
3	6	16	1	3	20	0.001	Apiti	Apiti	Tetrapediini → Xylocopinae	Xylocopinae
4	6	16	0	4	20	0.006	Apiti	Apiti	Tetrapediini → Xylocopinae	Xylocopini
5	6	16	0	4	20	0.009	Apiti	Apiti	Tetrapediini → Xylocopinae	Xylocopini
6	6	16	0	4	20	0.011	Apiti	Apiti	Tetrapediini → Megachilidae	Megachilidae
7	6	16	6	2	24	0.024	Apidae	Apidae	Xylocopinae	Xylocopinae
8	6	16	6	2	24	0.034	Apidae	Apidae	Xylocopinae	Xylocopinae
9	6	16	9	1	26	0.031	Apidae	Apidae	Apidae	Apidae
10	6	16	9	1	26	0.021	Apidae	Apidae	Apidae	Apidae
11	6	16	15	0	31	0.044	L-T	L-T	L-T	L-T

Co = codivergence, Du = duplication, Lo = extinction, Sw = host switching. [b]The prefix "early derivative" should be assumed before a host name. Apiti include Tetrapediini, Rhathymini, Ericrocidini, Melectini, Anthophorini, Centridini, and corbiculate Apinae; L-T = long-tongued bees (ancestor of Apidae and Megachilidae); → = host shift. Reconciliation corresponding to set 2 is presented on Fig. 41 *B*. Significance was estimated by the randomization test with 1000 permutations of P-trees at the 0.05 significance level.

Africa. The host associations and distribution of *Achaetodactylus* suggest a contemporaneous intercontinental dispersal to the Old World and host shift to *Ceratina*. This would imply either back intercontinental dispersal of the ancestor of *Chaetodactylus* (2–6) or independent intercontinental dispersal of the ancestor of *Sennertia* (1, Table 12). Judging from the relationships between early derivative groups of *Chaetodactylus*, host shifts were frequent and included bees with great dispersal abilities, such as *Lithurgus* (Megachilidae). Our maximum parsimony inference found *Chaetodactylus* associated with *Melitoma* as the earliest derivative taxon; Bayesian analysis, however, collapsed early derivative branches, suggesting that associates of *Lithurgus*, *Trichothurgus*, and *Diadasia* also can be potential ancestral hosts. Scenarios 2–6 (Table 12) also explain why the earliest derivative group of *Sennertia*, associated with *Xylocopa* (*Proxylocopa*) from the Mediterranean region and Middle Asia, does not occur in the New World. For the above reasons, we consider scenarios 2–6 as the most plausible. One of them (2) is reproduced in Fig. 41*B*.

In conclusion, historical associations of major groups of chaetodactylids and long-tongued bees are largely asymmetric, demonstrating a strong departure from a random pattern. Despite the fact that mites are strictly dependent on their hosts in terms of food, habitat, and means of dispersal codivergence seems to be not the major process structuring these relationships. Early derivative mite lineages are associated with derived bee hosts and vice versa, resulting in the symbiont phylogeny inversely corresponding to that of their host (Fig. 41). As a salient violation of Fahrenholz's rule, this model suggests the contribution of other coevolutionary phenomena, such as speciation by the parasite without the host (duplication), extinctions (sorting), host switches, and failure of symbiont to speciate in response to host speciation (Johnson *et al*., 2003).

Codivergence events, duplications, and extinctions are dependent on the hierarchy of the host phylogeny and may create distinct coevolutionary patterns, whether congruent or incongruent with the host topology. Similarly, host switching, mediated by certain geographic or ecological constraints may also be non-random, and even cause some degree of congruence in host-parasite systems (Percy *et al*., 2004). Sometimes, such scenarios may be misinterpreted in favor of codivergence and extinction, especially in the programs overestimating codivergence and if the divergence times are not taken into account (Percy *et al*., 2004). Recent analytical methods, when deriving an optimal coevolutionary solution, can give weights to each of these events (except for failure to speciate) and thus detect the relative importance of these processes in natural systems (Ronquist, 2003). Reconstruction of cophylogenetic events deep in host-symbiont history, however, often requires taking into account numerous uncertain and varying factors and the possibility of rare events drastically altering the outcome of coevolutionary interactions. One solution is to examine processes occurring in extant associations and make certain assumptions about events that occurred in the deep nodes of symbiont phylogeny. Another approach is to falsify some hypotheses with available paleogeographic and paleobiological data or molecular clock estimates of divergence times. For example, a codivergence event must involve contemporaneous speciation of a host and its symbiont, likewise host switches must be contemporaneous and include sympatric and syntopic hosts.

Through the above analyses of the mite biogeography, dispersal ecology, life history and nest architecture features of extant bees, we can begin to make generalizations about the biological factors that produced the non-random coevolutionary pattern. There is a certain degree of correspondence between mite and host lineages as they form monophyletic clades specific to one another. Aside from the derived mite genus *Chaetodactylus*, notorious for its dispersal and host switching abilities, chaetodactylid genera are associated with one or two bee genera (Table 8). Sometime, specialization also involves bee hosts developing an acarinarium used for mite transfer (*Roubikia-Tetrapedia*, *Achaetodactylus-Ceratina*, *Sennertia-Ceratina*, and *Sennertia-Xylocopa*). The strict host specificity of mites at the generic level of bees might suggest that they developed a substantial degree of specialization that restricts frequent shifts to unrelated hosts. Thus, host specificity of early derivative chaetodactylids was probably a factor influencing the non-random coevolutionary structure in this system but, at the same time, it has not resulted in any degree of cophylogenetic pattern.

Many cases of the above host specificity show some degree of correlation in certain ecological and biological characteristics. For example, hosts of *Centriacarus*, *Roubikia*, *Achaetodactylus*, most *Sennertia* and *Chaetodactylus* construct their nests in wood, with nest cells arranged in a linear sequence, and they are usually solitary, mass provisioning bees. If these features are considered to be independently distributed on the host phylogeny, the structured incongruence between bee and mite phylogenies should be attributed to resource tracking (Kethley & Johnston 1975), or, alternatively, to phylogenetically conserved host shifts (Percy *et al*., 2004).

The host shifts from *Centris* to *Tetrapedia* may be explained as follows. Females of *Centris* (*Heterocentris*) and *Tetrapedia* are known to construct their nests in wood using oily substances, soil or sand (Coville *et al*., 1983; Pereira *et al*., 1999; Michener, 2000; Alves-dos-Santos *et al*., 2002; Camillo, 2005). The nests of these two distantly related bee lineages are more similar to each other than nests between other closely related bees. For example, species of *Centris* nesting in the ground (Coville *et al*., 1983) completely lack chaetodactylids despite the fact the mites can be transferred from more derived wood nesting *Centris* by shared insect cleptoparasites or parasitoids (*e.g*., *Coelioxys*, *Anthrax*). Because the same insects may also attack *Tetrapedia* (Camillo, 2005), we consider the similarity in the *Heterocentris-Tetrapedia* nest architecture as a crucial factor influencing this host shift. Females of both *Tetrapedia* and *Centris* repeatedly visit the same small patches of dry soil to collect the soil and carry it on the scopae to their nests (Roubik, 1987), offering an additional opportunity for host switching.

The remaining shifts (Fig. 41*A*) are difficult to explain. The nests of *Tetrapedia* and *Ceratina*, bees belonging to different subfamilies, have little in common beside the fact that both are linear and constructed in wood. Species of *Ceratina* nest in pithy dead stems or twigs, while *Tetrapedia* in old burrows in wood (Michener, 2000). There are no known insect cleptoparasites shared between the two bee taxa, although common floral preferences or some generalist parasitoids such as conopid flies, might contribute to the mite transfer. Our cladogram shows that a substantial amount of morphological change occurred in the ancestor of the clade that shifted to xylocopine bees (Fig. 40), suggesting that much potentially useful information might be missing here. However, the shift is biogeographically possible as early derivative lineages of *Ceratina* appear to have a Neotropical origin (M. Terzo, pers. comm., 2005), and their mites are among early derivative lineages of *Sennertia*.

Bees of the genus *Ceratina* harbor two genera of chaetodactylid mites, *Achaetodactylus* and *Sennertia*. *Achaetodactylus* occurs only in Africa, while *Sennertia* is represented by at least four *Ceratina*-associated lineages distributed worldwide. Our cladogram indicates that a host shift from *Ceratina* to the large carpenter bees (*Xylocopa*) gave rise to the ancestor of the speciose genus *Sennertia*, whereas the lineages of *Sennertia* associated with *Ceratina* resulted from back shifts from *Xylocopa* to *Ceratina*. Extant bees of the genera *Ceratina* and *Xylocopa* are very different in terms of the body sizes, with *Xylocopa* being much larger than *Ceratina*. They are not known to utilize the same nest tunnels or share the same cleptoparasites. The simplest explanation of the host shifts between the two would involve the relatively high diversity of large and small carpenter bees in the tropics. However, without assuming phylogenetic constraints, it is very difficult to explain the host range of *Sennertia* lineages, as many alternative hosts with similar sizes and nest architecture are present.

In contrast to *Sennertia*, its sister taxon, *Chaetodactylus*, is associated with many unrelated hosts (Table 8). The ancestor of *Chaetodactylus* probably also had shifted from *Ceratina* to either apid or megachilid hosts (Fig. 41 *B*). The associations of this genus with Lithurgini and Osmiini, both belonging to Megachilidae and nesting principally in wood, are most diverse. Other associations involve one or a few species and may include bees nesting in soil such as *Chalepogenus* (Tapinotaspidini), *Diadasia*, *Ptilothrix*, *Ancyloscelis*, and *Melitoma* (Emphorini). All these associations, except for the last, are formed by derived mite taxa. The broad host range of *Chaetodactylus* may be explained by antagonistic interactions with its hosts. As *Chaetodactylus* often kills the developing bee larvae, evolutionary pressure may drive it to utilize new hosts. Other chaetodactylids (*Roubikia*, *Achaetodactylus*, *Sennertia*) seemingly adopted another strategy facilitating close adaptation with their hosts. In addition, unlike other chaetodactylids, *Chaetodactylus* may alter its life cycle and alternatively produce two types of deutonymphs. One of them is phoretic and similar to other chaetodactylid deutonymphs, while the other one is a nonphoretic, inert deutonymph. It can survive in the nest cavity and potentially infest any bee species reusing the burrow. For these reasons, some host shifts within this genus may be essentially random.

If the similar biologies and nest architecture are underlying factors that shaped the close associations of monophyletic lineages of hosts and symbionts, host specificity, therefore, occurs only when these qualities are shared among the hosts as the result of their common ancestry or otherwise. A host shift from an unrelated host may facilitate radiation of the associated organism to early derivative lineages of the new host group, as soon as they share a similar biology. Thus, the distribution of certain biological or ecological properties of hosts affecting their symbionts may create a strong non-phylogenetic signal in their coevolutionary history in the form of distinct event patterns, specifically host shifts and duplications (Liljeblad & Ronquist, 1998; Ronquist, 2003).

As chaetodactylids have adopted numerous mechanisms for lateral transfer (discussed above), a combination of host shifts and certain ecological constraints of bees (discussed above), seems the most plausible explanation for the observed negative congruence between the mite and bee phylogenies. In fact, our logistic regression model fitted to variables pertaining to the nest architecture and bee biology predicts the occurrence of mites on extant bees with 82.1% accuracy. Host switches concomitant with intercontinental dispersals were also postulated by our biogeographic reconstructions. Similarly, models involving host switching were selected by both TreeFitter and TreeMap analyses based on the lowest overall costs (Table 11, Table 12). Alternative models involving, codivergence-sorting, are difficult to accept because they postulate associations that probably could never exist due to strict biological incompatibility and unrealistic historical biogeography. We believe that the phenomenon of the negative correlation of phylogenies of chaetodactylid genera and their hosts (Fig. 41) may be explained by host shifts with subsequent colonization and speciation on early derivative lineages of the hosts. This corresponds to the duplication-sorting model selected by TreeFitter, suggesting that ecological constraints played an important role in the evolution of major lineages of chaetodactylids.

Phylogenetic Relationships among Species of *Chaetodactylus*

A 67 character matrix was constructed for heteromorphic deutonymphs of two outgroup and 25 ingroup species (Appendix 3). Eight characters with states that were difficult to assign into distinct groups were deleted, however, they may be useful for identification purposes for several taxa. Because of the presence of characters that may be considered apomorphic or plesiomorphic using either the close (*Achaetodactylus*) or distant (*Centriacarus*) outgroup, the monophyly of *Chaetodactylus* was not supported by characters that are variable in the ingroup taxa. Thus, we included 7 apomorphies of the genus *Chaetodactylus* and the *Chaetodactylus*+*Sennertia* clade (#58-64, Appendix 3) found in our previous analysis (Fig. 40). Enforcing the ingroup monophyly with topological constraints caused crashes in MrBayes and was not used. The resultant data matrix has 49 parsimony informative and 10 parsimony uninformative characters. Taxa with more than one character state were interpreted as polymorphisms. Burn-in values range from 30080 to 45880 in five different MrBayes analyses, each with 1 million generations. We did not analyze host-parasite associations with TreeMap or TreeFitter, because species level phylogenies are not available for the genera *Lithurgus* and *Osmia*. Otherwise, methods employed in this section are similar to those of the genus-level analyses (p. 76).

Parsimony analysis produced 18 most parsimonious trees (length = 146, CI = 0.596, RI = 0.771, HI = 0.452, RC = 0.460), the strict consensus of which is reproduced on Fig. 43. All topologies rendered *Ch. melitomae* associated with apid bees of the genus *Melitoma* in the New World and *Ch. ludwigi* s. l. associated with megachilid bees of the genus *Lithurgus* spp. and widely distributed in the eastern part of the Southern Hemisphere as early derivative clades of the genus. The sister clade of *Ch. ludwigi* includes two lineages that can be defined by distribution and host associations: the *lithurgi* and *osmiae* clades, and a weakly supported clade including species from the Araucanian region of southern South America.

The *lithurgi* clade is associated primarily with *Lithurgus* in North America with one western Palaearctic species occurring on *Megachile bombycina*. Two species, *Ch. furunculus* (California) and *Ch. antillarum* (Caribbean) form a monophyletic clade probably suggesting an old vicariance. The relationships of other species are uncertain. *Chaetodactylus gibbosi* and a pair of cryptic species *Ch. lithurgi*+*Ch. abditus* associated with *Lithurgus* species that collect pollen on flowers of Cactaceae in North America are very similar but lack any obvious synapomorphies, and the analysis rendered their relationships as an unresolved polytomy. *Chaetodactylus kouboy*, an enigmatic species known from a single collection from *Lithurgus apicalis* from New Mexico is placed to the root of the *lithurgi* clade by some analyses. The placement of the single western European species, *Chaetodactylus dementjevi*, in the *lithurgi*-group is relatively well supported, indicating a possible host shift.

The *osmiae* lineage includes Holarctic species mostly associated with *Osmia*, although three species occur on *Rhodanthidium*, *Hoplitis*, and *Chelostoma*. The earliest derivative species of this group, *Chaetodactylus azteca*, is associated with the subgenus *Diceratosmia* of the genus *Osmia* in Mexico, suggesting that mason bees were the ancestral hosts for the lineage. Two monophyletic lineages that we term the *micheneri* and *krombeini* groups deserve mention.

The *micheneri* group is represented by at least two species distributed throughout North America north of Mexico that are associated primarily with the endemic subgenus *Osmia* (*Cephalosmia*).

The formerly recognized Holarctic subgenus *Spinodactylus* was traditionally defined by autapomorphic characters, such as the inflation of the basal parts of some coxal setae (Fain, 1981b). In our analysis these species appear as is a highly derivative, monophyletic group within *Chaetodactylus*, and we place the name *Spinodactylus* as a junior synonym of *Chaetodactylus* **syn. n.**

The analysis considers *Ch. hirashimai* as an early derivative member of this lineage, having coxal setae *1a* only slightly inflated. Species in this lineage are associated with the bee subgenus *Osmia* (*s. str*.), but a host shift and speciation event occurred in the ancestor of *Ch. hopliti* now associated with *Hoplitis*. The ranges of the two closely related sister species, *Ch. krombeini* (North America) and *Ch. claviger* (Mediterranean), suggest either recent dispersal or vicariance.

The type species of the genus, *Ch. osmiae*, and similar species (*e.g.*, *Ch. claudus*, *Ch. nipponicus*) appear on the tree as a pectinate series basal to the above mentioned clade. The positions of *Ch. zachvatkini*, *Ch. anthidii*, and *Ch. reaumuri* may be questionable as they are based on a few highly homoplastic character states. However, if the larger lineage was ancestrally associated with *Osmia*, independent host shifts must be invoked in *Ch. birulai* to *Chelostoma* and *Ch. anthidii* to *Rhodanthidium*.

The analysis also identified a clade consisting exclusively of as yet unnamed species distributed in the Araucanian biogeographic region with each associated with distantly related hosts: *Trichothurgus*, *Anthidium*, and *Diadasia*. The group is supported by a single dubious apomorphic character pertaining to the ornamentation of the hysterosomal shield and may be in fact a paraphyletic or polyphyletic assemblage. However, a very peculiar, unique synapomorphy, the ventral striation of claws I–II joins *Ch. lassulus* and the undescribed species from *Anthidium espinosai* (character 48), indicating a relatively long isolation and independent host shifts in the group (or at least in these two species). Another host shift to Anthidiini had occurred independently in the Old World and gave rise to *Ch. anthidii*.

Analysis under implied character weights yielded four trees with the same parameters as for the general parsimony analysis. Strict consensus trees from the two analyses are similar except for the sister-group relationship of *Ch. birulai* and *Ch. reaumuri* in the implied weighting analysis.

Bayesian analysis reconstruction was different from that of maximum parsimony in several respects (Fig. 43). The relationships of the early derivative clades, *Ch. melitomae*, the *ludwigi* and *lithurgi*-groups, and the Araucanian species were unresolved, and the analysis placed them to the root of *Chaetodactylus*. Sister group relationships of the cryptic species *Ch. gibbosi* and *Ch. lithurgi* (*s. l.*) were recovered with a low posterior probability. The Araucanian group was partially recovered (except for the species associated with *Diadasia chilensis*). The *micheneri*-group is rendered as an early derivative lineage branching off from the sister clade of *Ch. azteca*. This arrangement probably should be preferred over the maximum parsimony solution because it does not require intercontinental dispersals. With the rearrangement of the *micheneri*-group, the analyses considers *Ch. zachvatkini* and *Ch. chrysidis* as more derived lineages, forming the sister clade to the remaining species. Unlike the parsimony analysis, *Ch. reaumuri* and *Ch. birulai* form a monophyletic clade, which is possibly a spurious grouping because the species are very dissimilar morphologically and ecologically.

Historical Biogeography of *Chaetodactylus*

We analyzed historical distribution of 22 terminal taxa of *Chaetodactylus* and the same set of areas as in the previous analysis (Table 8). To avoid polytomies, non-critical taxa were deleted (Appendix 3) and if that was not possible, polytomies were resolved arbitrarily to accommodate all possible changes.

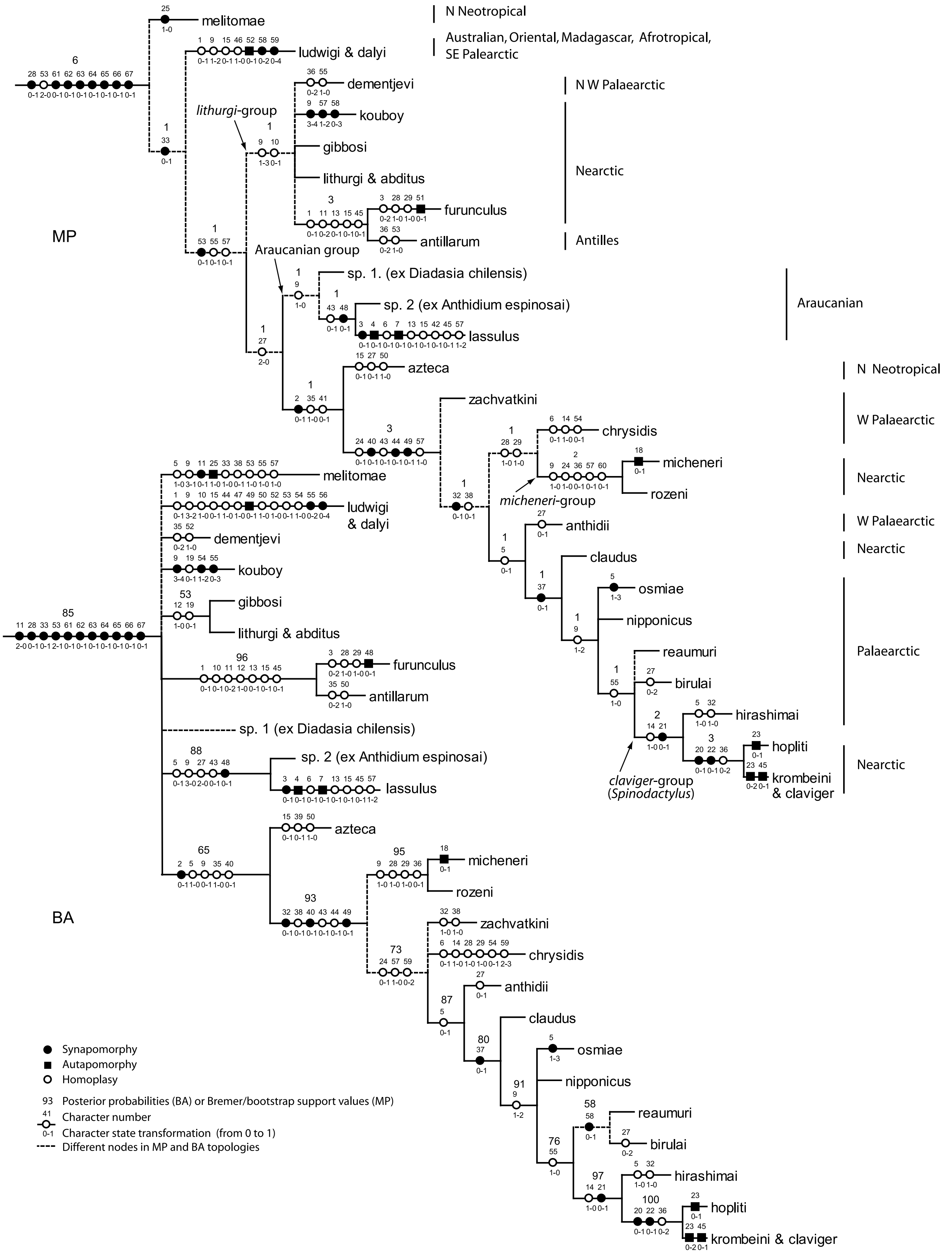

Fig. 43. Phylogenetic relationships in the genus *Chaetodactylus* reconstructed by maximum parsimony (MP) and Bayesian (BA) analyses. Two outgroups (*Centriacarus turbator* and *Achaetodactylus ceratinae*) are excluded. The data are shown in Appendix 3 (p. 168).

In the Bayesian topology, the unresolved early derivative clades were arranged according to the maximum parsimony topology. Six resultant trees (3 based on MP, 3 based on MCMC) were analyzed using DIVA with the parameter maxareas set to 9, 3, and 2 (Table 13).

Determination of the center of origin of *Chaetodactylus* faces the same challenges as finding the ancestral distribution the family itself. *Chaetodactylus melitomae*, the earliest derivative lineage of *Chaetodactylus* (Fig. 43), is known from the northern part of the Neotropical region. Another early derivative clade, the *ludwigi*-group (including one undescribed species) is broadly distributed throughout the entire Southern Hemisphere, but also in the Oriental region and marginally in the south-east Palaearctic. Given that the broad range of this group may represent a unique ability of its hosts to disperse with drifting wood and, therefore, may affect our analysis, we excluded this entire lineage. The results, however, were not drastically different, suggesting that the program correctly explains that this distributional pattern was shaped by dispersals.

DIVA reconstructions did not converge on a single area being an optimal ancestral area for the common ancestor of the genus. If the maxareas parameter is set to 2–3, the possibilities include either the Afrotropical and Neotropical regions and/or the Palaearctic and Neotropical regions. The inclusion of the Palearctic region is surprising because none of the early derivative lineages (*Centriacarus*-*Ch. melitomae*) occurs there. As the removal of the *ludwigi*-group apparently has no affect on the reconstructions, the heavy weighting of the Palearctic probably resulted from the fact that many derived lineages have Palearctic distributions. Given that many early derivative lineages (*Ch. melitomae*, undescribed species from the *ludwigi*-group, many members of *lithurgi*-group, and the Araucanian group, *Ch. azteca*) are distributed in the Neotropical region (here including the Antilles and Araucanian region), we believe that the Neotropical region was the center of origin of the genus. From this area, species probably spread to the Nearctic, Palaearctic, and Afrotropical regions.

Chaetodactylids of the Araucanian region display signs of endemism that might account for a long isolation of this interesting biogeographic region. At the level of genus, their host bees inhabit xeric areas of North and South America, which have never been connected to each other, and display amphitropical distributions (most notably, *Diadasia* and *Ptilothrix*). Their chaetodactylid associates, however, do not, indicating that their isolation and speciation occurred after the divergence of major bee genera. This small and endemic group is characterized by the greatest taxonomic diversity of hosts, suggesting independent host shifts (*e.g.*, to Anthidiini). Obviously, a more detailed study will be required to address this issue.

With the exception of the early derivative taxon, *Ch. azteca*, known from the northern Neotropical region, the remaining taxa form a Holarctic group (that occurs only marginally in other regions). Multiple dispersals across the Palaearctic and Nearctic were required to occur in this group by DIVA. At least two unambiguous dispersal events occurred in the most derivative lineage (*claviger*-group). Reconstructions of ancestral areas of other important lineages of *Chaetodactylus* are given in Table 13.

Table 13. Optimal distributions at selected nodes of the *Chaetodactylus* phylogeny (Fig. 43, MP (Analyses 1–3) and Bayesian analysis (Analyses 4–6)) reconstructed by DIVA with two different setting of the parameter maxareas.

	Analysis (maxareas = 9)					
Clade (a = ancestor)	**1**	**2**	**3**	**4**	**5**	**6**
a(*melitomae*, *ludwigi*+)	All, but Afr; All					
a(*ludwigi*, *antillarum*+)	All, but Afr and Neotr; All, but Neotr; All, but Afr; All					
lithurgi-group	Near-Antill; Hol-Antill	Hol-Antill	Near-Antill; Hol-Antill	Pal-Antill; Near-Antill; Hol-Antill	Pal-Antill; Hol-Antill	Near-Antill; Hol-Antill
Araucanian group	Arauc					
a(*azteca*+)	Pal-Neotr			Pal-Neotr, Near-Neotr, Hol-Neotr		
micheneri-group	Near					
claviger-group	Pal; Hol					
	maxareas = 2					
a(*melitomae*, *ludwigi*+)	Afr-Neotr; Pal-Neotr					
a(*ludwigi*, *antillarum*+)	Pal; Afr-Pal			Pal, Afr-Pal, Afr-Near		
lithurgi-group	Pal-Antill	Hol; Pal-Antill	Hol	Pal-Antill; Near-Antill	Hol; Pal-Antill	Hol; Near-Antill
Araucanian group	Arauc					
a(*azteca*+)	Pal-Neotr			Pal-Neotr, Near-Neotr		
micheneri-group	Near					
claviger-group	Pal; Hol					

All = 9 areas from Table 8 (after Michener, 2000), Afr = Afrotropical region, Antill = the Greater and Lesser Antilles, excluding Trinidad, Arauc = Araucanian region, Hol = Holarctic region, Near = Nearctic region, Palear = Palearctic region.

Phylogenetic Relationships among Species of *Sennertia*

Major groups, biogeography and host associations

The genus *Sennertia* was subdivided by Fain (1981b) and Kurosa (2003) into six subgenera and three species groups. The major characters used to establish these groupings were the relative length of the hysterosoma shield; the position of dorsal hysterosomal setae c_1, d_1, and e_1 on or off the shield; the length of setae *si* relative to *se*; the relative length of legs and tarsi IV; the development of the posterio-proximal and posterio-distal lobes of the caruncle of tarsi I–III; the modification of some leg setae into conical spines; and the presence or absence of setae *hT* I–II and *vF* IV. A brief review of the biogeography and host associations of these groups and two new groups is given below (traditional taxonomic hierarchy is not assumed, see also p. 147):

Subgenus *Amsennertia* Fain, 1981 (Type species: *Sennertia frontalis* Vitzthum, 1941). Identification: setae *si* and c_1 long *and* hysterosomal shield not triangular.

Distribution: Nearctic and Neotropical.

Hosts: virtually all major subgenera of New World *Xylocopa*; not found so far on the following subgenera: *Nanoxylocopa*, *Cirroxylocopa*, *Xylocospila*, *Ioxylocopa*, *Monoxylocopa*, *Diaxylocopa*, *Calloxylocopa*, *Xylocopina*.

Subgenus *Spinosennertia* Fain, 1981 (Type species: *Sennertia argentina* Vitzthum, 1941) Identification: posterio-proximal and posterio-distal lobes of the caruncle of tarsi I–III present, both transparent. Setae *si* distinctly longer than *se*.

Distribution: Neotropical.

Hosts: *Xylocopa* (*Neoxylocopa*).

Subgenus *Afrosennertia* Fain, 1981 (Type species: *Sennertia monicae* Fain, 1971)

Identification: hysterosomal shield short, about 1/3 of idiosoma; setae d_1 situated on soft cuticle.

Distribution: Afrotropical, Australian.

Hosts: *Xylocopa* (*Mesotrichia*), *X.* (*Koptortosoma*).

Subgenus *Asiosennertia* Fain, 1981 (Type species: *Sennertia "(Afrosennertia)" delfinadoae* Fain, 1981)

Identification: setae c_1 situated outside hysterosomal shield *and si* microsetae. We were unable to find any reliable apomorphy of this subgenus. Based on the reduction of anterior apodemes IV and the reduction of the hysterosoma shield, it should be included within *Afrosennertia*.

Distribution: Oriental, SE Palaearctic (Japan), Afrotropical.

Hosts: *Xylocopa* (*Biluna*), *Xylocopa* (*Xylomelissa* including *Perixylocopa*)

Subgenus *Eosennertia* Kurosa, 2003 (Type species: *Sennertia* (*Eosennertia*) *bifida* Kurosa, 2003)

Identification: *hT* I–II, *wF* IV absent. Originally defined by autapomorphies. Shared apomorphic characters suggest that it is related to other Old World *Ceratina*-associated *Sennertia* (*e.g.*, *S. indica*) traditionally grouped in *Sennertia* s. str.

Distribution: Japan.

Hosts: *Ceratina* spp.

Subgenus *Sennertia* Oudemans, 1905 (Type species: *Pediculus cerambycinus* Scopoli, 1763)

Identification: setae c_1 situated on hysterosomal shield *and* c_1 microsetae; probably a paraphyletic assemblage. Includes the following three previously recognized and three new species groups:

1. *horrida*-group *s. str.* (we include here *S. horrida, S. madagascarensis*, several undescribed species, and, probably, *S. potanini*)

   Identification: Setae *si* of medium length (40–100 μm) *and* ventral tarsal seta IV long *and* setae c_1 situated on hysterosomal shield *and* c_1 microsetae. Setae *si* on the same level or slightly anterior or posterior *se*.

   Distribution: Oriental region and Madagascar

   Hosts: *Xylocopa* subgenera *Nyctomelitta*, *Prosopoxylocopa*, *Zonohirsuta*, *Biluna*, *Nodula*, and ?*Koptortosoma*.

2. *japonica*-group

   Identification: Setae *si* microsetae *and* ventral tarsal seta IV long *and* setae c_1 situated on hysterosomal shield *and* c_1 microsetae. The monophyly of this group should be verified.

   Distribution: Oriental, Afrotropical, S Palaearctic.

   Hosts: *Xylocopa* subgenera *Alloxylocopa*, *Koptortosoma*, *Mesotrichia*, and *Rhysoxylocopa*.

3. *cerambycina*-group

   Identification: Setae *si* microsetae *and* ventral tarsal seta IV short *and* setae c_1 situated on hysterosomal shield *and* c_1 microsetae. The monophyly of this group should be verified, with respect to the *Ceratina*-associated lineage.

   Distribution: Palaearctic, Afrotropical, Oriental, Australian

   Hosts: *Xylocopa* and *Ceratina*.

4. *devincta*-group

   Identification: Setae c_1 long, nearly as long as *se*. Setae *si* nearly as long as *se*. Hysterosomal shield not triangle. Opisthosomal gland openings on hysterosomal shield. Tarsal ventral setae *w* IV long, distinctly longer than leg IV. Posterior apodeme IV present. Setae *1a*, *3a*, and *4b* conoidal; *c3*, *4a*, and *g* inflated at bases. Setae *wa* I–II bifid. It is probably a sister group to *Amsennertia*.

   Distribution: Neotropical.

   Hosts: Two species (*Sennertia devincta* and *S. sayutara*) are phoretic in the metasomal acarinaria of *Ceratina* (*Zadontomerus*).

5. *surinamensis*-group (new)

   Identification: Setae *si* of medium length, nearly as long as *se and* ventral tarsal seta IV short *and* setae c_1 situated on hysterosomal shield *and* c_1 microsetae.

   Distribution: Neotropical.

   Hosts: *Ceratina*.

6. *zhelochovtsevi*-group (new)

Identification: Setae c_1 and *se* are long *and* hysterosomal shield triangle.

Distribution: Palaearctic: Mediterranean and Middle Asia.

Hosts: *Xylocopa* (*Proxylocopa*)

Character incongruence and its possible causes

Most of the above groups have clear morphological boundaries, and distinct host and geographical ranges, suggesting their potential monophyly. Exceptions include *Asiosennertia*/*Afrosennertia*, *Eosennertia*/*cerambycina*-group associated with *Ceratina* if one considers any member of these pairs alone. The *cerambycina*-group itself is extremely heterogeneous and probably paraphyletic with respect to most of the other groups.

In contrast to *Chaetodactylus*, where numerous and probably recent transcontinental dispersals have apparently occurred, none of the above lineages of *Sennertia* displays any apparent connection between the Old and New Worlds. The hosts of *Sennertia*, bees of the genera *Xylocopa* and *Ceratina*, are mainly tropical and subtropical and probably had limited opportunities to disperse over land bridges and island chains. Leys *et al.* (2002) demonstrated that such dispersal was rare and occurred in the early history of the genus *Xylocopa*. The ancestor of the North American species of *X.* (*Xylocopoides*) probably dispersed across land bridges in the North Atlantic or the Bering Strait as long as 34 Mya or later. This host subgenus does not have any mites shared among its Old World sister-taxa or two early derivative lineages, *Copoxyla* and *Lestis*. Instead, its mites apparently belong to *Amsennertia*, the lineage associated with the so-called American clade of *Xylocopa*. This clade is related to the East Palaearctic *Proxylocopa* and Oriental *Nyctomelitta*, suggesting that its common ancestor dispersed into America from Eurasia, probably across the Bering Strait, approximately at the same time with *Xylocopoides* (Leys *et al.*, 2002). The above relationships of the New and the Old World host lineages have some degree of congruence with the comparative morphology of their mites: *Amsennertia* associated with the American clade and *Xylocopoides*, *Spinosennertia* associated with Neotropical *Neoxylocopa*, the *zhelochovtsevi*-group associated with *Proxylocopa*, and the *horrida*-group associated with *Nyctomelitta* and other related subgenera. All these three groups have long setae *si* (also in the *surinamensis*-group from New World); *Amsennertia* and the *zhelochovtsevi*-group share long setae c_1 and setae d_1 and e_1 longer than h_1 (some species in *Amsennertia*); *Spinosennertia* and the *zhelochovtsevi*-group share the shape of the hysterosomal shield; and finally the two Neotropical species of the *devincta* group have extremely long tarsal setae *w* IV, similar to the *horrida*-group.

The role of the dual hosts and the relationships of the *Ceratina* and *Xylocopa* associated lineages in this system are unclear. The *Amsennertia*, *horrida*, and *zhelochovtsevi*-groups occur exclusively on *Xylocopa*; the *devincta* and *surinamensis*-groups and a lineage in the *cerambycina*-group (including *Eosennertia*) are associated only with *Ceratina*. The elongation of the body and the tarsi I–III, as well as the short posterior edge of hysterosoma not protruding past legs IV indicate possible links between the two *Ceratina*-associated lineages (except for the *devincta*-group). However, these character states may have evolved convergently in response to the small size and the general absence of vestiture in *Ceratina*, and the different lengths of setae *si* contradicts a possible sister-group relationship of the Old and New World *Ceratina*-associated lineages. In addition, these characters occur in some *Xylocopa*-associated lineages. Although the nest biology of recent species of *Xylocopa* and *Ceratina* gives little opportunity for host switching, frequent cross-generic host shifts in the early evolution of *Sennertia* and its hosts, *Xylocopa* and *Ceratina*, seem to be a reasonable explanation for these phenomena. Mites phoretic on these two bee genera undergo at least two different types of selective pressures shaping their structural adaptations: phoresy on small and smooth *Ceratina* requires greater development of the attachment organ, while phoresy on *Xylocopa* requires development of claws as the primary means of attachment to the dense pubescence of their hosts. Phoresy inside isolated "pouches", such as acarinaria, is another factor that could drastically affect the morphology of mites. Unfortunately any definitive conclusions about the groundplan of such mites cannot be drawn so far. We suspect that the reduction of the hysterosomal shield and the development of inflated ventral setae may be one of the attributes of such mites. The former is typical of common evolutionary trend in derived chaetodactylids, the progressive reduction of idiosomal sclerotization. If the hysterosomal shield is fully developed, as in *Centriacarus* and *Roubikia*, it serves for insertion of the musculature of the attachment organ (p. 21) (posterio-central part) and the ventro-dorsal musculature (p. 16) (lateral parts). The former operates the attachment organ, and the latter creates hydraulic pressure, a very important component in mite locomotion. Mites lack protractor muscles, and protraction/extension of various appendages, including locomotory ones, is accomplished solely by hydraulic pressure. In some *Sennertia* and *Chaetodactylus*, the hysterosomal shield is reduced and the ventro-dorsal muscles insert on the soft cuticle lateral to the shield. As the two types of muscles are essentially antagonistic, their partial structural separation probably ensures their relative independence and the possibility to operate simultaneously.

Different selective constraints imposed by structural differences of the hosts, probable multiple reciprocal cross-generic host shifts, and heterogeneous ontogeny facilitating the existence of multiple character states in different ontogenetic instars (p. 53) might create substantial plasticity in the phenotypic expression of morphological features and correlated multiple changes in associated mites, and, as a result, favor homoplasies. Even the few examples above are sufficient to show a great amount of morphological disparity among *Sennertia* species. Based on different character sets, the four New World groups may either have a common ancestor with the two Old World groups, or either of them has a common ancestor with an Old World clade: (*Amsennertia*, *zhelochovtsevi*-group), (*Spi-*

nosennertia, *zhelochovtsevi*-group), (*surinamensis*-group, *horrida*-group), and (*devincta*-group, *horrida*-group). The relationships among the *Ceratina*-associated lineages are even more mysterious, with some characters showing similarity to each other or to different lineages associated with *Xylocopa*.

Irrespective of the true relationships between the New and Old world clades and the role of *Ceratina* in the system, the hypothesis about long-term isolation of their xylocopine hosts (Leys *et al*., 2004) and, therefore, the absence of recent mite exchange across the continents, seems likely.

The outgroup

The two close outgroups of *Sennertia*, *Chaetodactylus* and *Achaetodactylus*, were identified by our previous analyses of genus level-relationships (p. 76). There is variation in the length of the dorsal setae in *A. decellei* and *Ch. ludwigi*; they are longer, and in *A. leleupi*, *A. ceratinae*, and *Ch. melitomae* they are much reduced, represented by microsetae. This variation may create ambiguity in determining the direction of the character state transformation, since a majority of characters used in defining species groups in *Sennertia* pertain to the relative length of dorsal idiosomal setae. In *Roubikia*, a more distant outgroup, dorsal idiosomal setae are relatively long, suggesting that this may be the ancestral state for *Achaetodactylus*, *Chaetodactylus*, and *Sennertia*. It is interesting that an apparent trend in having non-uniform setae of the posterior idiosoma in *Centriacarus*, *Roubikia*, and *Achaetodactylus decellei* persists in the *zhelochovtsevi*-group and some species of *Amsennertia*. In these supposedly early derivative taxa setae h_1 are always substantially shorter than d_1.

Possible phylogenetic relationships

We coded the 14 characters discussed above for 16 taxa representing all lineages in the genus; one invariant character was added to support the ingroup monophyly. Except for the relationships of *Asiosennertia* and *Afrosennertia*, general parsimony analyses resulted in a large polytomy, influenced by a large number of homoplastic characters. To extract a possible phylogenetic signal from the data, implied character weighting was applied to the same data matrix. The resultant cladograms (Fig. 44) confirm our empirical assessments that the New World lineages have sister group relationships with early derivative Old World lineages. On the consensus cladogram, SW Palaearctic *S. zhelochovtsevi*, Neotropical *S. ignota* and a clade including other New and Old World taxa form basal a trichotomy. The derived Old World taxa form a monophyletic group, while the New World taxa represent a paraphyletic assemblage. This may be true with respect to the *surinamensis*-group and *Spinosennertia*, but this is probably not true for *Xylocopa*-associated members of *Amsennertia*, which appear paraphyletic on the cladogram. The *horrida* group is a sister group to the remaining derived Old World lineages, which include four taxa with unresolved relationships: *cerambycina* (*s. str*.), *Eosennertia* (*s. lat*.), *japonica*-group, and *Afrosennertia* (*s. lat*.). As in the maximum parsimony analysis with equal weight, *Asiosennertia* is sister to *Afrosennertia*, and probably the two should be consid-

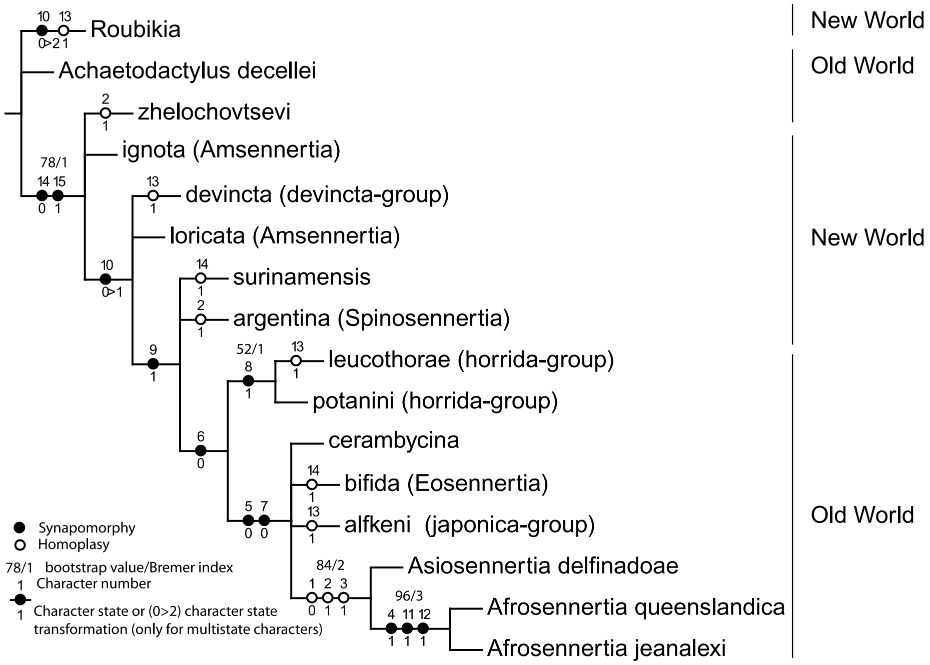

Fig. 44. Consensus tree of 17 most parsimonious cladograms of phylogenetic relationships in *Sennertia* obtained under implied weighting (Goloboff fit = −12.56, CI = 0.516, RI = 0.700, HI = 0.484). Datamatrix includes 15 characters, 2 outgroup and 13 ingroup taxa (Appendix 4). The topology should not be considered as the real phylogeny of the group.

ered as a single group. The position of this group is questionable because, based on the reduction of the hysterosomal shield, it may be a sister taxon to New World *Spinosennertia*. The occurrence of *Asiosennertia* on such early derivative *Xylocopa* as *Biluna* and "*Perixylocopa*" (*Xylomelissa*) may also indicate the antiquity of this lineage. It is interesting that either or both of the host subgenera are rendered as early derivative sister-groups to the remaining *Xylocopa* in the analyses of Leys *et al*. (2002). If recent host-associations of these subgenera are as old as the host divergence, the phylogenetic positions of *Biluna* and *Xylomelissa* should be reevaluated. Judging from the mite fauna, they evolved after the origin the American clade of *Xylocopa*.

CRYPTIC SPECIES

Ninety out of 112 chaetodactylids are described only from heteromorphic deutonymphs, the single instar phoretic on adult bees that can be easily collected. This instar facultatively appears in the middle of the life cycle and is adapted exclusively for phoresy on its host. The adult males and females usually live in the bee nests and are recovered only occasionally. Adults are described for 21 species of chaetodactylids, and 18 of them are correlated with corresponding deutonymphs. Despite the great importance for species definitions and phylogenetic reconstructions, the relationship between the adult and deutonymphal morphologies still remains unclear. Because of the heterogeneity of the habitats and life history strategies, one may assume that deutonymphal and non-deutonymphal instars experience two different vectors of natural selection, therefore many aspects of their morphologies may be independent from one another. If this is true, deutonymphs of different species may exhibit no obvious differences in contrast to the adults, or vise versa. In reality, neither the two vectors of selection, nor the deutonymphs and feeding instars, are independent from each other. Indeed, bee hosts and their nest environment are strictly interlinked, and a failure of one component will result in the failure of the other. Thus, the two selective vectors affecting chaetodactylid evolution should be considered as a single ordered sequence rather than two independent factors. We showed above (p. 56) that in the course of evolution, deutonymphs and feeding instars of chaetodactylids undergo correlated structural reductions, for example in the leg setation. Deutonymphs, however, may have some unique reductions or additions, which are phylogenetic constraints rather than evidence for their "independence" from the feeding instars. Finally, the presence of characters in two or more different states throughout chaetodactylid ontogeny (Table 5) is better explained by a reticulate rather than hierarchical pattern, meaning that the adult and deutonymphal morphologies can 'influence' each other. Because there are not two independent 'evolutions' for deutonymphal and non-deutonymphal instars in astigmatid mites, morphological differences in adults, to some extent, should be accompanied by differences in heteromorphic deutonymphs and vice versa. Unfortunately, this 'extent' is not always qualitative but may be quantitative and, in some cases, it approaches zero.

To avoid excessive interspecific mating, adults of many mite species develop mechanisms of effective prezygotic isolation, namely different shapes of the aedeagus in males and the spermatheca and copulatory canal in females. Given that deutonymphs do not face this challenge, one could expect a lower amount of interspecific morphological variation among them. Thus, the validity of species boundaries established on only qualitative characters from deutonymphs of Chaetodactylidae might be questioned. The presence of cryptic species has been documented in astigmatid mites, including chaetodactylids, using different approaches or their combinations: hybridization experiments, gene sequencing, and multivariate morphometrics (Klimov *et al*., 2004; Klimov & OConnor, 2004). The latter technique seems redundant if mite cultures or material properly preserved for DNA sequencing are available. However, it is not always the case, especially for chaetodactylids, the majority of which were collected from old museum bee specimens and mounted in a DNA degrading medium. In such situations, multivariate analyses are a powerful tool capable of finding discontinuities in 'hidden' dimensions of character space, irrespective of whether they are continuous measurements of qualitative characters. The resulting models could be verified by other methods. The primary advantage of multivariate techniques is their ability to accommodate multiple variables in an attempt to understand the complex relationships not possible with univariate and bivariate methods. Multivariate techniques analyzing differences in predefined groups, for example canonical variates analysis (CVA) and binomial logistic regression (LR)[6], create a model explaining variation in the predefined groups, and the predictive power of this model can be assessed using a set of statistical estimators as well as external data. Some types of multivariate analyses do not require an *a priori* group definition and may be used as exploratory techniques to aid in the explanation of variance in terms of a small set of factors that can account for all the common and unique variance in a large set of variables and assist in variable selection (Principal Component Analysis, PCA). At this point, multivariate morphometrics is an indispensable complement to traditional morphological comparisons and uni- and bivariate data. Because of the importance of these techniques for determining species boundaries in chaetodactylid deutonymphs, we will here briefly discuss their potential advantages and pitfalls along with some relevant aspects of data acquisition.

Geometric Versus Traditional Morphometrics

Two- and tree-dimensional coordinates of landmark points are the usual data choice for geometric morphometrics, while traditional morphometrics relies on the study of interpoint distances. Profound disagreements exist over the two approaches (*e.g.*, Lela, 1991; Bookstein, 1991). Coordinate-based methods focus on shape differences rather than shape itself. Traditional

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[6] We discuss only binomial LR because some researchers believe that CVA should be used in place of multinomial LR.

morphometrics may also consider shape as an intrinsic property of an organism (Jungers *et al*., 1995).

For a comparative analysis of chaetodactylids, we prefer interpoint over other data types for the following reasons. (i) In chaetodactylids, most of the informative variation for species delineation is localized in the length differences of the body and leg setae. Because a seta has only one fixed point on the cuticle, and the orientation of the free end often varies randomly, selection of simple measurements is a natural choice for such objects. Standardizing coordinates for the free end of a seta is a challenging task for geometric morphometrics, and as far as we know, it is not programmatically implemented. (ii) It is almost impossible to control for all factors that may affect uniform mounting of specimens on slides, and therefore uniform landmark preservation. Some of these factors include initial specimen fixation, temperature, humidity, and differential pressure. Low pressure usually results in legs being flexed to the midline of the body making it impossible to acquire accurate measurements for many leg setae. Excessively high pressure will crush the mite and deform its structures. As indicated below, comparison of mites mounted with different methods may generate substantial artificial differences in the shape and length of three-dimensional structures (*e.g.*, length of body parts). Two-dimensional structures, such as setae, are usually less prone to such mounting-specific artifacts and, therefore, an analysis of such data will be less biased. (iii) Some techniques of geometric morphometrics require homologous points, and in some cases their selection may be extremely difficult. (iv) Data acquisition in geometric morphometrics requires taking a digital picture of a specimen with subsequent computer-assisted plotting of the landmarks. Although it may be viewed as a more objective technique, its application to small organisms such as chaetodactylid mites will create substantial measurement artifacts. Due to low resolution of pictures/monitors, the end points of some very thin and transparent setae will be inevitably difficult to determine. Moreover, sometimes it is difficult to determine 3D orientation of a structure on a 2D picture, and therefore to estimate errors associated with the different orientation of objects in the z-axis. Data for traditional morphometrics may be acquired directly from the microscope, and its setting may be directly adjusted to ensure proper contrast for thin and transparent objects. The ability to use direct measurements is particularly useful if unknown specimens are classified based on an already developed model, as it does not require taking a digital picture and the use of special software. (v) Results of a traditional morphometric analysis may be directly incorporated to a morphological description or a key and are easily interpretable.

Sampling

All multivariate techniques require data collection in which every individual in the population has an equal chance of being selected, and significance tests generated by statistical packages are based on the assumption of simple random sampling. The infestation rate of nest cells is usually very low, and chaetodactylids phoretic on a single bee specimen or multiple bee specimens originating from the same nest are most likely the offspring of a small number of related females. Because of this intrinsic dependency, morphometric properties of even a large sample from a few hosts may not be identical to or even closely approach those of the general population. Conclusions drawn from an analysis of such data run the risk of biased estimates as the assumption of random sampling is violated. In practice, available material is often limited to several dozen, rarely over a hundred host specimens. On the other hand, data acquisition from extensive material may be extremely time-consuming, especially if many variables are measured, and therefore not practically justified. An analysis of mites originating from different geographic localities often alleviates the problem or, at least, it can demonstrate the presence of a strong bias due to non-random sampling. Results obtained from potentially non-random data sets should be evaluated using external validation, rather than using standard statistical estimators.

Missing Data

In mounted chaetodactylid mites some structures may be broken or deformed, not allowing accurate measurements. If a number of variables are measured, such specimens may be common, and their exclusion from the analysis is impractical. The easiest solution is to delete variables with a high percentage of missing values and input the remaining missing data. There are many approaches dealing with imputation of missing data, and it is beyond the scope of this work to give a complete review of them. The use of mean values or values predicted by a linear regression is the most commonly used approach. Missing data raise the issue of the generalization of the results. If missing data occur in material mounted using a uniform technique, then they are probably randomly scattered throughout the observations. If missing data do not occur randomly, for example, when old or excessively compressed slides and freshly mounted material, or material originating from alcohol preserved vs. dried samples are analyzed, some distinct patterns of missing data may emerge. Any statistical results based on these data would be biased to the extent that the variables included in the analysis are influenced by the missing data process. As in the previous example, it is highly recommended to validate the results from such analyses using external data sets.

Sources of Variation

Chaetodactylid populations typically vary geographically and from host to host across a species' range. These differences may arise as the result of chance occurrences (founder effect, genetic drift) or systematically, especially if the environment in various places/hosts exposes individuals to different optima for survival and reproduction. Spatial, temporal, and host-related barriers restricting gene flow were discussed in detail in the section on host specificity and possible isolation mechanisms (p. 70). Genetic and non-genetic components of morphological variation are both affected by these factors, and sometimes they are difficult or impossible to separate without elaborate rearing experiments and reciprocal transplants. Traditionally, variation in shape is attributed to the genetic component and variation in size to the non-genetic component. This is not always true. Morphometric analyses of deutonymphs of *Sancassania salasi* (Acaridae) obtained in the field and from laboratory cultures demonstrated substantial differences in shape among the two groups, however, these differences were much lower than interspecific differences of this and another sibling species (Klimov *et al*., 2004).

Data Transformation

The goal of many comparative studies is to assess similarity or dissimilarity among taxa after size, and, therefore, much of the non-genetic component of variation, is eliminated. In other words, if smaller individuals of one species are compared with larger individuals of another without adjusting for gross differences in scale, this analysis probably would not discover much beyond the obvious fact that one species is larger than the other. Fain & Pauly (2001) recognized "small" and "large" forms of phoretic deutonymphs of *Chaetodactylus ludwigi* that were believed to exhibit biological differences as well. If this distinction is real, the use of raw, size-related characters may be misleading in interspecific comparisons. There are 11 techniques for size-adjustment. Jungers *et al*. (1995) evaluated their performance on simulated data sets and concluded that only variables in the Mosimann family of shape ratios allow correct identification of different sized individuals of the same shape after accounting for overall size differences. Darroch and Mosimann shape variables may or may not be correlated with size (Jungers *et al*., 1995). In this study, we follow Darroch & Mosimann (1985) and explicitly define size as the geometric mean of all variables.

Darroch and Mosimann shape variables may be created in a form of Y/GM, where Y is a value of the variable, and GM is the geometric mean of all variables of the given specimen.

Principal components of raw data can be contrasted with the principal components of shape variables to determine the extent to which overall differences among individuals can be attributed to a combination of size and shape versus shape only (Darroch & Mosimann, 1985).

Darroch and Mosimann size-correction usually results in a better overall discrimination among groups since "noisy" variation unimportant for taxonomic comparison, may be eliminated. Sometimes analyses on raw data outperforms that of shape data in terms of classification accuracy, indicating that size may be a latent shape variable as well. Mosimann shape ratios, if log-transformed, sometimes cause some variables to fail the tolerance test in CVA. We are not aware of any work dealing with this problem.

Logarithmic transformation is recommended to achieve or approximate lognormality and homoscedasticity, but this cannot be guaranteed. Homoscedasticity is an assumption of CVA.

Data Reduction

If fewer original predictors were used in the classification rule without compromising classification accuracy, it would be less costly in obtaining data on the predictors for the purpose of classifying new specimens. In CVA, the following methods of variable selection can be used: stepwise elimination of variables based on the lowest potency index (Hair *et al*., 1998), stepwise CVA, and the best-subset analysis (Huberty, 1994). The former two methods are not guaranteed to arrive at the most optimal subset(s) of variables and should be used with caution. The best-subset method tests every combination of the variables and usually produces an array of equally best subsets of variables. Classification accuracy in either resubstitution, internal or external data sets is an explicit criterion for the variable selection. This method guarantees finding the 'best' subsets of variables and should be used in place of the two previous methods when the number of original variables allows the completion of the computations in a reasonable time (the analysis estimates $2^{\wedge n}$-1 combinations, where n = number of variables). Neither stepwise CVA nor best-subset analyses as implemented in standard statistical packages can be performed for size-corrected variables, as construction of a new shape matrix is required at each step of these analyses. We created a simple script that generates all combinations for a given number of variables and prints an *OMS* command file performing size-correction at each CVA/LR in the program SPSS 12. The script is freely available at: http://insects.ummz.lsa.umich.edu/ACARI/Tools/Best_Subset/Best_Subset_SPSS.htm.

Data reduction in PCA can be achieved by calculating scores for each underlying dimension and substituting them for the original variables. This procedure should be used with caution, because PC scores may not have any biological meaning, and principal components may be influenced by variation other than that which accounts for intergroup differences. If the number of variables is too large or there is a need to better represent a smaller number of groups as in comparative morphological analyses, PCA can assist in selecting a representative subset of variables.

Multivariate Classification Models

Multivariate models summarize all the variation of large data sets in the form of a concise formula that contains essential and comprehensive information about the groups and has predictive power. A canonical variates model can be represented as a latent variable that is created as a linear combination of independent variables,

$$CV = b1 * x1 + b2 * x2 + \cdots + bn * xn + c, \tag{1}$$

where the b's are coefficients, the x's are independent variables, and c is a constant.

If there are n groups, n − 1 CV's are calculated. For assignment purposes, the estimated posterior probability of group membership is calculated, or, when multivariate normality of the independent variables is assumed, the value of CV can be equivalently used. If CV of an unknown is less than the cutting score, then it is classified as taxon 0, if more, then as taxon 1.

The logistic regression (LR) model can be expressed as the following equation,

$$P(0) = \frac{\exp(b1 * x1 + b2 * x2 + \cdots + bn * xn + c)}{1 + \exp(b1 * x1 + b2 * x2 + \cdots + bn * xn + c)}, \quad (2)$$

where P(0) is the probability of an unknown specimen being taxon 0; other notations are the same as for CVA above. If P(0) exceeds 0.5 then the unknown belongs to taxon 0, otherwise to taxon 1.

Both (1) and (2) are metric latent variables and have coefficients, independent variables, and the constant in common, but the ways in which an unknown specimen is classified are rather different. CVA, in general, estimates posterior probabilities of group membership, while binomial LR scores can be compared directly with the cutting score.

A great advantage of LR over CVA is that it is a direct posterior probabilities estimator. It calculates the class posterior probabilities without ever estimating the classes' individual density functions, which requires additional data (group means, prior probabilities, and the value of mean square within groups). The cutting scores in CVA can only be used for classification purposes if the assumption about multivariate normality of the independent variables is met. This is rare in real data. In practice, calculations of posterior probabilities for a CVA model may be substituted by plotting canonical function values on a territorial map usually provided by major statistical packages. However, if there are more than three groups, the programs assume that canonical functions 3 and above are equal to zero. JavaScript implementations of both LR and CVA classification models for chaetodactylids and other mites are available at http://insects.ummz.lsa.umich.edu/beemites/Morphometrics.html. These models automatically classify unknown specimens once the required measurements are entered.

Principal Component Analysis

PCA is an interdependence technique of data reduction. It usually reduces original variables to fewer components by maximizing explanation of the entire data set. If there is no previous knowledge about the data, a frequent case in chaetodactylid morphometrics, PCA is a useful exploratory technique since it does not predict a dependent variable like CVA and LR. PCA, unlike factor analysis, considers the total variance and derives factors that contain small proportions of unique variance and error variance. However, the first few components do not contain enough unique or error variance to distort the overall factor structure (Hair *et al.*, 1998; Tabachnick & Fidell, 2001). If all variables are in the same metrics, PCA is conducted on the covariance matrix. If data of different types are analyzed, then the correlation matrix is used instead. In a morphometric study, an example of the latter is a combined analysis of measurements and counts. To avoid performing PCA on a correlation matrix and to ensure interpretability of results, ratios and angles should always be entered to the analysis as their original measurements. This applies to all multivariate analyses.

Canonical Variates Analysis

CVA predicts group membership by analyzing the relationships between a single nonmetric (categorical) dependent variable and a set of metric independent variables. A canonical variates function is a latent variable that is created as a linear combination of discriminating (independent) variables, such as that represented above (1). Groups must be defined in advance before running a CVA, for example, based on *a priori* knowledge or results of PCA. There must be two or more specimens for each group of the dependent, and the maximum number of independents is the sample size minus two. However, it is recommended that there be at least four or five times as many individuals as independent variables.

A Wilks' lambda test is used to test if the canonical variates function as a whole is significant. Standardized canonical coefficients or loadings that show the correlations of each variable with each discriminant function are used to compare the relative importance of the independent variables. In relation to variable selection, loadings are used for calculation of the potency index (see this and other methods of variable selection above).

The classification table is a pivotal part of CVA, showing the percentage of specimens correctly classified (hit ratio) by the analysis. The hit ratio and Jackknife resubstitution (cross-validation) may be used for assessing the predictive power of a CVA model in the case of a limited number of specimens. Usually these estimators are positively biased and should be used with caution. External validation provides less biased assessment of classification accuracy. The sample is randomly split into two subsamples: a training sample, and a test or holdout sample. A classification rule is determined using the training sample data and then applied to the holdout data. Variable selection (see above) may be conducted if there is a concern about the cost of obtaining measurements for the holdout subset. The resulting classification model may be evaluated with a smaller holdout data set containing newly collected specimens.

Classification accuracy may also be biased if group sizes are grossly unequal. Proportional chance criterion, maximum chance criterion, and Press' *Q* statistics are used to test if it substantially exceeds the classification accuracy expected by chance (Hair *et al.*, 1998; Huberty, 1994; Tabachnick & Fidell, 2001).

Logistic Regression

Logistic regression (LR) is used in place of two-group CVA because it usually involves fewer violations of assumptions, is robust, has coefficients that are easier to interpret, and can accommodate both metric and non-metric independent variables. Logistic regression is preferred when data are heteroscedastic, not normal in distribution, or group sizes are very unequal (Hair *et al.*, 1998). LR, unlike CVA, is a direct posterior probabilities estimator. It calculates the class posterior probabilities without estimating the classes' individual density functions. Although the analysis overcomes several violated assumptions of CVA, some other assumptions still apply, for example, no multicollinearity and large samples.

The success of an LR analysis can be assessed by a classification table showing correct and incorrect classifications. Model chi-square (likelihood ratio test) provides a significance test for a logistic model. The Wald statistic tests the significance of individual independent variables and may justify exclusion of insignificant variables from the model. If the log-likelihood test statistic is significant and the Wald statistic is insignificant, the latter should be ignored as it is biased toward Type II errors.

Logit coefficients correspond to b coefficients in the prediction equation (2) above. Many statistical packages also provide an odds ratio, which is the natural logarithm to the b power. If the logit is b = 2.303, then its log odds ratio is 10, meaning that when the independent variable increases one unit, the odds that the dependent (for example, taxon) equals 1 increase by a factor of 10 when other variables are controlled (Menard, 2001).

Like CVA, an LR classification model can be overfitted, and it is recommended to evaluate the results by employing external validation.

Multivariate Discrimination of *Chaetodactylus* associated with *Lithurgus* in North America

The presence of three cryptic species was demonstrated by PCA and CVA using 27 morphometric variables measured from 111 specimens (Klimov & OConnor, 2004).

Among them, *Chaetodactylus gibbosi* (Florida) is geographically isolated from *Ch. lithurgi* distributed in Texas, New Mexico, Arizona, Colorado, and Idaho. Sympatric *Ch. lithurgi* and *Ch. abditus* (USA: Arizona, Mexico: Socorro Is.) are seasonally isolated in Arizona. *Chaetodactylus gibbosi* is associated with a single bee species, *Lithurgus gibbosus* Smith in Florida. The host range of *Ch. lithurgi* includes several species flying predominantly in the spring: *L. apicalis*, *L. littoralis*, and western *L. gibbosus*. *Chaetodactylus abditus* is associated with *L. planifrons* and *L. echinocacti*, flying predominantly in the fall in Arizona.

Both shape and size-and-shape variables were analyzed. However, only the latter were used to build a classification model. A six-variable model developed by the best subset CVA and estimated by jackknife resampling and external validation (n = 100) is capable of classifying the three species with 100% accuracy. Later, a 3 bp difference was found in 28S rDNA of *Chaetodactylus abditus* and *Ch. lithurgi* confirming their genetic isolation.

The two canonical functions are as follows (all raw variables (μm) must be converted to natural logarithms):

$$\mathrm{CV1} = 12.511 + 6.371 * d_1 + 1.099 * vF\,\mathrm{II} + 5.488 * hT\,\mathrm{II} + 2.338 * c_1 - 4.973 * h_2 - 9.365 * \text{hysterosomal shield, width at } f_2 \text{ level}$$

$$\mathrm{CV2} = 6.259 + 2.205 * d_1 - 6.686 * vF\,\mathrm{II} - 2.539 * hT\,\mathrm{II} + 5.609 * c_1 + 3.241 * h_2 - 1.294 * \text{hysterosomal shield, width at } f_2 \text{ level}$$

Identification of unknown specimens based on these functions can be performed online at: http://insects.ummz.lsa.umich.edu/beemites/Morphometrics/Chaetodactylus_Lithurgus.htm

Multivariate Discrimination of *Chaetodactylus* Associated with *Osmia*, Subgenus *Cephalosmia*

Canonical variates analysis of 100 morphometric variables demonstrated the existence of three morphs associated with bees of the genus *Osmia*, subgenus *Cephalosmia*. *Chaetodactylus micheneri* sp. n. form 1 (western United States and southwestern Canada) and form 3 (USA: Michigan, subarctic Canada) are associated with *Osmia subaustralis*, while form 2 is associated primarily with *Osmia californica*, *O. marginipennis*, *O. montana*, and *O. grinnelli* in the western United States. We refrain from calling these groups species as their distinctiveness is not yet demonstrated by independent data (*e.g.*, gene sequences). The morphs could be identified using a preliminary CVA model built from a subset of 11 shape variables and 71 specimens with overall error rates of 3.8% (external validation, n = 156), 1.4% (jackknife sampling), and 0.0% (internal validation). Computer identification based on this model is available at http://insects.ummz.lsa.umich.edu/beemites/Morphometrics/Chaetodactylus_Cephalosmia.htm.

Morphometric Analysis of the *Sennertia frontalis*-group Complex

Mites of this complex are the most abundant *Sennertia* on large *Xylocopa* ranging from southern continental North America through South America, as well in the Caribbean and Hawaiian islands. An analysis of the *frontalis* complex is essential for proper identification of specimens from the southern United States and Mexico relevant to this study. Up to now, three species belonging to this complex were described: *Sennertia frontalis* (on *Xylocopa frontalis*, Argentina), *S. augustii* (on *Xylocopa augusti*, Argentina), and *S. shimanukii* (on *Apis mellifera*, Guatemala) (Alzuet & Abrahamovich, 1990; Baker & Delfinado-Baker, 1987; Vitzthum, 1941). Although the authors of the latter two species differentiated their taxa from *S. frontalis*, the oldest described species in the group, our investigation of type material of *S. shimanukii* and topotypical material from the typical hosts of *S. frontalis* and *S. augustii* revealed that the original diagnostic characters or measurements are inaccurate or largely overlap those of *S. frontalis*.

Initial investigation of data, variable selection

For initial investigation, we measured 94 morphometric variables of 31 specimens, including the abovementioned three groups, US samples, as well as a sample from *X. nautlana* with long setae *w* IV (Table 14, Appendix 5). Sixteen variables with missing values in more than five specimens were excluded. For the remaining 78 variables, four PCAs were conducted on raw, log-transformed (base e), and normal (DM) and log-transformed Darroch and Mosimann (log-DM) variables.

PCA on raw and DM data resulted in separation of *S. augustii* versus all other groups, largely on PC2. PCA on log-transformed data identified three groups: (*S. shimanukii*+US samples), (specimens *ex X. nautlana* + *S. frontalis*), and *S. augustii* with one specimen misidentified. For log-raw data, separation occurred on PC2 for the former two groups and on PC1 for the latter, while log-DM transformation provided generally better resolution, largely on PC1, for all the groups.

Compared to the size-and-shape analyses, the total variance reduced from 99.9% and 44.1%, for the raw and log-transformed shape data, respectively. The decrease represents an isometric vector that was explicitly removed by the size-correction procedure. Because the shape data provided a better overall group separation, they were chosen for further analyses.

Sixteen variables with high (≥0.6) loadings on PC1-2 of either shape or log-shape analyses were selected (Table 14, Appendix 5) and another PCA was conducted. It resulted in nearly the same pattern of variation (the separation was generally worse in respect to *S. augustii*), indicating that these 16 variables may represent all the complexity of our dataset and deserve further consideration.

Measurements from 106 additional specimens were converted to DM and log-DM shape variables and subjected to the best-subset analysis (Table 15). The analyses found one optimal and one suboptimal subset of variables. The log-shape data provided generally better discrimination; the optimal 11 variable subset and suboptimal 6-variable subset were capable of classifying the three groups with 93.4 and 92.0% accuracy, respectively. The shape analysis yielded a single optimal subset of 9 variables with a 92.7% hit rate (Table 15, Appendix 5). Three variables (hysterosomal shield, anterior width; hysterosomal shield, width at f_2 level; and *d* I) were absent from any of the above subsets, indicating that they may be dropped from the model without loss of classification accuracy.

Data for all measured specimens are given in the Systematic part (*Sennertia shimanukii* and *S. frontalis*) and Appendix 1 (p. 165) (*Sennertia augustii*).

Evaluation of the classification models

Despite the high hit rate estimated by internal validation and jackknife resubstitution, the predictive power of the subsets obtained by the best-subset analyses may be positively biased. Some of the important sources of potential bias were discussed above: non-random sampling resulting from the dependency of mites originating from a single host; the sampling may not adequately reflect the complexity of the problem; and overfitting. The best-subset analysis (and any method of variable selection) may even exaggerate these problems by maximizing the sampling bias. In order to estimate the predictive power of the above models, the optimal and suboptimal subsets were evaluated using 90 specimens originating from hosts not sampled for either 78- or 16-variable analyses (Table 14, Appendix 5).

The classification accuracy for the 6-, 9- and 11-variable models applied to the external data was 74.4, 68.9, and 58.9%. The dramatic decrease of the hit ratio compared to the values of internal validations and jackknife resubstitution suggests that these models cannot be used confidently for classification purposes, and, therefore, original ‘diagnostic’ characters of all species are invalid. Judging from the consecutive increase of the misclassification rate, overfitting is probably the major factor influenced by the low predictive power of the models. However, this pattern may appear by chance alone.

Another best-subset analysis on 13 variables comprising the 6-, 9- and 11-variable data sets also produced 4–9 variable models with acceptable external classification accuracy (80–84%). However, revalidation of these models on a small set (n = 15) representing the three groups indicated that their predictive power is also much lower than estimated. This may be caused by insufficient sampling, the complexity of the data, or incorrect original group assignment. Since the highest misclassification rate was among *Sennertia shimanukii* and *S. augustii*, which both have long dorsal idiosomal setae, dropping of *S. augustii* from the model will potentially reduce the complexity in the data. The two group data set allows conducting of both binomial logistic regression and canonical variates analyses. Below we describe an experimental 3-group model, as well as 2-groups models obtained by both CVA and LR.

Three-group model

Since best-subset analyses conducted on 13 shape and log-shape variables produced models that are substantially biased toward our sample, we report here a descriptive CVA. Inclusion of more samples in the future will potentially give more conclusive results that reflect the complexity of variation in the *frontalis* group.

CVA on the 13-variable subset produced two significant ($p < 0.001$) functions. The first function (CV1) accounts for 74.7% percent of the variance explained by the two functions. The total amount of variance explained by CV1 is 85.7%. CV2 explains 52.1% of the remaining variance (14.3%). Therefore, the total variance explained by both functions is 93.2% of the total variation in the dependent variable. Box’s M test showed that the assumption of CVA about equality of covariance matrices is not met ($p < 0.001$). However, some researchers believe that CVA is robust enough even if this assumption is violated (Hair *et al*., 1998). All 13 variables passed the tolerance test. The unstandardized discriminant coefficients that may be used to calculate discriminant scores for purposes of classifying unknown specimens are given in Table 17. As noted above, this can only be done if the assumption of multivariate normality is met. Discriminant loadings ordered from highest to lowest by the absolute size of loadings are also reported in Table 17. Values of the loadings indicate that their respective variables substantially contribute to the group discrimination, except for the variables *vF* IV, *ra* II, and hysterosomal shield length, where the loading was low. CV1 is a clear contrast of the variables σ I and gnathosomal solenidion versus mostly other leg setae. CV2 is a contrast of the variables pertaining to dorsal idiosomal setae (e_2 and d_2) versus measurements of some body parts (Table 17).

CV1 primarily serves for classification of *S. shimanukii* versus *S. frontalis*, while CV2 separates *S. augustii* from the two above groups (Fig. 45). The performance of the classification model is given in Table 18. A high misclassification rate in the holdout sample (n = 90) indicates that the model is positively biased, especially for *S. shimanukii*.

Press' *Q* statistic for the analysis and holdout samples are 228.1 and 36. 5, respectively. Because the critical value at the 0.01 significance level is 6.63, the discriminant analysis can confidently be described as predicting group membership better than chance.

The maximum chance criterion (48.0%) outperforms the proportional chance criterion (37.0%). If we establish the threshold as 25% greater than the maximum chance criterion value, the hit ratio must exceed 60.0% (48.0 ∗ 1.25). The classification accuracy of both 94.2% (analysis sample) and 91.2% (jackknife resubstitution) both substantially exceed this criterion, however the 63.3% hit rate of the holdout sample is only marginally greater than this value. The threshold value is substantially less than any hit ratio of the three groups in internal analysis and cross-validation (Table 18), indicating a good performance of the classification rule in explaining the observed cases. In external validation, the classification accuracy of putative *Sennertia frontalis* and *S. augustii* also exceeds the threshold value, while for *S. shimanukii* it is substantially lower (42 versus 60.0%) (Table 18). Thus, our model has an adequate level of accuracy for *Sennertia frontalis* and *S. augustii* only; it should not be used for classification of *S. shimanukii*.

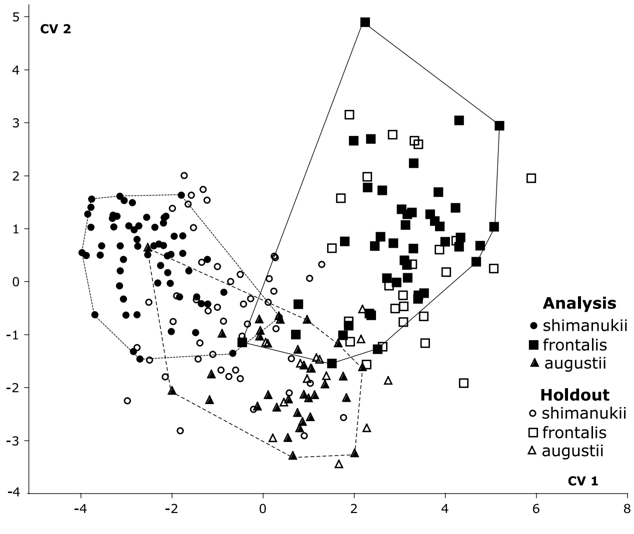

Fig. 45. 13-variable canonical variates analysis: Combined-group plot.

In conclusion, the maximum classification accuracy that can be achieved by our morphometric data is about 80%. Several subsets selected by the best subset analysis of shape data, *e.g.*, v02 v03 v04 v05 v06 v07 v10 v11 v13, v03 v04 v05 v06 v07 v10 v11 v13, and v02 v03 v05 v07 v10 v12 (variable numbered as arranged in Table 14 for 13-variable analysis), gave a hit ratio of 80% or more when applied to the small (n = 15) holdout dataset.

Two-group models

LR and CVA best subset analyses were conducted on the shape and log-shape matrices (Table 16). All four analyses selected 4- and 3-variable models (Table 16) on the basis of their overall performance when applied to external data. The 4-variable model has the following variables: hysterosomal shield length, gnathosomal solenidion, c_3, and d_2. The 3-variable model has all these variables but the first, and it has slightly lower (1.4%) hit ratio values for the log-transformed shape data. These values were the same (94.7%) for the shape data for both LR models. Below we present the 3-variable LR model obtained from the shape variables.

3-variable logistic regression model. The overall model test, -2 Log Likelihood, is highly significant ($p < 0.001$), rejecting the null hypothesis that none of the independent variables are linearly related to the log odds of the dependent variable being equal to 1 (*S. frontalis* = original groups 2, 5). A good assessment of model fit, the Hosmer-Lemeshow test, indicates by non-significant chi-square value (10.859, df = 8, $p = 0.210$) that there are no differences between the observed and predicted classifications. The estimated coefficients and the constant of the model were evaluated using the Wald statistic (Table 20). This shows that the logit coefficient for the variable c_3 is significant, while for the remaining variables and constant the coefficients are insignificant. However, the log-likelihood test evaluates the model as well-fitted ($p < 0.001$). For large logit coefficients, as in this case, standard error is inflated, lowering the Wald statistic and leading to Type II errors (Menard, 2001). Also, the Wald statistic is sensitive to violations of the large-sample assumption of logistic regression. The overall classification accuracy for the model is very high, 97.1% for the analysis and 94.7% for the holdout samples (Table 19, Fig. 46). One specimen of putative group 0 (*shimanukii*) (ex *X. varipuncta*, Texas) and two specimens of putative group 1 (*frontalis*) (ex *X. frontalis*, Argentina) were misidentified by the analysis. In external validation (n = 90), only species assigned to putative group 0 were misclassified: two ex *X. varipuncta* from Texas and two ex *X. fimbriata* from Guatemala. The latter specimens belong to the same sample, indicating that the error associated with non-dependent sampling may still be present, or this sample was originally identified incorrectly. All other misclassified specimens originate from different samples. Logit coefficients and the constant of the model are presented in Table 20.

Classification based on the 13-variable logistic regression model is as follows:

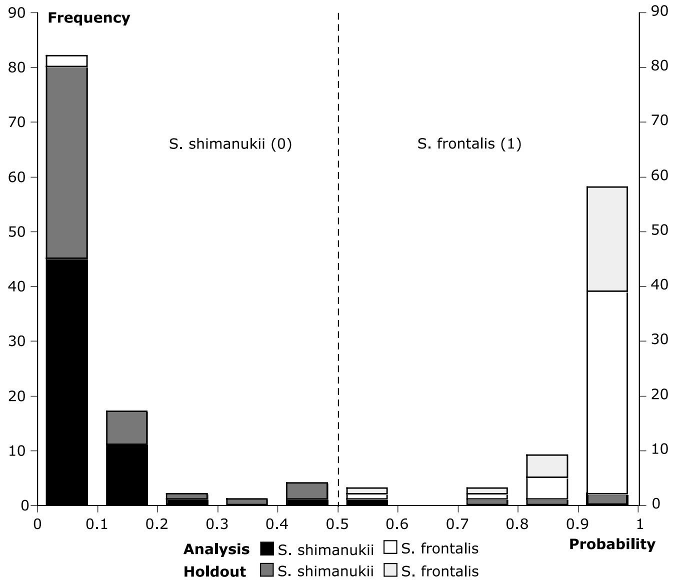

Fig. 46. Three-variable logistic regression model: Observed groups and predicted probabilities.

$$P(S.\ frontalis) = \mathrm{Exp}(-119.993 + 317.819 * \text{gnathosomal solenidion} + 31.373 * c_3 + 4.646 * d_2) / (1 + \mathrm{Exp}(-119.993 + 317.819 * \text{gnathosomal solenidion} + 31.373 * c_3 + 4.646 * d_2))$$

where P is the probability of an unknown specimen being *S. frontalis*; the numbers in the equation are coefficients and the constant from Table 20; the critical value is 0.5. If $P > 0.5$, the unknown specimen is predicted to be *S. frontalis*, whereas if $P < 0.5$, the unknown specimen is predicted to be *S. shimanukii*. Gnathosomal solenidion, c_3, and d_2 are shape variables calculated as

$$DM = Y/GM$$

where DM is a shape variable, Y is a measurement of the structure expressed in micrometers, and GM is the geometric mean of all measurements (here gnathosomal solenidion, c_3, and d_2).

An example of the calculations. A specimen from *Xylocopa varipuncta varipuncta* from Texas has the following measurements in micrometers (taken with a 100× objective under immersion with 0.5 μm precision):

gnathosomal solenidion 1, c_3 25, and d_2 72 (Y_1, Y_2, Y_3).

1. The geometric mean GM is $(1 * 25 * 72)^{1/n} = 12.164$ ($n = 3$ is the total number of variables)
2. Shape variables (DM) are:

$$DM_1 = 1/12.164 = 0.0822$$

$$DM_2 = 25/12.164 = 2.0552$$

$$DM_3 = 72/12.164 = 5.9189$$

3. Logit coefficients (B from Table 20) multiplied by corresponding shape variables ($B_i * DM_i$) are:

$$317.819 * 0.0822 = 26.1270 \text{ (gnathosomal solenidion)}$$

$$31.373 * 2.0552 = 64.4771\ (c_3)$$

$$4.646 * 5.9189 = 27.4993\ (d_2)$$

4. The odds (the ratio of the probability that the unknown specimen is *S. frontalis* is true divided by the probability that it is *S. shimanukii*) is:

$$\exp(-119.993 + 26.1270 + 64.4771 + 27.4993) = 0.1511$$

(-119.993 is the constant from Table 20, while the other numbers are from step 3)

5. The probability of the unknown of being *S. frontalis* is:

$$P(S.\ frontalis) = \text{odds}/(1 + \text{odds}) = 0.1313$$

6. Since P(*S. frontalis*) is less than the cutting score (0.5), the unknown specimen is classified as *S. shimanukii*.
7. The classification accuracy of our model was estimated as 94.7%. In reality, it may be less, especially if aberrant and non-randomly selected specimens are measured. We suggest repetition of steps 1–6 for at least 5–10 specimens originating from the same population.

A JavaScript application that performs these calculations is available online at http://insects.ummz.lsa.umich.edu/beemites/Morphometrics/Sennertia_frontalis_groupLR.htm.

Discussion

The *Sennertia frontalis* group comprises three nominal species (*S. frontalis*, *S. shimanukii*, and *S. augustii*), each described from a few specimens originating from one or a few localities or bee hosts. Univariate measurements of 78 morphometric variables revealed broad overlaps between the three species, raising the question about the validity of the original diagnostic characters and, therefore, the status of the taxa they define. Our analyses suggest that only *S. frontalis* and *S. shimanukii* may be diagnosed in multivariate space of at least four variables and therefore may formally be considered as separate entities.

Because *S. augustii* had the highest misclassification rate with *S. shimanukii*, it was removed from the 2-group analysis. Combining these two taxa in a single group resulted in a poor performance of the classification rule, indicating potential complexity of the data that cannot be accounted for because of the limitation of available material. Intergroup variation substantially exceeding within-group variation and a clear dependence of the same samples from a single host are factors also contributing to the problem. In some cases, morphometric data themselves cannot guarantee accurate discrimination between reproductively incompatible cryptic species (Burks & Heraty, 2002). Using additional data such as gene sequences and rearing experiments that can lay the groundwork for an objective *a priori* group assignment for the dependence multivariate analyses is not currently possible for *Sennertia*. PCA used for this purpose may capitalize on environmentally induced variations that were not completely removed by the size-correction procedure (Klimov *et al*., 2004), as well as sampling, preservation, and measurement biases. Our analyses, therefore, should be considered as an attempt to describe variation in our data set rather than to develop a predictive rule that can be generalized to all populations of the *frontalis* group. However, the two-group model (*S. frontalis* and *S. shimanukii*) has acceptable confidence limits and can be used for prediction purposes.

If the above limitations are ignored and the notion that morphological discontinuities correspond to genetic ones is accepted, the pattern of variation detected by our analyses can be explained as follows. There are two species of the *frontalis* group in the New World. One of them, *S. frontalis*, is predominantly associated with *Xylocopa frontalis* and *Xylocopa nautlana* throughout their ranges (Central and South America). Another species, *S. shimanukii*, is associated with multiple species of *Xylocopa* in Central and North America. Judging from the distinctiveness of the groups, gene flow is impossible or severely limited between them in Central America, the sympatric part of their range. The relationships of *S. shimanukii* and *S. augustii* associated with *Xylocopa augustii* in South America are not clear as the latter group was not included in the 2-group analysis. *Sennertia augustii* and *S. shimanukii* are partially overlapping in multivariate space, indicating that even if gene flow exists between the two, it is limited. If this is true, the name *S. augustii* should be considered as a junior synonym of *S. shimanukii* based on the principle of priority. However, because the populations of *S. augustii* and *S. shimanukii* are considerably allopatric and because additional data are necessary to confirm our finding, we refrain from synonymizing them formally.

The existence of two sympatric and almost completely separated groups over a broad range in the New World may be alternatively explained by simply assuming them as phenotypical morphs that appear in response to some ecological factors, for example the nest architecture and the conditions inside the nest.

Irrespective of whether the differences between the two above groups are genetic or non-genetic, one may speculate that all discussed groups are, in fact, a single species. This "species" would have a very complex internal structure, with some populations restricted to certain hosts or geographic areas. Indeed, as discussed previously (p. 63), the nest biology of carpenter bees offers ample opportunity for host switching, thus facilitating gene flow between populations from different host species. Thus, a single mite species utilizing multiple parapatric hosts may expand its range over the combined ranges of all its hosts and still have an opportunity for occasional gene exchanges. This is the case for *Kuzinia* (Acaridae) and its *Bombus* (Apidae) hosts in the Nearctic region (our data, unpublished). If this hypothesis is true, the species name *S. frontalis* is available to include all the three taxa of the *frontalis* group.

In conclusion, our analyses offer little beyond the proof that the original diagnostic characters/variables are invalid as uni- or bivariate discriminators and the existence of two, partially separated groups. Additional data (*e.g.*, gene sequences, rearing experiments) will be required to test the true genetic/evolutionary relationships in the *frontalis* complex.

SYSTEMATICS

Family **Chaetodactylidae** Zachvatkin, 1941

Trichodactyliens Donnadieu, 1868: 69 (denoting "*Trichodactyle* Dufour"; as "subsection of Sarcoptides"; nom. preocc. Trichodactylidae H. Milne Edwards, 1853 in Decapoda)

Chaetodactylinae Zachvatkin, 1941: 347 (part., as subfamily of Glycyphagidae); Turk, 1953: 82 (as subfamily of Glycyphagidae); Baker, 1962b: 1 (part., as subfamily of Glycyphagidae).

Chaetodactylidae: Baker, 1962a: 229 (part.); OConnor, 1982: 149; OConnor, 1993a: 345 [only selected references are given].

Sarcoptides: Donnadieu, 1868: 69 (part.).

Sarcoptidae: Canestrini & Kramer, 1899: 132 (part.), with genus "*Trichotarsus*" (including species now in *Chaetodactylus*, *Sennertia, Horstia*); Trägårdh, 1904: 156; Trägårdh, 1905: 113 (part.); Trägårdh, 1907: 12.

Tyroglyphes: Donnadieu, 1868 (part.)

Tyroglyphini: Canestrini & Berlese, 1885: 207 (part.)

Tyroglyphidae: Canestrini, 1888b: 14 (part); Berlese, 1895: 100 (part.), with genus *Trichotarsus* (=*Chaetodactylus*, *Sennertia*, Winterschmidtiidae: *?Vidia*); Tietze in Canestrini, 1899: 937 (part.); Michael, 1901: 190 (part.) with genus "*Trichotarsus*" (=*Chaetodactylus*, *Sennertia, Horstia, Tortonia, Sennertionyx, Cerophagus*); Trouessart, 1904a: 234; Türk & Türk, 1957: 60 (part.); Vitzthum, 1912d: 293 ("Tyroglyphiden", part., with genus *Trichotarsus* (=*Chaetodactylus*, *Sennertia*, *Horstia*, *Tortonia*)); Vitzthum, 1943: 877 (part.)

Tyroglyphinae: Canestrini & Kramer, 1899: 132 (as subfamily, part.; with genus "*Trichotarsus*" (=*Chaetodactylus*, *Sennertia, Horstia*)); Oudemans, 1901: 84 (as subfamily, part.; with genus "*Trichotarsus*" (=*Chaetodactylus*, *Sennertia, Horstia*)); Oudemans, 1903a: 149 (as subfamily, part.; with genus "*Trichotarsus*" (=*Chaetodactylus*, *Sennertia, Horstia, Tortonia*)); Trägårdh, 1905: 119 (part., as subfamily of Sarcoptidae); Trägårdh, 1907: 12 (as subfamily of Sarcoptidae); Oudemans, 1908: 53 (part., includes many non-psoroptidian taxa, as subfamily of Acaridae)

Tyrogtyphidae Canestrini, 1897: 473 (part.) [lapsus pro Tyroglyphidae, with genus "*Trichotarsus*" (=*Sennertia, Horstia*)]

Acaridae: Murray, 1877: 227 (part); Oudemans, 1908: 53 (part., =Astigmata)

Hypopidae: Murray, 1877: 227 (as subfamily, part.).

Acarini: Canestrini & Fanzago, 1878: 169 (part., as family)

Adisci Canestrini, 1888b: 14 (inferior category of Tyroglyphidae; part.)

Ameri Canestrini, 1888b: 15 (inferior category of Tyroglyphidae; part.)

Glycyphagina: Berlese, 1897: 100 (as subfamily, part.), with genus *Trichotarsus* (=*Chaetodactylus*, *Sennertia*, Winterschmidtiidae: *?Vidia*)

Glycyphagidae: Vitzthum, 1929: 76 (part.); Womersley, 1941: 476 (part.); Zachvatkin, 1941: 276 (part.); Baker & Wharton, 1952: 350; Fain, 1971: 264.

Glycyphaginae: Türk & Türk, 1957: 183 (part., as subfamily); Vitzthum, 1943: 885 (part., as subfamily).

Notes. OConnor (1993a) indicated that the family-name is a junior homonym of Chaetodactylini Tschitscherin, 1903 (Coleoptera). The systematics of the family was developed by Zachvatkin (1941), Fain (1981a, 1981b), and OConnor (1993a).

Diagnosis. The supracoxal sclerites are enlarged and modified (Fig. 6). External vertical setae *ve* are absent or reduced to alveoli in all instars. Tarsal setae *aa* I, *u* and *v* I–IV are absent from all instars. Solenidion ω_3 is shifted to the posterior part of tarsus I in tritonymphs and females (in males it is on the anterior side). In non-deutonymphs, the anterior oblique ridge of the gnathosoma is well-developed, starting near the posterior transverse ridge and extending anteriorly, meeting the internal wall of the palpcoxae. In heteromorphic deutonymphs, supracoxal setae *scx* are vestigial, with rounded or blunt tips; setae *e* and *ba* I–II are absent.

Key to Genera of the Family Chaetodactylidae of the World

Heteromorphic deutonymphs

1 Coxal fields III open. Tarsus III with 4 setae (*w*, *r*, *q*, and *p* absent). Tarsus IV with maximum of 5 setae (*s*, *p*, *q* always absent). Setae *1a* and *3a* touching posterior borders of respective coxal fields *and* filiform at least distally. Gnathosomal setae absent. Dorsal setae c_2 distinctly anterior to level of c_1. Condylophores of tarsi I–III well-developed, long and distinctly asymmetrical: anterior longer, posterior shorter or absent (*Sennertia argentina*, *S. donaldi*). Worldwide 3

\- Coxal fields III closed. Tarsus III with 7–8 setae (*w*, *r*, and *p* always present). Tarsus IV with 8 setae (*s*, *p*, *q* present). Setae *1a* and *3a* not touching posterior borders of respective coxal fields, if touching then inflated. Gnathosomal setae present. Setae c_2 on same transverse level as c_1. Condylophores of tarsi I–III short, almost symmetrical. Neotropical, southern Nearctic 2

2(1) Free palpi present. Empodial claws I–III not spirally twisted. Tarsi I–II with 7 setae (*p* and *q* present). Tarsus III with 8 setae (*q* present). Tarsal setae *w* IV longer than leg IV. Coxal fields IV open. Associated with *Centris* . . . . **Centriacarus** Klimov & OConnor (p. 99)

\- Free palpi absent. Empodial claws I–III spirally twisted. Tarsi I–II with 5 setae (*p* and *q* absent). Tarsus III with 7 setae (*q* absent). Tarsal setae *w* IV distinctly shorter than leg IV. Coxal fields IV closed. Associated with *Tetrapedia* . . . . **Roubikia** OConnor (p. 100)

3(1) Transverse medial extension of posterior apodemes IV well-developed. Gnathosomal solenidion absent. Setae *se* situated on prodorsal shield. Setae e_2 situated on hysterosomal shield. Associated with Afrotropical *Ceratina* . . . . **Achaetodactylus** Fain (=*Chaetodactylus* (*Ochaetodactylus*) Fain, **syn. n.**) (p. 96)

\- Transverse medial extension of posterior apodemes IV absent. Gnathosomal solenidion present. Setae *se* situated on soft cuticle. Setae e_2 situated outside hysterosomal shield or touching it. Associated with Megachilidae and Apidae. Worldwide 4

4(3) Prodorsal shield and free palpi present. Posterior apodemes II not extending to posteriorly anterior apodemes III. Cupules *ih* incorporated into lateral sclerotized borders of attachment organ. Solenidion σ III absent, represented by alveolus. Solenidion ϕ IV present. Associated with Lithurgini, Osmiini, Megachilini, Anthidiini (Megachilidae), Emphorini, and Tapinotaspidini (Apidae) . . . . **Chaetodactylus** Rondani (p. 108)

\- Prodorsal shield and free palpi absent. Posterior apodemes II extending posteriorly to anterior apodemes III. Cupules *ih* situated on sides of attachment organ. Solenidion σ III present. Solenidion ϕ IV absent. Associated with Xylocopini and Ceratinini (Apidae) . . . . . **Sennertia** Oudemans (p. 145)

Adults*

1 Anterior paraxial process of cheliceral body developed; fenestrate area *fe1* of cheliceral body vertically striated (Fig. 1 *D*). Solenidion ω_2 I proximal to seta *d* I. Tarsal setae *w* III, *r* III–IV, and tibial seta *kT* IV present. *Females*. Proximal ends of anterior apodemes I and pregenital sclerite separated. Inseminatory canal cylindrical, well sclerotized, protruding inside spermatheca. *Male*. Tarsal setae *e* III–IV absent; *p* III–IV absent, *q* III–IV present. Sclerotized portions of condylophores fused and incorporated to the distoventral sclerotized tarsal wall, pretarsal suckers not developed (Fig. 16 *A*). Heteromorphic males present . . . . **Roubikia** OConnor (p. 100)

\- Anterior paraxial process of cheliceral body absent; fenestrate area *fe1* of cheliceral body not striated (Fig. 1 *A*,*B*). Solenidion ω_2 I distal to *d* I or on same level. Tarsal setae *w* III, *r* III–IV, and tibial seta *kT* IV absent. *Female*. Proximal ends of anterior apodemes I and pregenital sclerite fused. Inseminatory canal trumpet-shaped or funnel shaped, weakly sclerotized, not protruding inside spermatheca. *Male*. Tarsal setae *e* III–IV present; both *p* and *q* III–IV absent. Sclerotized portions of condylophores separate, anterior condylophore modified to bilobed pretarsal sucker (Fig. 16 *C,D, F,G*). Heteromorphic male absent 2

2(1) *Female*. Proximal ends of anterior apodemes I fused, forming sternum. *Male*. Main part of progenital sclerites anterior to genital capsule (medial sclerite) (Fig. 10 *F*, Fig. 12 *A–E*). Progenital sclerites completely fused forming large unpaired sclerite (Fig. 10 *F*, Fig. 12 *B–E*). Lateral processes (horns) of dorsal supporting sclerite of genitalia with secondary processes (Fig. 12 *D*). Tarsi I–IV distinctly thicker than in females, with distinct anterio-dorsal protuberance (Fig. 16 *F*). *Larva*. Claparède's organ present. . . . . **Chaetodactylus** Rondani (p. 108)

\- *Female*. Proximal ends of anterior apodemes I separated from each other by large pregenital sclerite. *Male*. Main part of progenital sclerites lateral to genital capsule (Fig. 10 *A–E*). Progenital sclerites separate (Fig. 10 *A–E*). Lateral processes (horns) of dorsal supporting sclerite of genitalia simple or vestigial (Fig. 10 *A*). Tarsi I–IV as thick as in females, without distinct anterio-dorsal protuberance. *Larva*. Claparède's organ absent . . . . **Sennertia** Oudemans (p. 145)

*unknown for *Centriacarus* and *Achaetodactylus*

Genus *Centriacarus* Klimov & OConnor, 2007

Centriacarus Klimov & OConnor, 2007; 814; Klimov *et al.*, 2007a: 1370.

Type species *Centriacarus turbator* Klimov & OConnor, 2007, by original designation

Description. *Phoretic deutonymph*. Gnathosomal solenidion, free palpi and their setae present. Alveoli *ve* dorsal, distinctly anterior to *se*. Prodorsal shield striation longitudinal anteriorly and transverse posteriorly. Prodorsal shield present. Posterior edge of prodorsal shield shorter than its lateral edges. Setae *se* situated on soft cuticle. Setae c_2 situated on same transverse level as c_1. Setae e_2 situated on hysterosomal shield. Setae *1a* and *3a* touching posterior borders of respective coxal fields and filiform. Cupules *ia* situated on hysterosomal shield. Cupules *im* distinctly posterior to acetabula III, situated off line between d_2 and e_2. Cupules *ip* anterior to setae f_2. Cupules *ih* situated on sides of attachment organ. Posterior part of posterior apodemes of coxal fields II not displaced posteriorly to anterior apodemes III. Coxal fields III closed. Coxal fields IV open. Transverse medial extension of posterior apodemes IV well-developed. Anterior extension of posterior apodemes IV present, connecting with anterior apodeme III. Ventral longitudinal sclerites of progenital chamber conspicuous at posterior part. Ventral longitudinal sclerites of progenital chamber conspicuous at anterior part. Posterior and lateral cuticular suckers (Fig. 8 *A*) present. Anterior cuticular suckers (Fig. 8 *A*) present. Bases of anterior cuticular suckers inserted on separate apodeme (may touch or overlap posterio-lateral sclerotized border of the attachment organ) (Fig. 8 *A, C*). Apodemes of ps_1 separated. Setae *wa* I–II submedial, *f* I–II apical, near tarsal apices. Solenidion ω_2 present. Empodial claws I–III not twisted. Dorsal cuticular folds of ambulacra I–III absent (Fig. 17 *J*). Condylophores of tarsi I–III weakly developed, almost symmetrical. Supporting sclerites of condylophores (latero-apical sclerites of tarsus) indistinct from tarsus, not connected by dorsal bridge (Fig. 17 *J*). Disto-dorsal lobe of distal part of caruncle (*e.g.*, Fig. 17 *B*) absent. Dorsal condylar plate of femur-tibia joint (Fig. 14 *A*) broad. Tarsi I–II with 7 setae (*p* and *q* present). Tarsal setae *ra* and *la* I–II foliate. Genual seta *cG* I longer or only slightly shorter than genu I and modified. Genual setae *cG* I longer than *cG* II. Tarsal setae *q* III present. Tarsal setae *w*, *r*, and *p* III present. Tarsal seta *s* III foliate. Sigma III absent, represented by alveolus. Tarsus IV with 8 setae (*s*, *p*, *q* present). Tarsal setae *e*, *f* IV foliate or slightly lanceolate. Tarsal setae *w* IV longer than leg IV. Tibial setae *kT* IV present. Solenidion ϕ IV absent, represented by alveolus.

Feeding instars and *immobile deutonymph* unknown.

Biology and host associations. Associated with *Centris* (*Heterocentris*).

Distribution. Neotropical region.

Etymology. The generic name is formed from *Centris* (bee host genus) and *acarus* (a mite), and is masculine in gender.

Notes. Feeding instars of the *Sennertia vaga* complex have been collected on the same hosts, sometimes together with deutonymphs of *Centriacarus*. They have poorer leg chaetotaxy and belong to an early derivative lineage that probably does not form deutonymphs.

Key to species of *Centriacarus*

Phoretic deutonymphs

1 Free palpi longer than basal width. Lateral margins of prodorsal shield distinctly longer than its posterior margin. Posterior ends of posterior apodemes II not bent, directed inward. Lateral longitudinal hysterosomal sclerites at level of leg acetabula IV narrower than cupule *im*, extending anteriorly approximately to level of middle of acetabula III and not touching attachment organ posteriorly. Coxal fields I–II finely striated longitudinally. Setae *3a* shorter than c_3. Setae *4a* situated on sclerite fused with sclerotized paraxial border of coxal apodeme IV. Setae *mG* II shorter than combined length of femur-tibia II (ratio 0.6–0.8 (0.7 ± 0.05)). Solenidion σ I not reaching alveolus of ϕ and base of *cG* I. Setae *kT* and *w* IV smooth. Base of seta *p* IV approximately equidistant *e* and *r* IV. Brazil (type locality), Peru, Panama, Mexico: Jalisco. On *Centris vittata* . . . . **Centriacarus turbator** Klimov & OConnor, 2007 (p. 100)

\- Free palpi shorter than basal width. Lateral margins of prodorsal shield only slightly longer or shorter than its posterior margin. Posterior ends of posterior apodemes II bent, directed outward. Lateral longitudinal hysterosomal sclerites at level of acetabula IV wider than cupule *im*, extending anteriorly almost to level of *ia*, and posteriorly to attachment organ. Coxal fields I–II smooth. Setae *3a* distinctly longer than c_3. Setae *4a* situated on unsclerotized cuticle. Setae *mG* II nearly equal to or longer than combined length of femur-tibia II (ratio 0.8–1.2 (1.1 ± 0.10)). Solenidion σ I reaching alveolus of ϕ and base of *cG* I. Setae *kT* and *w* IV finely barbed. Base of seta *p* IV closer to *r* IV than to *e* IV. Venezuela. On *Centris* sp . . . . **Centriacarus guahibo** Klimov and OConnor, 2007

Centriacarus turbator
Klimov & OConnor, 2007

Centriacarus turbator Klimov & OConnor, 2007: 816; Figs. 2 *A*, *C–D*; 3–4; Klimov *et al.*, 2007a: 1371.

Material. Holotype: HDN—**BRAZIL**: **Mato Grosso do Sul**, Aquidauana, ex *Centris vittata* propodeum, 11–12 Dec 1919, R.E. Harris, CUIC, BMOC 95-0422-026; Paratypes: same data as holotype—14 HDNs; 5 HDNs—same data, BMOC 95-0422-025; 2 HDNs—**Matto Grosso**, Vila Vera, 12°46′S 55°30′W, ex *C. vittata* propodeum, 1 Oct 1973, M. Alvarenga, AMNH, BMOC 04-0508-229; 1 HDN—same data, on posterior wing bases, BMOC 04-0508-230; 13 HDNs—**COLOMBIA**: **Magdalena**, Socorpa Mission, Sierra de Perijá, ex *C. vittata* propodeum, 5–25 Aug 1968, B. Malkin, AMNH, BMOC 04-0508-234; 17 HDNs—**MEXICO**: Jalisco, Chamela (Estación de Biologia), ex *Centris* sp1 on propodeum, 6 Oct 1965, J. Rozen, AMNH, BMOC 04-0508-237; 16 HDNs—**PANAMA: Colón**, Isla Guacha [label reads Canal Zone, Barro Colorado Is.], ex *C. vittata* propodeum, 30 Jun 1934, Otis E. Shattuck, AMNH, BMOC 04-0508-236; 3 HDNs—**PERU**: **Loreto**, Pucallpa, 600 ft., ex *C. vittata* propodeum, 8 Nov 1946, J. C. Pallister, AMNH, BMOC 04-0508-235. Holotype in CUIC, paratypes in AMNH, CUIC, ESALQ, MUSM, OSAL, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 47, Fig. 48). Setae c_1 usually not reaching bases of d_1, c_1/c_1-d_1 0.7–1.0 (0.8 ± 0.09). Setae *3a* and *4b* distinctly shorter than c_3. Ratio $3a/c_3$ 0.4–0.7 (0.5 ± 0.07), $4b/c_3$ 0.4–0.8 (0.6 ± 0.10). Setae *1a* nearly equal to c_3, $1a/c_3$ 0.8–1.2 (1.0 ± 0.13). See key above for other diagnostic characters.

Hosts. *Centris* (*Heterocentris*) *vittata* (type host), *Centris* sp. (Mexico)

Distribution. Brazil: Mato Grosso do Sul (type locality), Peru, Colombia, Panama, Mexico: Jalisco.

Etymology. Turbator (a troubler) is a Latin noun in the masculine gender. The species name is a noun in apposition.

Genus *Roubikia* OConnor, 1993

Roubikia OConnor, 1993a: 347; Eickwort, 1994: 221; Van Asselt, 2000: 225; Okabe & Makino, 2002: 82; Klimov & OConnor, 2007: 818; Klimov *et al.*, 2007a: 1370; Klimov *et al.*, 2007b: 117.

Chaetodactylus (non Rondani): Baker *et al.*, 1987: 65 (part.); Roubik, 1987: 75; Qu *et al.*, 2003: 60 (part.).

'*Chaetodactylus*' OConnor, 1988: 341.

Type species *Chaetodactylus panamensis* Baker, Roubik & Delfinado-Baker, 1987, by original designation.

Description. *Phoretic deutonymph*. Gnathosomal solenidion *and* gnathosomal setae present *and* free palpi absent. Alveoli *ve* dorsal, distinctly anterior to *se*. Prodorsal shield striation longitudinal anteriorly and transverse posteriorly. Prodorsal shield present. Its posterior edge longer than lateral edges. Setae *se* situated on soft cuticle. Setae c_2 situated on same transverse level as c_1. Setae e_2 situated on hysterosomal shield. Setae *1a* and *3a* touching posterior borders of respective coxal fields and filiform. Cupules *ia* situated on hysterosomal shield. Cupules *im* distinctly posterior to acetabula III, situated off line between d_2 and e_2. Cupules *ip* anterior to setae f_2. Cupules *ih* situated on

Fig. 47. *Centriacarus turbator*, heteromorphic deutonymph (BMOC 95-0422-026, holotype). A, B - ventral and dorsal view.

sides of attachment organ. Posterior part of posterior apodemes of coxal fields II not displaced posteriorly to anterior apodemes III. Coxal fields III closed. Coxal fields IV closed. Transverse medial extension of posterior apodemes IV well-developed. Anterior extension of posterior apodemes IV present, connecting with anterior apodeme III. Ventral longitudinal sclerites of progenital chamber conspicuous at anterior and posterior parts. Posterior and lateral cuticular suckers (Fig. 8 *A*) present. Anterior cuticular suckers (Fig. 8 *A*) present. Bases of anterior cuticular suckers inserted on separate apodeme (may touch or overlap posterio-lateral sclerotized border of the attachment organ) (Fig. 8 *A*). Apodemes of ps_1 partially fused anteriorly. Setae *wa* I–II apical or subapical, *f* I–II at level or proximal to *wa* I–II and far from tarsal apices. Solenidion ω_2 present. Empodial claws I–III twisted. Dorsal cuticular folds of ambulacra I–III weakly developed, with distal part smaller than proximal (Fig. 17 *H*). Condylophores of tarsi I–III weakly developed, almost symmetrical. Supporting sclerites of condylophores (latero-apical sclerites of tarsus) indistinct from the tarsus, not connected by dorsal bridge (Fig. 17 *G,H*). Disto-dorsal lobe of distal part of caruncle (*e.g.*, Fig. 17 *B*) absent. Dorsal condylar plate of femur-tibia joint (Fig. 14 *A*) broad. Tarsi I–II with 5 setae (*p* and *q* absent). Tarsal setae *ra* and *la* I–II foliate. Genual seta *cG* I longer or slightly shorter than genu I and modified. Genual setae *cG* I longer than *cG* II. Tarsal setae *q* III absent. Tarsal setae *w*, *r*, and *p* III present. Tarsal seta *s* III foliate. Sigma III absent, represented by alveolus. Tarsus IV with 8 setae (*s*, *p*, *q* present). Tarsal setae *e*, *f* IV foliate or slightly lanceolate. Tarsal setae *w* IV distinctly shorter than leg IV or absent. Tibial setae *kT* IV present. Solenidion ϕ IV absent, represented by alveolus. *Larva*. Claparède's organ shaft slightly asymmetrical, distinctly narrowing terminally and ending in button-shaped dome.

Inert heteromorphic deutonymph unknown.

Adults. Second anterior tooth of fixed cheliceral digit (*tf2''*) not forming crown (Fig. 1 *D*). Anterior paraxial process of cheliceral body developed (Fig. 1 *D*). Fenestrate area fe1 of cheliceral body vertically striated (Fig. 1 *D*). Paraxial and antiaxial rutellar lobes (*rlp* and *rpa*) fused ventrally, paraxial lobe distinct only dorsally (Fig. 4 *C*). Supracoxal seta spiniform, with rounded tip, situated on supracoxal sclerite lateral to outer

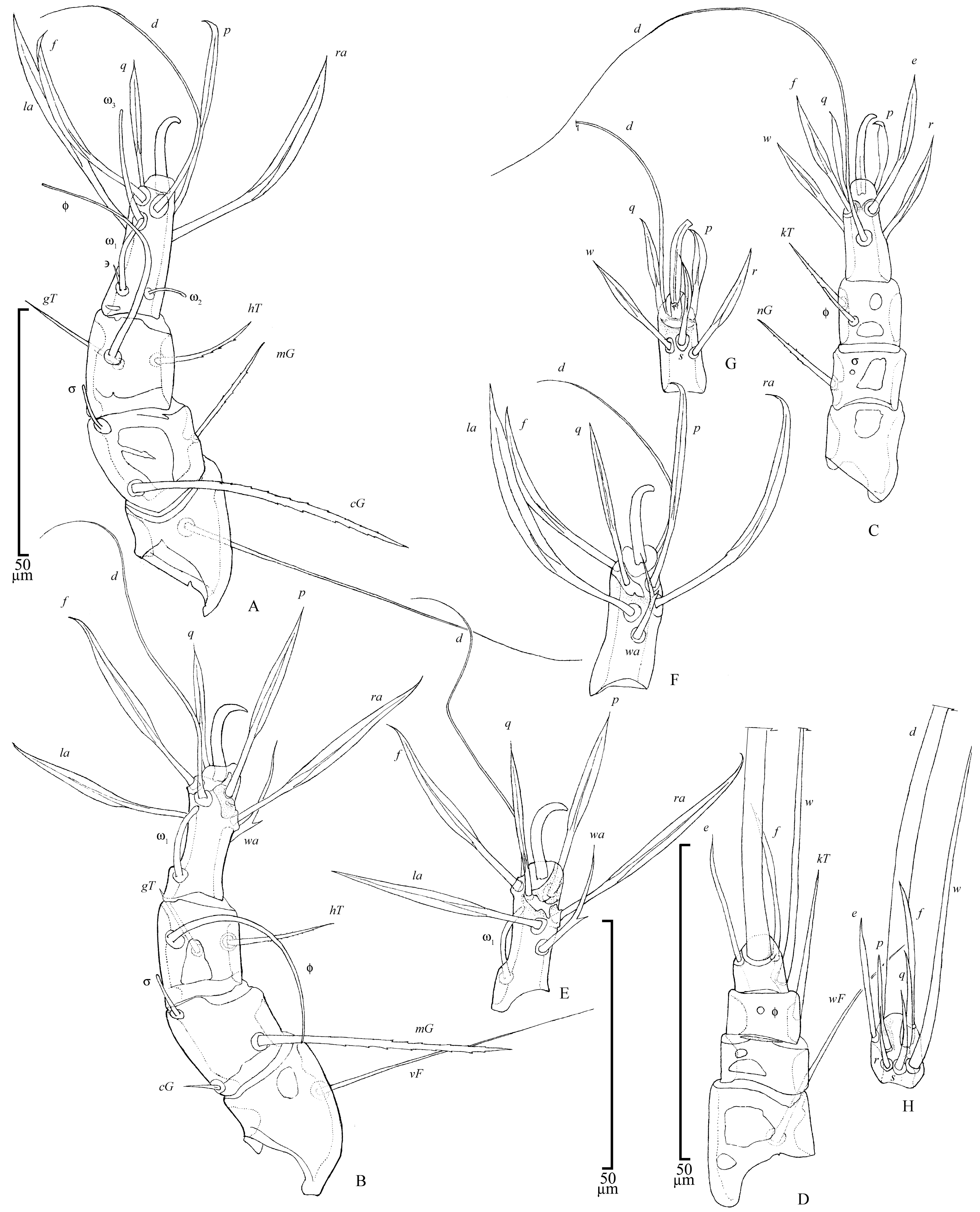

Fig. 48. *Centriacarus turbator*, heteromorphic deutonymph (BMOC 95-0422-026). A–D - legs I–IV, dorsal view, respectively; E–H - tarsi, I–IV, ventral view, respectively.

ridge of supracoxal sclerite. Anterio-lateral ridge of supracoxal sclerite (Fig. 6 *D*) absent. Setae h_3 medial to h_2. Cupules *im* ventro-lateral (correlated with HDN). Cupules *ip* anterior to setae f_2 (correlated with HDN). Disto-dorsal lobe of distal part of caruncle absent (correlated with HDN). Dorsal condylar plate of femur-tibia joint narrow, posterior. Solenidion ω_2 I distal to *d* I or on same level. Solenidion ω_2 II present in female and homeomorphic male, absent in heteromorphic male. Setae *w* III present (correlated with HDN). Tarsal setae *r* III–IV present. Setae *kT* IV present (correlated with HDN).

Female. Proximal ends of anterior apodemes I and pregenital sclerite separated. Proximal ends of anterior apodemes I fused forming sternum. Spermatophores present. Inseminatory canal cylindrical, well sclerotized, protruding inside spermatheca. Posterior ends of supporting sclerite of preoviporal canal situated near area of genital papillae. Condylophores with short sclerotized portion and distinct proximal unsclerotized portion connected to the tarsus.

Male. Main part of progenital sclerites anterior to genital capsule (medial sclerite) (Fig. 10 *F*, Fig. 12 *A–E*). Progenital sclerites touching each other (Fig. 12 *A*). Lateral processes (horns) of dorsal supporting sclerite (Fig. 12 *A*) simple or vestigial. Body of dorsal supporting sclerite developed posterior to base of aedeagus. Genital setae represented by transparent disk. Genital setae distinctly (more than their diameter at base) anterior to progenital folds. Tarsal setae *q* II present in homeomorphic male, absent in heteromorphic male. Tarsal setae *e* III–IV absent. Tarsal setae *q* III–IV present. Setae *s* and *w* IV separated, *w* submedial, *s* subapical. Tarsi I–IV as thick as in female. Sclerotized portions of condylophores fused and incorporated into disto-ventral sclerotized tarsal wall, pretarsal suckers not developed. Distinct anteriodorsal protuberance on tarsi I–IV absent.

Heteromorphic males present (see p. 41 for description).

Biology and host association. The four species (see p. 103) are associated exclusively with *Tetrapedia* (Apidae: Tetrapediini). *Roubikia panamensis* and *R. imberba* occur on cleptoparasitic bees of the genus *Coelioxoides* (Apidae: Tetrapediini) attacking their principal host (Alvez-dos-Santos *et al*., 2002). *Roubikia latebrosa* was found to be phoretic in the metasomal acarinarium of *Tetrapedia* sp. Probably *Roubikia* are commensals feeding on the nest materials and fatty acids from floral oils. Biology is only known for *Roubikia panamensis* (see below, p. 94).

Distribution. Neotropical region.

Key to Species of *Roubikia*

Heteromorphic deutonymphs

1 Dorsal extensions of apodemes I–II usually completely surrounding setae *scx*. 0–2 gnathosomal setae. Setae *si* usually exceed distance from lateral edge of prodorsal shield to base of *si* + distance between *si*. Seta *mG* I slightly pectinate. Seta *mG* II equal to or exceeding length of leg II (with claw). *ex Tetrapedia* sp. and cleptoparasites *Coelioxoides waltheriae* and *C. exulans*, Argentina. . . . . **Roubikia imberba** Klimov & OConnor, 2007

- Dorsal extensions of apodemes I–II not completely surrounding setae *scx*. 2 gnathosomal setae. Other characters variable 2

2(1) Setae *si* about 2 or more times longer than *se*. Setae *si* usually as long as distance from lateral edge of prodorsal shield to base of *si* + distance between *si*. Seta *mG* I slightly pectinate. Seta *mG* II nearly as long as leg II (with claw). *ex Tetrapedia* sp. Peru . . . . **Roubikia latebrosa** Klimov & OConnor, 2007

- Setae *si* less than 2 times longer than *se*. Other characters variable 3

3(2) Setae *mG* I pectinate (sometimes only slightly). Setae *mG* II usually longer than combined length of femur-tibia II. *ex Tetrapedia* sp. (type host), *Tetrapedia diversipes*, *T. peckoltii* and cleptoparasites *Coelioxoides waltheriae*. Panama (type locality), French Guiana, Brazil, Bolivia, Mexico. [possibly a complex of cryptic species]. . . . . **Roubikia panamensis** (p. 103)

- Setae *mG* I smooth. Setae *mG* II distinctly shorter than combined length of femur-tibia II. *ex Tetrapedia maura*. Mexico . . . . **Roubikia officiosa** Klimov & OConnor, 2007 (p. 107)

Roubikia panamensis
(Baker, Roubik & Delfinado-Baker, 1987)

Chaetodactylus panamensis: Baker *et al*., 1987: 67; Roubik, 1987: 75.
Roubikia panamensis OConnor, 1993a: 345; Van Asselt, 2000: 225; Klimov & OConnor, 2007: 819; Klimov *et al*., 2007a: 1371; Klimov *et al*., 2007b: 116.
'Chaetodactylus' panamensis OConnor, 1988: 341.
Chaetodactylus panamaensis Qu *et al*., 2003: 60 (lapsus)

Material. Holotype: female—**PANAMA**: **Panamá**, Curundú, nest of *Tetrapedia* sp. (aff. *maura*), 19 Sep 1982, D. Roubik, USNM (Note date is different from that originally published). Paratypes: 2f, 1m hmm, 7PNs, 1L—same data as holotype; 1f, 1m htm, 13PNs, 3L—same data, 31 Jul 1984; 1+3 HDNs—same data, ex *Tetrapedia* sp. leg hairs + hind leg, 25 Apr 1984, D. Roubik, USNM. Additional material: 20 HDNs—same data, ex *Tetrapedia maura* on 1st metasomal tergite, 16 Dec 1981, D. Roubik #12, USNM, BMOC 96-0510-208; 1HDN—**Darien** Prov., Bayano Bridge, ex *Tetrapedia* dorsal pronotum, 16 May 1980, D. Roubik #6, UMMZ BMOC 91-0103-002; 8 HDNs—same data, lateral and ventral mesosoma, BMOC 91-0103-004; 1 HDN—same data, on propodeum, BMOC 91-0103-005; 14 HDNs—**BOLIVIA**: Santa Cruz, Santa Cruz Jardín Botanico, *Coelioxoides waltheriae* on 1st metasomal tergite, 2 Aug 1976, Porter & Calmbacher, AMNH, BMOC 04-0508-245; 15 HDNs—**BRAZIL**: **Minas Gerais**, Varginha, ex *Tetrapedia* sp 1 on propodeum, Feb 1972, M. Alvarenga, AMNH, BMOC 04-0508-253; 19 HDNs—**Pará**, ex *Tetrapedia diversipes* on mesosoma & metasoma (Cornell lot 546, sub 262), no date, Baker coll., CUIC, BMOC 87-0606-002; 14 HDNs—**São Paulo**, Campinas, ex *Tetrapedia diversipes* on mesosoma, 5 Jun 1972 R.M. Bohart USNM, BMOC 96-0510-207; 22 HDNs—Jundiaí, ex *Tetrapedia peckoltii* on mesosoma & behind head, 14 Mar 1909, Schrottky, CUIC, BMOC 87-0606-001; 9 HDNs—ex *Tetrapedia* on mesosoma (Cornell lot 298), no date, Hammar coll., CUIC, BMOC 87-0606-003; 19 HDNs—**FRENCH GUIANA**, 3 km W. Kourou, ex *Tetrapedia* sp. anterior metasoma, legs II–III, some scattered over mesosoma, wings & head, 30 May 1981, D. Roubik #41, BMOC 91-0103-006; 20 HDNs—same data, lateral mesosoma, legs II–III and anterioventral on metasoma, BMOC 91-0103-007; 4 HDNs—**MEXICO: Chiapas**, Tuxtla Gutiérrez, ex *Tetrapedia* sp. on 1st metasomal tergite, 26 Jul 1987, F.D. Parker, USNM, BMOC 96-0510-211; 13 HDNs—**Nayarit**, La Bajada, near San Blas, ex *Tetrapedia* sp. on 1st metasomal tergite, 21 May 1983, F.D. Parker, USNM, BMOC 96-0510-210; 5 HDNs—**Tamaulipas**, 17mi W Sotola Marina, ex *Tetrapedia* sp. on 1st metasomal tergite, 2 Jun 1978, Gillaspy USNM, BMOC 96-0510-209. Voucher specimens in AMNH, CUIC, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 51). Diagnostic description given in the key on p. 103. *Larva* and *adults* described on p. 100, see also Fig. 49 and Fig. 51.

Hosts. *Tetrapedia* sp. (type host), *Tetrapedia diversipes*, *Tetrapedia peckoltii*, also phoretic on *Coelioxoides waltheriae* (cleptoparasite of *Tetrapedia diversipes*).

Distribution. Panama (type locality), Mexico: Chiapas, Nayarit, Tamaulipas; French Guiana, Brazil, Bolivia.

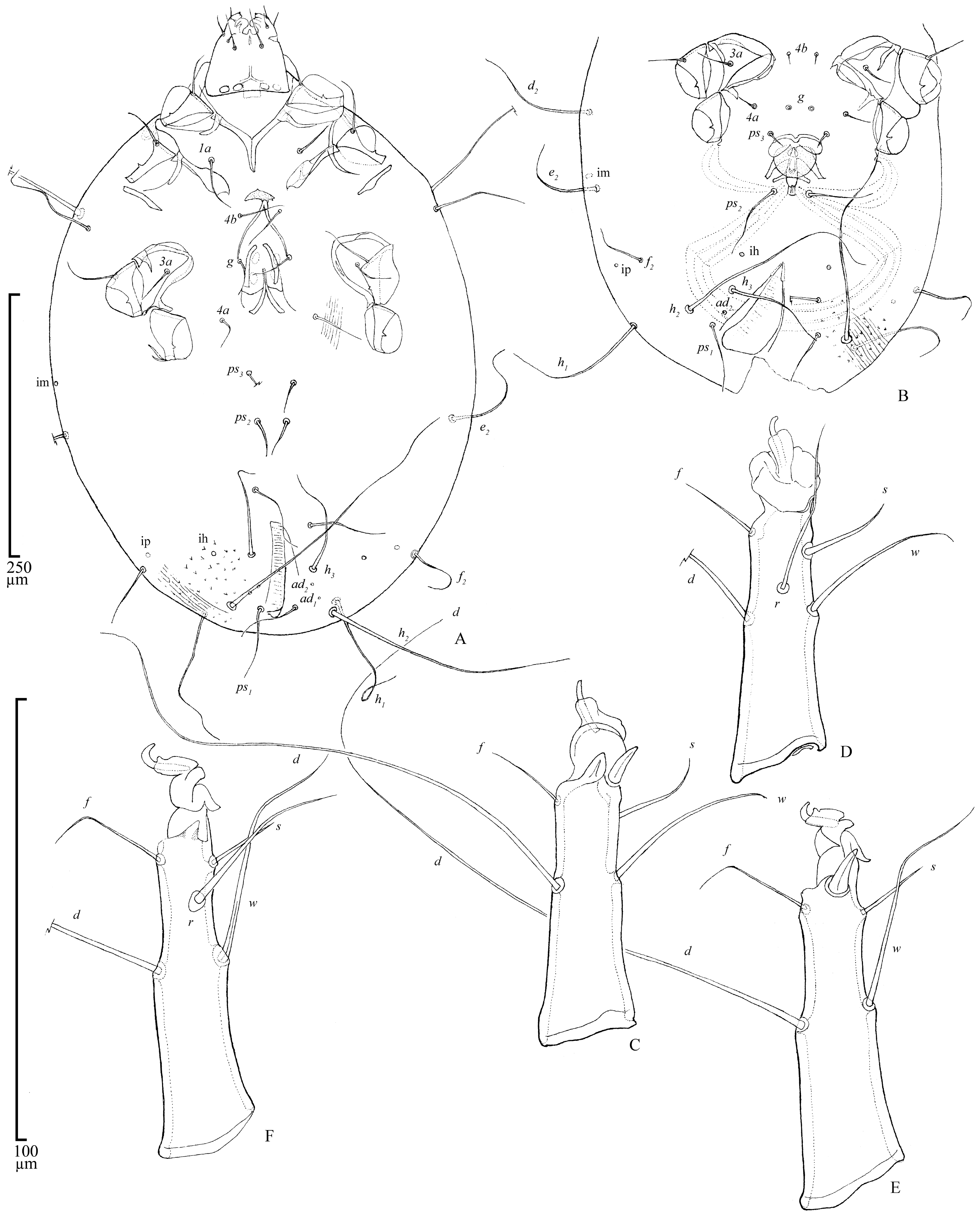

Fig. 49. *Roubikia panamensis*, adults (paratypes). A - female, ventral view of idiosoma; B - homeomorphic male, ventral view of idiosoma; C, D - tarsus III, E, F - tarsus IV.

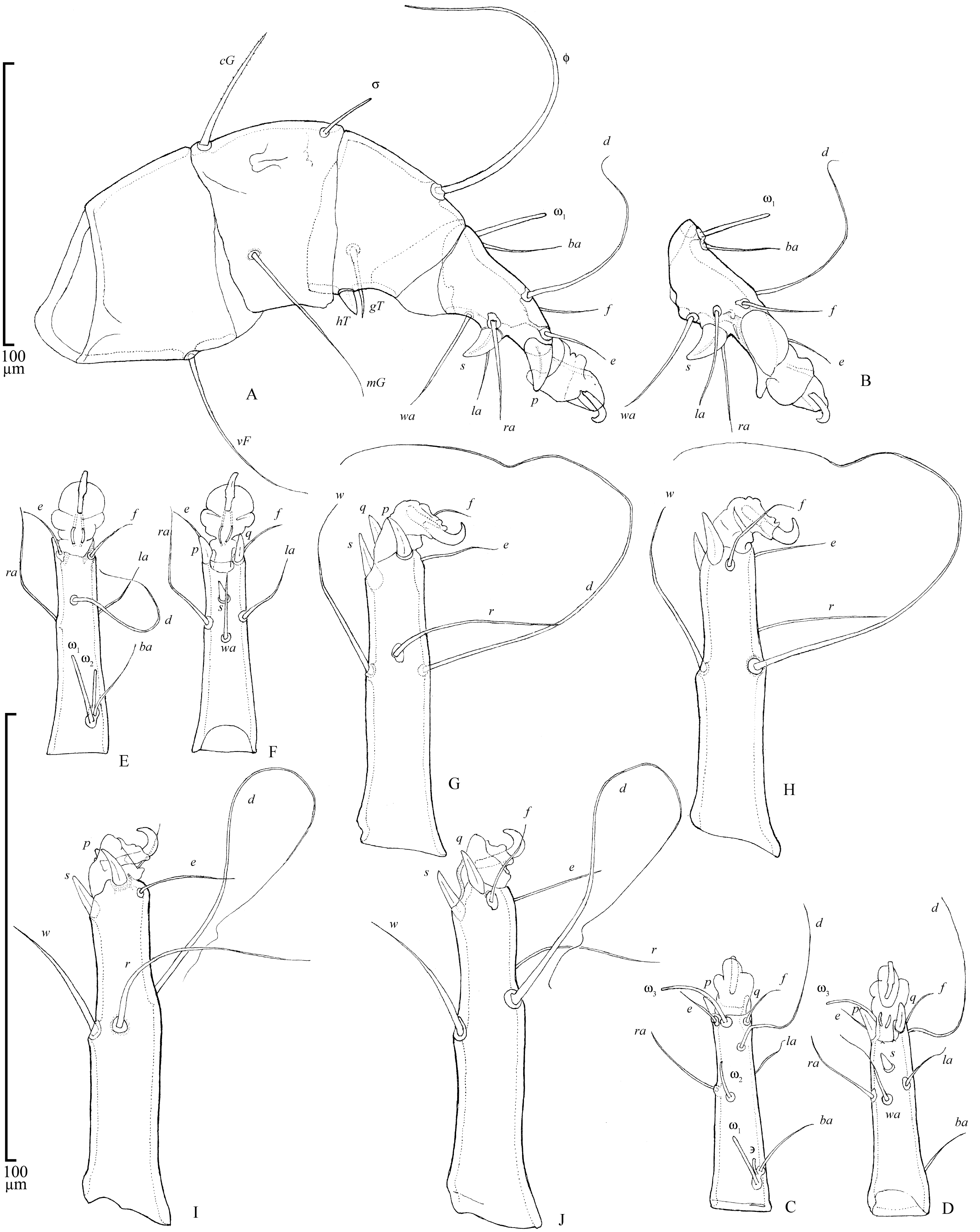

Fig. 50. *Roubikia panamensis*, legs of adults (paratypes). A - leg II, heteromorphic male; B - tarsus II; C, D - tarsus I, female, dorsal and ventral view; E, F - tarsus II, female, dorsal and ventral view; G, H - tarsus III, female; I, J - tarsus IV, female.

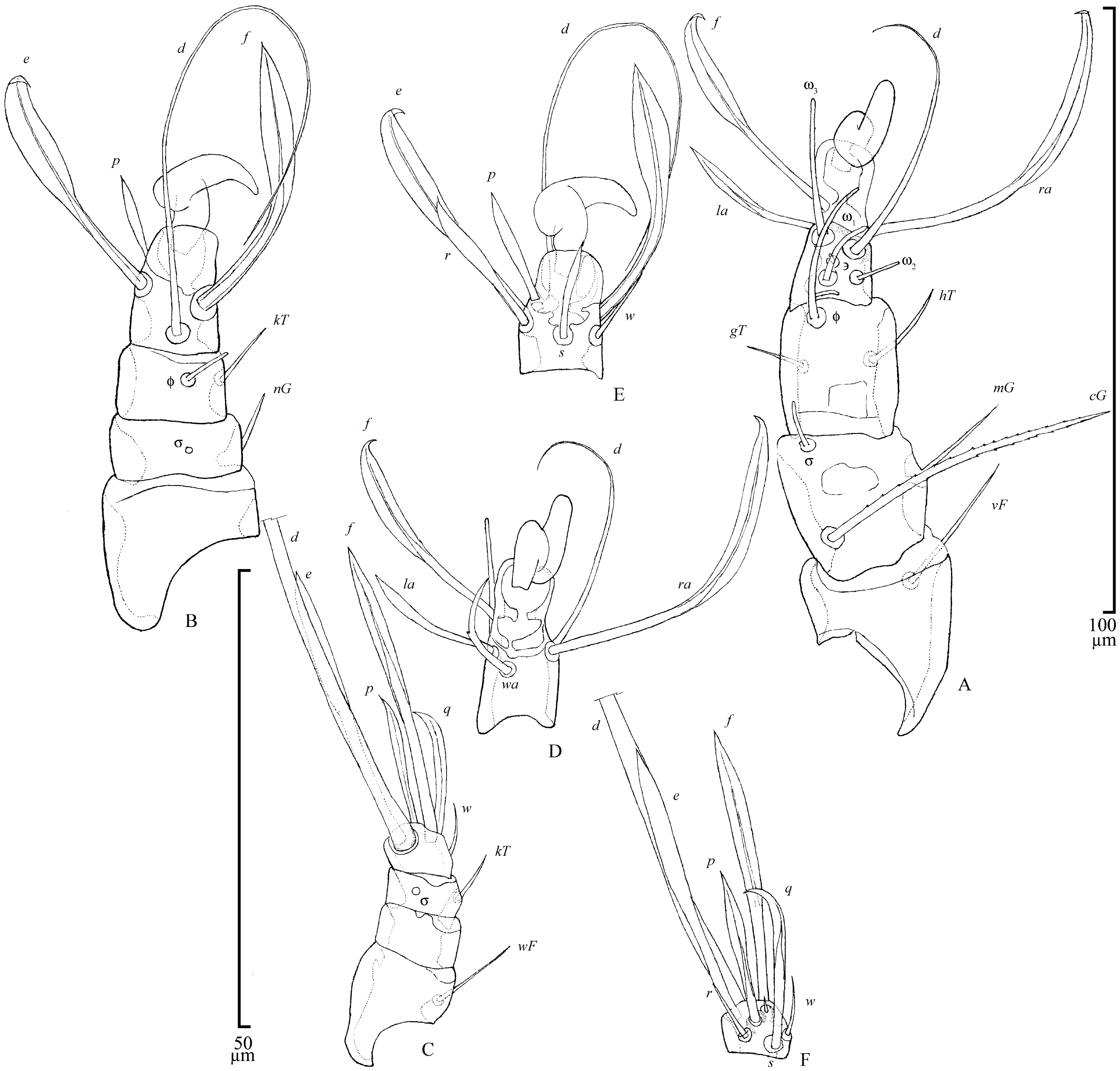

Fig. 51. *Roubikia panamensis*, heteromorphic deutonymph (BMOC 91-0103-003). A–C - legs I, II, IV, dorsal view, respectively; D-F - tarsi, I, II, IV, ventral view, respectively.

Biology. In Panama, *Tetrapedia* sp. nests primarily from the late dry season until the early wet season (April to July), and occasionally in the early dry season (November to February). The *Tetrapedia* female collects floral oils to combine with pollen provisions, and gathers dry soil to make partitions between the cells. Both materials are carried on the hairs of the tibial scopae. Soil in the cell partitions appeared to be admixed with a resinous substance and much of it formed small, shiny pellets less than a half of millimeter in diameter. Mature larvae produced fecal pellets, which are about 1.2 mm long and another, cigar-shaped. Several hundred mites were scattered among the two types of pellets. This was the approximate mite abundance in each of three completed nests having 5–6 bee cells. A nest containing young larvae had several mites in the loose soil fill between each cell and also on the pollen provision. The mites presumably fed on materials in the cells, and possibly on the fatty acids from floral oils mixed with some of the fill dirt. Mites were much more apparent in nests from which bees had emerged than in the nest containing young larvae. Adults of *Tetrapedia* routinely harbor mites on the basal metasomal tergites and hind legs, particularly on the scopae. A characteristic of *Tetrapedia* is their repeated visitation to small patches of dry soil in which females collect soil for nest construction. The mites apparently disperse to new nests by leaving a nest with emerging bees. An individual mite was seen wandering within a small (10 cm diameter) area in which three female *Tetrapedia* had been seen collecting loose dirt. The mites thus possibly disperse among female bees at such a restricted foraging spot, and they probably arrive at the nests of more than one apid bee in this manner (Roubik, 1975).

The shape and internal structure of the "nematodes" reported in the female spermathecae (OConnor, 1993a) are consistent with those of astigmatid mite spermatophores (Griffiths & Boczek, 1977)

Note. Probably a complex of species. Specimens from Panama have setae *mG* II as long as leg II (including claw), while in specimens from Mexico and Brazil, these setae are distinctly longer.

Roubikia officiosa

Klimov & OConnor, 2007

Roubikia officiosa Klimov & OConnor, 2007: 821, Fig. 9 *A–C*.

Material. Holotype: HDN—**MEXICO**, **Jalisco**, Chamela, ex *Tetrapedia maura* on propodeum & metasoma, 21 Jun 1983, S.H. Bullock #1534, LACM, BMOC 97-0331-028. Paratypes: 9 HDNs—same data as holotype. Holotype in LACM, paratypes in LACM, UMMZ, UNAM.

Description. *Phoretic deutonymph*. Diagnostic description given on p. 103. Differs from all known species by the following characters: setae *mG* I smooth, setae d_1 nearly as long as c_1, and setae *mG* II distinctly shorter than combined length of femur-tibia II.

Other instars unknown.

Hosts. *Tetrapedia maura*.

Distribution: Mexico: Jalisco

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Roubikia%20officiosa&-max=200&-find

Etymology. Officiosus (=full of courtesy, complaisant, serviceable) is a Latin adjective.

Genus *Achaetodactylus* Fain, 1981

Chaetodactylus (*Achaetodactylus*) Fain, 1981b: 2; Fain & Pauly, 2001: 125; OConnor, 1993a: 354.

Chaetodactylus (*Ochaetodactylus*) Fain, 1981b: 2 (type species *Chaetodactylus decellei* Fain, 1974, by original designation); OConnor, 1993a: 354, **syn. n.**

Chaetodactylus: Fain, 1974a: 214 (part.).

Achaetodactylus: Klimov *et al.*, 2007a: 1370; Klimov *et al.*, 2007b: 119.

Type species *Chaetodactylus leleupi* Fain, 1974, by original designation.

Description. *Phoretic deutonymph*. Free palpi, gnathosomal solenidia and setae absent. Alveoli *ve* usually weakly developed, dorsal, distinctly anterior to *se*. Prodorsal shield present, with longitudinal striation. Posterior edge of prodorsal shield longer than lateral edges. Setae *se* situated on prodorsal shield. Setae c_2 situated distinctly anterior to level of c_1. Setae e_2 situated on hysterosomal shield. Setae *1a* and *3a* not touching posterior borders of respective coxal fields, if touching then inflated and elongated. Cupules *ia* situated outside hysterosomal shield. Cupules *im* distinctly posterior to leg acetabula III, laterad of line connecting d_2 and e_2. Cupules *ip* posterior to setae f_2. Cupules *ih* situated on sides of attachment organ. Posterior part of posterior apodemes of coxal fields II displaced posteriorly to anterior apodemes III. Coxal fields III open. Coxal fields IV open. Transverse medial extension of posterior apodemes IV well-developed. Anterior extension of posterior apodemes IV present, connecting with anterior apodeme III. Ventral longitudinal sclerites of progenital chamber conspicuous at anterior and posterior parts. Posterior and lateral cuticular suckers absent (Fig. 8 *B*). Anterior cuticular suckers (*e.g.*, Fig. 8 *A*) vestigial or absent. Bases of anterior cuticular suckers incorporated into the border (Fig. 8 *B*). Apodemes of ps_1 completely fused. Setae *wa* I–II apical or subapical, *f* I–II at level or proximal to *wa* I–II and far from tarsal apices. Solenidion ω_2 present or absent. Empodial claws I–III twisted. Dorsal cuticular folds of ambulacra I–III well-developed, with distal part distinctly larger than any of proximal folds (*e.g.*, Fig. 17 *C*). Condylophores of tarsi I–III well-developed, distinctly asymmetrical with anterior longer, posterior shorter, incorporated into posteriolateral lobe. Supporting sclerites of condylophores (lateroapical sclerites of tarsus) distinct from the tarsus, connected by dorsal bridge (*e.g.*, Fig. 17 *C*). Disto-dorsal lobe of distal part of the caruncle (*e.g.*, Fig. 17 *B*) present, well developed. Dorsal condylar plate of femur-tibia joint (Fig. 14 *A*) absent or indistinct. Tarsi I–II with 5 setae (*p* and *q* absent). Tarsal setae *ra* and *la* I–II simple or spiniform. Genual seta *cG* I distinctly shorter than genu I and unmodified (*A. ceratinae*) or slightly shorter than genu I and modified (*A. decellei* and *A. leleupi*). Genual seta *cG* I–II subequal (*A. ceratinae*) or *cG* I longer than *cG* II (*A. decellei* and *A. leleupi*). Tarsal seta *q* III absent. Tarsal setae *w*, *r*, and *p* III absent. Tarsal seta *s* III simple. Sigma III absent, represented by alveolus. Tarsus IV with maximum 5 setae (*s*, *p*, *q* always absent). Tarsal setae *e*, *f* IV simple or absent. Tarsal seta *w* IV distinctly shorter than leg IV or absent. Tibial seta *kT* IV absent. Solenidion ϕ IV absent, represented by alveolus.

Feeding instars and *immobile deutonymph* unknown.

Biology. All three known species are associated with *Ceratina* spp. in the Afrotropic region.

Species included. *Achaetodactylus leleupi* (Fain, 1974), **comb. n.** (from *Chaetodactylus*), *Achaetodactylus ceratinae* (Fain, 1974), *Achaetodactylus decellei* (Fain, 1974), **comb. n.** (from *Chaetodactylus*) (see also p. 187).

Notes. The three known species can be distinguished using the key of Fain (1981b).

Genus *Chaetodactylus* Rondani, 1866

Trichodactylus Dufour, 1839: 276 (type species *Trichodactylus osmiae* Dufour, 1839 by monotypy) (nom. preocc. Latreille, 1828 in Decapoda); Gervais, 1844: 266 (part.); Donnadieu, 1868: 70 (also as *Trichodactyle*, French vernacular form of *Trichodactylus* Dufour), part.; Dujardin, 1849: 245 (as *Trichodactyle*, French vernacular from of *Trichodactylus* Dufour); Mégnin, 1873a: 129; Mégnin, 1873b: 492; Mégnin, 1874: 225; Murray, 1877: 251 (part); Canestrini & Fanzago, 1878: 169 (authorship attributed to Dugès); Mégnin, 1880: 146 (part.).

Chaetodactylus Rondani, 1866: 183 (nom. n. pro *Trichodactylus* Dufour, 1839); Berlese, 1920: 21 (part.); Oudemans, 1924: 329; Vitzthum, 1929: 76; Vitzthum, 1943: 886; Baker & Wharton, 1952: 351; Turk, 1953: 82; Türk & Türk, 1957: 207; Krombein, 1962: 237; Fain, 1974a: 213 (part.); Sherbef & Duweini, 1980: 245; Fain *et al*., 1992: 337; OConnor, 1993: 345 (part.); Fain & Baugnée, 1996: 23; Fain & Pauly, 2001: 127 (part.); Qu *et al*., 2003: 60 (part.); Klimov *et al*., 2007a: 1370; Klimov & OConnor, 2007: 821.

Chaetodactylus (*Chaetodactylus*): Fain, 1981b: 1; OConnor, 1993: 345; Fain & Pauly, 2001: 127 (as subgenus).

Saproglyphus (non Berlese, 1890): Hirashima, 1957: 200.

Trichotarsus Canestrini, 1888b: 7 (nom. n. pro *Trichodactylus* "Dugès", part.); Canestrini, 1888a: 394 (part.); Berlese, 1897: 105 (part., with genus *Eutarsus* Hessling, 1852 as junior synonym); Berlese, 1898: fasc. 89, n. 12 (part); Canestrini & Kramer, 1899: 148 (part.); Giard, 1900: 377 (part.); Banks, 1902: 176 (part.); Oudemans, 1900: 115 (part); Oudemans, 1901: 82 (part.); Michael, 1903: 13 (part.); Oudemans, 1903a: 144 (part.); Oudemans, 1903b: 13 (part.); Ludwig, 1904: 216; Trouessart, 1904a: 234; Trouessart, 1904b: 365; Oudemans, 1905a: 21 (part.); Trägårdh, 1905: 119 (part.); Oudemans, 1908: 53; Vitzthum, 1912b: 181 (part.); Vitzthum, 1912d: 289 (part.); Vitzthum, 1919: 31 (diagnosis); Vitzthum, 1933: 168; Knülle, 1959: 385.

Trichotarsus group C Oudemans, 1903a: 147.

Chaetodactylus (*Spinodactylus*) Fain, 1981b: 2 (type species *Chaetodactylus claviger* Oudemans, 1928, by original designation); OConnor, 1993a: 354, **syn. n.**

Tricholarsus Vitzthum, 1912d: 292 (lapsus).

Type species *Trichodactylus osmiae* Dufour, 1839 by monotypy.

Description. *Phoretic deutonymph*. Gnathosomal solenidion present *and* setae on free palpi absent *and* free palpi present. Alveoli *ve* dorsal, approximately at level of *se*. Prodorsal shield striation longitudinal anteriorly and transverse posteriorly. Posterior edge of prodorsal shield longer than lateral edges. Prodorsal shield present. Setae *se* situated on soft cuticle. Setae c_2 situated distinctly anterior to level of c_1. Setae e_2 situated outside hysterosomal shield or touching it. Setae *1a* and *3a* not touching posterior borders of respective coxal fields, or if touching then inflated and elongated. Cupules *ia* situated outside hysterosomal shield. Cupules *im* distinctly posterior to bases of legs III, laterad of line connecting d_2 and e_2. Cupules *ip* posterior to setae f_2. Cupules *ih* incorporated into lateral sclerotized borders of attachment organ. Posterior part of posterior apodemes of coxal fields II not displaced posteriorly to anterior apodemes III. Coxal fields III open. Coxal fields IV open. Transverse medial extension of posterior apodemes IV absent. Anterior extension of posterior apodemes IV absent, if present then not connected. Anterior and posterior ventral longitudinal sclerites of progenital chamber inconspicuous. Posterior and lateral cuticular suckers (*e.g.*, Fig. 8 *A*) absent. Anterior cuticular suckers (*e.g.*, Fig. 8 *A*) present, vestigial or absent. Bases of anterior cuticular suckers if present, touching the border (Fig. 8 *E*). Apodemes of ps_1 completely fused. Setae *wa* I–II apical or subapical, *f* I–II at level or proximal to *wa* I–II and far from tarsal apices. Solenidion ω_2 present. Empodial claws I–III twisted. Dorsal cuticular folds of ambulacra I–III well-developed, with distal part distinctly larger than any of proximal folds (*e.g.*, Fig. 17 *C*). Condylophores of tarsi I–III well-developed, distinctly asymmetrical with anterior longer, posterior shorter, incorporated into posterio-lateral lobe. Supporting sclerites of condylophores (latero-apical sclerites of tarsus) distinct from tarsus, connected by dorsal bridge (*e.g.*, Fig. 17 *C*). Disto-dorsal lobe of distal part of caruncle (*e.g.*, Fig. 17 *B*) present, well developed. Dorsal condylar plate of femur-tibia joint (Fig. 14 *A*) absent or indistinct. Tarsi I–II with 5 setae (*p* and *q* absent). Tarsal setae *ra* and *la* I–II simple or spiniform. Genual seta *cG* I longer or slightly shorter than genu I and modified. Genual setae *cG* I longer than *cG* II. Tarsal setae *q* III absent. Tarsal setae *w*, *r*, and *p* III absent. Tarsal seta *s* III simple. Sigma III absent, represented by alveolus (present but short in *Ch. furunculus*). Tarsus IV with maximum of 5 setae (*s*, *p*, *q* always absent). Tarsal setae *e*, *f* IV simple or absent. Tarsal seta *w* IV distinctly shorter than leg IV or absent. Tibial seta *kT* IV absent. Solenidion ϕ IV present.

Immobile deutonymph present (p. 38).

Adults. Second anterior tooth of fixed cheliceral digit ($tf2''$) forming long, blade-shaped crown, extending to posterior group of teeth (Fig. 1 *A*). Anterior paraxial process of cheliceral body absent (Fig. 1 *A*). Fenestrate area fe1 of cheliceral body not striated (Fig. 1*A*). Paraxial and antiaxial rutellar lobes (*rlp* and *rpa*) free, paraxial lobe separate ventrally and dorsally (Fig. 4 *A,B*). Supracoxal seta filiform, situated on supracoxal sclerite lateral to outer ridge of supracoxal sclerite. Anterio-lateral ridge of supracoxal sclerite present (Fig. 6 *E-I*). Setae h_3 external to h_2. Cupules *im* ventral (correlated with HDN). Cupules *ip* posterior to setae f_2 (correlated with HDN). Disto-dorsal lobe of distal part of the caruncle present, well developed (correlated with HDN). Dorsal condylar plate of femur-tibia joint broad, sometimes medially incised, submedial. Solenidion ω_2 I proximal to *d* I. Solenidion ω_2 II absent. Seta *w* III absent (correlated with HDN). Tarsal setae *r* III–IV absent. Seta *kT* IV absent (correlated with HDN).

Female. Proximal ends of anterior apodemes I and pregenital sclerite fused. Proximal ends of anterior apodemes I fused forming sternum. Inseminatory canal trumpet-shaped or funnel shaped, weakly sclerotized, not protruding inside spermatheca. Posterior ends of supporting sclerite of preoviporal canal situated near area of genital papillae. Condylophores with long sclerotized portion, distinct proximal unsclerotized portion absent.

Male. Main part of progenital sclerites anterior to genital capsule (medial sclerite) (Fig. 10 *F*, Fig. 12 *B–E*). Progenital sclerites completely fused forming large unpaired sclerite (Fig. 10 *F*, Fig. 12 *B–E*). Lateral processes (horns) of dorsal supporting sclerite with secondary processes (Fig. 12 *B–E*). Body of dorsal supporting sclerite developed posterior to base of aedeagus. Genital setae on progenital folds. Genital setae short, transparent mammillae. Tarsal seta *q* II absent. Tarsal setae *e* III–IV present. Tarsal setae *q* III–IV absent. Setae *s* and *w* IV both subapical, close to each other. Tarsi I–IV distinctly thicker than in females. Sclerotized portions of condylophores separate, anterior condylophore modified to a bilobed sucker. Pretarsal suckers present. Distinct anterio-dorsal protuberance on tarsi I–IV present.

Heteromorphic males absent.

Larva. Claparède's organ shaft more or less cylindrical, constricted apically; dome spherical.

Biology and host associations. Species of this genus are associated with Megachilidae, tribes Lithurgini (*Lithurgus*, *Trichothurgus*, *Microthurge*), Osmiini (*Osmia*, *Hoplitis*, *Chelostoma*), Anthidiini (*Rhodanthidium*, *Anthidium*), and Megachilini (*Megachile*), and with Apidae, tribes Emphorini (*Melitoma*, *Diadasia*, *Ptilothrix*, *Ancyloscelis*), and Tapinotaspidini (*Chalepogenus*). Most species occur on *Lithurgus* and *Osmia*, while only one species is associated with each of the remaining host genera.

The mites usually kill young bee larvae and feed on provisioned pollen and nectar. In nests with partitions (*Osmia*), bees that develop in the innermost cells chew their way out of the nest, and phoretic deutonymphs from the opened cells may attach to them. The mites in the innermost cell would possibly die because of their inability to break through the partition. In nests without partitions (*Lithurgus*), some young bees possibly complete development and transform to adults that disperse the mites.

The presence of the inert non-phoretic deutonymph along with the phoretic deutonymph is the most conspicuous feature in the life-cycle of this genus. This is a highly regressive, cyst-like morph with legs and most setae greatly reduced (Fig. 24). It is capable of surviving in old bee nests and infesting new hosts that reuse these nests or nest material. Inert deutonymphs are very important for the mite survival when mites are trapped in innermost cells of an infested nest or all bee larvae are killed and therefore cannot transfer mites to a new nest as adults.

Biology has been studied for *Chaetodactylus osmiae* (Chmielewski, 1993; Fain, 1966; Popovici-Baznosanu, 1913; Lith, 1957), *Ch. birulai* (Lith, 1957), and *Ch. krombeini* (Krombein, 1962, 1967) (see below).

Distribution. *Chaetodactylus* is associated with megachilid bees on a worldwide basis (except Antarctica), while species associated with apid bees are only found in the Neotropical region. *Chaetodactylus* is associated with *Hoplitis* species in the Nearctic region, but not in the Old World where this host bee genus also occurs. Similarly, no records are known for *Chaetodactylus* associated with North American *Chelostoma* and *Megachile*, while the mites do occur on these hosts in the western Palaearctic. The close similarity of species of the *osmiae*-lineage and *Ch. anthidii* associated with *Rhodanthidium sticticum* suggests a recent host shift from *Osmia* and subsequent vicariance in the Palaearctic region. No *Chaetodactylus* are positively known from New World Anthidiini, although we were able to find one on *Anthidium* spp. in Chile. The distribution patterns of *Ch. krombeini* + *Ch. claviger* and *Ch. claudus* + *Ch. osmiae*, sister species living in the Nearctic and southwestern Palaearctic regions, respectively, indicate their recent vicariance. The *ludwigi-dalyi* lineage has a broad distribution in the Australian, Oriental, Afrotropical, Neotropical, and south Palaearctic regions, which may imply intercontinental dispersal events or an ancient Gondwanan origin of this early derivative lineage.

Key to Species of the Genus *Chaetodactylus* of the World

Phoretic heteromorphic deutonymphs*

1 Solenidion ϕ IV longer than combined length of genu and tibia IV. Tarsal setae *w*, *r*, *f*, and *e* IV longer than tarsus IV and nearly uniform in length; all stiff ("non-bendable"). Suckers ad_3 larger than inner unsclerotized area of suckers ad_{1+2}. Associated with *Melitoma* (Apidae). Mexico: Chiapas, Oaxaca, Tabasco; Honduras: Yoro . . . . **Chaetodactylus melitomae** Klimov & OConnor, 2007 (p. 113)

\- Solenidion ϕ IV shorter than combined length of genu and tibia IV. At least one of tarsal setae *w*, *r*, *f*, and *e* IV shorter than tarsus IV, if all longer then they are non-uniform in length and width; long setae, if present, filiform ("bendable"). Suckers ad_3 smaller or equal to inner unsclerotized area of suckers ad_{1+2}. Associated with Megachilidae or rarely Apidae 2

2(1) Setae *mG* II and *vF* II shorter than combined length of femur, genu, and tibia II. Posterior apodeme II absent, if present than interrupted and less than half of distance separating base of leg II and apodemes III (3/4 of lateral edge of sternal shield in *Ch. lassulus*). Primarily associated with *Lithurgus*, one species with *Megachile bombycina*. 17

\- At least one setae, *mG* II or *vF* II, equal to or exceeding combined length of femur, genu, and tibia II. Posterior apodeme II well-developed, at least 1/2 length of distance separating base of leg II and apodemes III. Primarily associated with *Osmia*, *Hoplitis*, *Chelostoma*, and *Rhodanthidium*. 3

3(2) Tarsal setae *e* and *f* IV longer than length of tarsus IV. Primarily associated with *Osmia*, *Hoplitis*, *Chelostoma*, and *Rhodanthidium*. Holarctic . . 4

\- Tarsal setae *e* and *f* IV microsetae, shorter than width of tarsus IV, or absent. Primarily associated with *Osmia* subgenera *Cephalosmia*, *Diceratosmia*, *Helicosmia*. Nearctic 15

4(3) Setae c_2 situated outside prodorsal shield. Both tarsal setae *e* and *f* IV, or only *e* IV shorter or slightly longer than legs IV. Setae *wa* I–II not widened or only slightly widened at bases 5

\- Setae c_2 situated on prodorsal shield (in small specimens of *Ch. chrysidis* may be outside the shield). Both tarsal setae *e* and *f* IV longer than legs IV. Setae *wa* I–II usually distinctly widened at bases. 11

5(4) Setae *si* not extending beyond posterior edge of prodorsal shield, shorter than *se*, situated anterior to transverse level of c_2 and c_p. Setae *e* and *f* IV subequal, both shorter or roughly equal to leg IV, in one species (*Ch. reaumuri*) setae *e* IV longer than legs IV and more than 2 times longer than *f* IV. Associated with *Osmia* or *Anthidium*. Holarctic 6

\- Setae *si* extending beyond posterior edge of prodorsal shield and almost as long as *se*, situated almost on same transverse level with c_2 and c_p. Setae *e* IV longer than legs IV and more than 2 times longer than *f* IV. Setae e_1 as long as d_1. Associated with *Chelostoma florisomne* and *Chelostoma rapunculi* (Megachilidae), also found on its parasites, *Sapyga quinquepunctata* and *S. clavicornis* (Hymenoptera: Sapygidae). Russia: Kirovskaya Oblast'; Czech Republic; Netherlands . . . . **Chaetodactylus birulai** Zachvatkin, 1941 (=*Chaetodactylus poetae* Samšiňák, 1973, **syn. n.**)

6(5) Setae *mG* and usually *cG* I shorter or equal to combined length of genu and tibia I. Western Palaearctic. 7

- Setae *mG* and *cG* I distinctly longer than combined length of genu and tibia I. Holarctic 8

7(6) Setae *si* distinctly shorter than 1/2 of distance between them. Setae d_1 shorter or nearly equal to 1/2 of distance between them. Most of prodorsal shield usually with transverse linear pattern. Associated with *Osmia tricornis* (type host), *O. niveata*, *O. cornuta*, and *O. latreillei*. Italy (type locality), Spain, Tunisia. . . . . **Chaetodactylus zachvatkini** sp. n., nom. n. pro *Ch. osmiae* sensu Zachvatkin, 1941 (part., non Dufour, 1839)[7]

- Setae *si* nearly as long as 1/2 of distance between them. Setae d_1 distinctly longer than 1/2 of distance between them. Most of prodorsal shield with scale-like pattern . . . Associated with *Rhodanthidium sticticum*. Tunisia (type locality), France . . . . **Chaetodactylus anthidii** (Oudemans, 1911)

8(6) Setae *f* IV about 3 times shorter than *e* IV; *e* IV much longer than leg IV. On "*Osmia rufiventris* Panzer"[8] (type host), *O. niveata*, *O. leucogastra*, *O. brevicornis*, *O. tricornis*, also phoretic on cleptoparasite of *Osmia*: *Stelis murina* . Czech Republic (type locality), Germany, Italy, Spain, Turkey, Greece, Ukraine, Georgia, Tunisia. . . . . **Chaetodactylus reaumuri** (Oudemans, 1905)

- Setae *f* and *e* IV subequal, both shorter than leg IV 9

9(8) Conoids ps_2 less than 8 in diameter; anterior edges of their bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Distance between cupules *ih* and bases of ps_2 nearly equal to diameter of latter. Associated with *Osmia ribifloris*. USA: Texas, Utah . . . . **Chaetodactylus claudus**, sp. n. (p. 133)

- Conoids ps_2 exceeding 8 in diameter; anterior edges of their bases anterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Distance between cupules *ih* and bases of ps_2 less than diameter of latter. Palaearctic 10

10(9) Posterior edge of bases of conoids ps_2 posterior to center of inner unsclerotized areas of suckers ad_{1+2}. Unsclerotized elements of pattern of prodorsal and hysterosomal shields lens-like. Associated with *Osmia rufa* (type host), *O. tricornis*, *O. niveata*, *O. cornuta*. France (type locality), Belgium, England, Spain, Germany, Hungary, Croatia, Romania (only verified records listed). . . . . **Chaetodactylus osmiae** (Dufour, 1839) (=*Ch. mahunkai* Samšiňák, 1973)

- Posterior edge of bases of conoids ps_2 anterior to center of inner unsclerotized areas of suckers ad_{1+2}. Unsclerotized elements of pattern of prodorsal and hysterosomal shields represented by short lines. On *Osmia cornifrons* (type host), *O. excavata*, *O. pedicornis*, *O. taurus*. Japan . . . . **Chaetodactylus nipponicus** Kurosa, 1987

11(4) Coxal setae *1a* not inflated at bases, situated on soft cuticle. Seta *si* not reaching posterior edge of prodorsal shield. Tarsus IV with only one ventromedial seta (*w* IV). Anterior and posterior apodemes IV connected on outer edge of coxal field IV. Posterior apodemes IV without protruding medial end. Lateral angles of prodorsal shield attenuated. Associated with *Osmia aurulenta*, and its parasite, *Chrysura trimaculata* (Chrysididae) (type host). Belgium (type locality), Germany . . . . **Chaetodactylus chrysidis** Fain and Baugnée, 1996 (=*Ch. chrysidis aurulenticola* Fain & Baugnée, 1996, **syn. n.**[9])

- Coxal setae *1a* inflated at bases (only slightly in *Ch. hirashimai*), situated on sclerite fused with anterior apodemes II. Tarsus IV with both ventro-medial setae (*w* and *s* IV) present. Seta *si* distinctly extending beyond posterior edge of prodorsal shield. Anterior and posterior apodemes IV disjunct on outer edge of coxal field IV. Posterior apodemes IV with protruding medial end. Lateral angles of prodorsal shield not attenuated. Holarctic 12

12(11) Sclerites surrounding alveoli of *4b* and *3a* represented by thin margins around bases of setae; sclerites of *3a* not fused to anterior coxal apodemes IV. Coxal setae *3a* and *4b* only slightly widened at bases, almost filiform. Posterior end of sternal apodeme usually simple. Associated with *Osmia* and *Hoplitis* 13

- Sclerites surrounding alveoli of *4b* and *3a* large, irregularly shaped; sclerites surrounding alveoli of *3a* fused to anterior coxal apodemes IV. Coxal setae *4b* and *3a* usually more distinctly widened at base. Posterior end of sternum usually distinctly bifurcated. Associated with *Osmia* 14

13(12) Setae *1a* distinctly inflated at bases. Seta *se* reaching transverse level of c_2. Associated primarily with *Hoplitis* spp. USA: Michigan, North Carolina, New York, Ohio, Tennessee, Idaho . . . . **Chaetodactylus hopliti** sp. n. (p. 137)

- Setae *1a* only slightly widened at bases. Seta *se* not reaching transverse level of c_2. Associated with *Osmia excavata* (type host), *O. cornifrons*, *O. imaii*, *O. pedicornis*. Japan . . . . **Chaetodactylus hirashimai** Kurosa, 1987

14(12) Posterior end of anterior coxal apodeme II without large sclerite. Setae h_3 0.9–1.3 (1.1 ± 0.1, n = 10) times longer than h_2. Associated primarily with *Osmia lignaria*. USA, Canada . . . . **Chaetodactylus krombeini** Baker, 1962 (p. 141)

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[7] This species was described and depicted by Zachvatkin (1941) as *Chaetodactylus osmiae* (Dufour). Van Asselt (2000) redescribed *Chaetodactylus osmiae* from Belgium (which is very close to the type locality) and from the type host, *Osmia rufa*. He believed that Zachvatkin had the same species but erroneously depicted its dorsum without prodorsal shield (actually it is present on the figure and mentioned in the description and in the key) and short dorsal setae (longer in true *Ch. osmiae*). Because Zachvatkin describes *Ch. osmiae* as having "lateral suckers [=ps_2] situated on the same transverse level with central ones [ad_1+ad_2]" (as in true *Ch. osmiae*) but figures mites with shorter setae, we believe that he dealt with two very similar species and one of them, having "shorter" setae, is new, *Chaetodactylus zachvatkini* nom. n. Unfortunately, we could not find any specimens that match *Ch. osmiae* sensu Zachvatkin, 1941 or even true *Ch. osmiae* in his collection in Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (ZIN). We designate the holotype of *Chaetodactylus zachvatkini* with the following data: **ITALY**: Liguria, San Remo, ex *Osmia tricornis* (male), collection of F. Morawitz, BMOC 03-0523-005. Paratypes: 19 HDNs—same data as holotype; 10 HDNs—Calabria, *Osmia tricornis* (female), BMOC 03-0523-005, other data as for holotype; 1 male, 1 female—**SPAIN**: Cataluña, Barcelona, *Osmia cornuta* nest#: BCN (31), 1991 J. Bosch, GCE 91-0517-19, UMMZ BMOC 05-0310-003; 2 males, 1 female, 1 HDN—ex *Osmia niveata* nest BCN OF (33), 1991, J. Bosch, GCE 91-0517-1, UMMZ BMOC 05-0310-001; 2 HDNs—ex *Osmia latreillei*, nest BCN (29), 1991 J. Bosch GCE 91-0517-24, UMMZ BMOC 05-0310-005; 2 females—ex *Osmia* sp nest host nest#: BCN x1 (26), 1991, J. Bosch, GCE 91-0517-29, UMMZ BMOC 05-0310-006; 2 HDNs—*Osmia* sp BCN x2 (27), 1991, J. Bosch, GCE 91-0517-27, UMMZ BMOC 05-0310-007; 2 HDNs, 2 males—ex *Osmia* sp., nest BCN x2 (28), 1991, J. Bosch, GCE 91-0517-30; UMMZ BMOC 05-0310-008; 2 HDNs, 2 females—ex *Osmia* sp nest BCN D17 (35), 1991, J. Bosch, GCE 91-0517-34, UMMZ BMOC 05-0310-009; 2 HDNs—Granadella, ex *Osmia latreillei* nest GRA 143(1) (no. 4), 1991, J. Bosch, GCE 91-0517-23, UMMZ BMOC 05-0310-004; 2 HDNs—Taradell, ex *Osmia niveata* nest TAR 1–6(N) (11), 1991, J. Bosch, GCE 91-0517-8, UMMZ BMOC 05-0310-002; 1 HDN—**TUNISIAN REPUBLIC**: Tunis, ex *Osmia tricornis* (ventral mesosoma), no date Graeffe, KU BMOC 93-0329-001. The holotype is in ZIN, paratypes are in ZIN and UMMZ. Material from Italy was collected by Dr. S. V. Mironov in the insect collection of ZIN on our request. Since insect-associated mites described by Zachvatkin (1941) were collected in ZIN and this author mentioned that *Ch. osmiae* occurs in Italy on *Osmia tricornis* (p. 398), we believe that our mites originated from the same bee hosts that were sampled by Zachvatkin.

[8] Probably lapsus pro *Osmia fulviventris* now known as *Osmia* (*Helicosmia*) *niveata*

[9] Intermediate forms between *Ch. chrysidis* s. str. (larger, with tongue-like projection on posterior hysterosoma) and *Ch. chrysidis aurulenticola* (smaller, without projection) occur on a single bee *Osmia aurulenta* from Germany (BMOC 95-0315-002), suggesting that the differences between the two subspecies represent rather allometric variation of *Ch. chrysidis*.

- Posterior end of anterior coxal apodeme II with large sclerite. Setae h_3 1.2–2.0 (1.5 ± 0.2, n = 8) times longer than h_2. Associated primarily with *Osmia tricornis*. Italy (type locality), France, Egypt . . . **Chaetodactylus claviger** Oudemans, 1924

15(3) Setae d_2 situated outside hysterosomal shield. Prodorsal setae *si* distinctly longer than 1/2 of distance between their bases. Seta h_3 shorter than femur I. Posterior apodeme II, approximately 1/2 the length of lateral edge of sternal shield. Anterior and posterior apodemes IV not connected on outer edge of coxal field IV. Setae *mG* II more than 2 times shorter than *vF* II. Associated with *Osmia* (*Diceratosmia*) *azteca*. Mexico: Chiapas . . . . **Chaetodactylus azteca**, sp. n. (p. 127)

- Setae d_2 situated on hysterosomal shield. Prodorsal setae *si* shorter than 1/2 of distance between their bases. Seta h_3 longer than femur II. Posterior apodeme II exceeding 3/4 the length of lateral edge of sternal shield. Anterior and posterior apodemes IV connected on outer edge of coxal field IV. Seta *mG* II longer than *vF* II 16

16(15) Setae h_3 equal or exceeding combined length of femur, genu, and tibia I. Associated primarily with *Osmia* (*Cephalosmia*): *O. subaustralis*, *O. montana*, *O. marginipennis*, *O. californica*, and *O. grinnelli*. Northwestern, southwestern, and northeastern USA; western and subarctic Canada. See p. 94 for identification of 3 partially overlapping morphs . . . . **Chaetodactylus micheneri** sp. n. (p. 127)

- Setae h_3 distinctly shorter than combined length of femur, genu, and tibia I. Associated with *Osmia* (*Helicosmia*) *georgica*. USA: North Carolina . . . . **Chaetodactylus rozeni** sp. n. (p. 132)

17(2) Hysterosomal setae d_2 situated outside hysterosomal shield *and* setae c_1 on anterior edge of this shield. Tarsal setae *la* I–II lanceolate (filiform in undescribed species from Neotropics). Tarsal seta *w* IV more than 1.5 times shorter than *s* IV; seta *e* IV more than 2 times shorter than *f* IV. Seta *s* III submedial. Afrotropical, Oriental, Australian, southeastern Palaearctic, Neotropical regions 18

- Both hysterosomal setae d_2 and c_1 situated *either* on hysterosomal shield *or* outside this shield. Tarsal setae *la* I–II filiform. Tarsal seta *w* and *s* IV subequal; setae *e* and *f* IV subequal or absent. Seta *s* III subterminal. Holarctic and Neotropical 19

18(17) Setae *4b* not reaching transverse level of anterior coxal apodemes IV. Associated with *Lithurgus atratus* (type host), *L. scabrosus*. Micronesia (type locality), Indonesia, New Caledonia, French Polynesia, South India . . . . **Chaetodactylus ludwigi** (Trouessart, 1904)

- Setae *4b* slightly extending beyond transverse level of anterior coxal apodemes IV. Associated with *Lithurgus pullatus* and *L. aethiops*, few specimens collected on *Ceratina* (*Pithitis*) *turneri* (type host). South Africa (type locality), Zimbabwe, Mozambique, Madagascar . . . . **Chaetodactylus dalyi** Fain, 1974

19(17) Setae c_1 and d_2 situated outside hysterosomal shield. Tarsus I elongated and solenidion ω_1 and ω_3 distinctly separated, distance exceeds 3 diameters of alveolus of famulus (ε). Legs IV 2.8–3.6 times shorter than idiosoma. 20

- Setae c_1 and d_2 situated on edges of hysterosomal shield. Tarsus I not elongated and solenidion ω_1 and ω_3 close to each other, distance less than 3 diameters of alveolus of famulus (ε). Relative length of legs IV variable 22

20(19) Prodorsal shield small, not extending anteriorly beyond *se*. Setae *si* situated outside prodorsal shield. Posterior apodemes II exceed half the length of lateral edges of sternal shield. Longitudinal striation between coxae III–IV present. Ventral side of claws I–III finely striated. Setae *e* and *f* IV vestigial or absent. Associated with *Trichothurgus dubius*, *T. herbsti*. Chile . . . . **Chaetodactylus lassulus** Klimov and OConnor, 2007

- Prodorsal shield larger, extends anterior of *se*. Setae *si* situated on prodorsal shield. Posterior apodemes II absent or shorter than 1/3 of lateral edges of sternal shield. Longitudinal striation between coxae III–IV absent. Ventral side of claws I–III smooth. Setae *e* and *f* IV longer than width of tarsus IV. 21

21(20) Dorsal idiosomal setae relatively short: d_2 not reaching anterior margin of hysterosomal shield and reaching e_2, *si* and e_1 shorter than half the distance between corresponding pairs. Alveolus of *vi* indistinct. Solenidion σ I usually about 0.6 of genu I length. Proximal acetabular extensions IV connected. Solenidion σ III present, short. Associated with *Lithurgus listrotus*. USA: California . . . . **Chaetodactylus furunculus** sp. n. (p. 116)

- Dorsal idiosomal setae longer: d_2 extending beyond anterior margin of hysterosomal shield and reaching e_2, *si* and e_1 distinctly longer than half the distance between corresponding pairs. Alveolus of *vi* distinct. Solenidion σ I nearly as long as genu I or longer. Proximal acetabular extensions IV disjunct. Solenidion σ III absent. Associated with *Lithurgus antilleorum*. Jamaica, Dominican Republic . . . . **Chaetodactylus antillarum** sp. n. (p. 113)

22(19) Setae *e* and *f* IV longer than width of tarsus IV. Genual seta *mG* I extending beyond base of tarsus I. Legs IV 3.2–3.5 times shorter than idiosoma. Seta *si* more than 1.5 times shorter than d_2 and e_2. Associated with *Megachile bombycina* and *M. ligniseca*. Western Palaearctic . . . . **Chaetodactylus dementjevi** Zachvatkin, 1941

- Setae *e* and *f* IV shorter than width of tarsus IV. Genual seta *mG* I not extending beyond base of tarsus I. Legs IV 4.1–5.3 times shorter than idiosoma. Seta *si* less than 1.5 times shorter than d_2 and e_2. Associated with *Lithurgus*. Nearctic 23

23(22) Setae *si*, d_2, and e_2 represented by microsetae, shorter than 1/4 of prodorsal shield length. Setae of hysterosomal shield represented by microsetae (Fig. 58 *A*). All idiosomal setae smooth. Apical tarsal setae *e* and *f* IV absent. On *Lithurgus apicalis*. USA: New Mexico . . . . **Chaetodactylus kouboy** sp. n. (p. 121)

- Setae *si*, d_2, and e_2 longer than 1/4 of prodorsal shield length. On hysterosomal shield, at least setae f_2 are not microsetae. Idiosomal setae smooth or some long setae pectinate. Apical tarsal setae *e* and *f* IV present or absent 24

24(23) Ratio of length of prodorsal shield/length of seta d_1 4.7–7.3 (5.8 ± 0.70). Associated with *Lithurgus gibbosus*. USA: Florida . . . . **Chaetodactylus gibbosi** Klimov & OConnor (p. 124)

- Ratio length of prodorsal shield/length of seta d_1 2.4–4.4 (3.2 ± 0.43) 25

25(24) CV 1 and 2 fall within *lithurgi* group (p. 94). Ratio length of seta *vF* II/length of seta h_2 1.2–2.6 (1.6 ± 0.26). Associated with *Lithurgus apicalis*, *L. littoralis*, and *L. gibbosus*. USA: Texas, New Mexico, Arizona, Colorado, Idaho . . . . **Chaetodactylus lithurgi** Klimov and OConnor (p. 121)

- CV 1 and 2 fall within *abditus* group (p. 94). Ratio *vF* II/h_2 2.2–3.4 (2.7 ± 0.31). Associated with *Lithurgus planifrons* and *L. echinocacti*. USA: Arizona; Mexico: Socorro Is . . . . **Chaetodactylus abditus** Klimov & OConnor (p. 124)

Immobile heteromorphic deutonymphs**

1 Legs I–II more than 2 times longer than their bases, some articles distinct. Attachment organ situated on distinct posterior projection . . . **Ch. ludwigi**

- Legs I–II less than 2 times longer than their bases, without distinct articulation. Posterior body rounded 2

2(1) Anterior apodemes IV developed as well as apodemes I–II. Hysterosoma with distinct border situated outside legs II–IV . . . . **Ch. krombeini** (p. 141)

- Anterior apodemes IV not developed. Border outside legs I–II absent 3

3(2) Legs III–IV longer than their bases . . . . **Ch. micheneri** (p. 127)

- Legs III–IV shorter than their bases . . . . . . **Ch. osmiae** and **Ch. claudus**

Females***

1 Central part of dorsal opisthosoma more or less uniformly covered with small (1.5–2.0) mammillae (2.0–4.0 in *Ch. claudus*); at least some mammillae conical or subconical, with attenuated, darker tips. Adanal setae ad_3 extending well beyond *ih*. (-) Setae c_3 almost reaching or extending beyond trochanters IV. Position of setae ps_3 relatively *4a* variable. Sclerotized lining of outer end of inseminatory canal shorter than 0.4 length of inseminatory canal. Setae *gT* I–II smooth, filiform; *hT* I–II only slightly barbed, almost smooth 4

- Central part of dorsal opisthosoma covered with fleshy tubercles (2.0–3.5), usually with rounded, transparent tips. Adanal setae ad_3 extending at most only slightly beyond *ih*. Setae ps_3 posterior to *4a* level. Other charcters variable 2

2(1) Some tubercles of central part of dorsal opisthosoma larger (2.5–3.0), partially fusing together. On peripheral part, tubercles arranged in transverse rows ultimately forming distinct linear pattern. Transverse linear pattern extending ventrally covering almost all ventral opisthosoma. Tibial setae *gT* I–II barbed, distinctly widened. Sclerotized lining of outer end of inseminatory canal longer than 0.4 length of inseminatory canal (Fig. 9 *B*). (-) c_3 extending beyond trochanters IV. ps_3 slightly posterior to *4a* level. Inseminatory canal trumpet-shaped, about 2 times longer than its width at spermatheca (Fig. 9 *B*). Setae *gT* I–II distinctly barbed, spiniform. Copulatory tube very short, trapezoidal. . . . . **Chaetodactylus reaumuri**

- Tubercles of central part of dorsal opisthosoma smaller (2.0–3.0), usually not partially fusing together and not forming distinct linear pattern on peripheral part of dorsal and on most part of ventral opisthosoma. Tibial setae *gT* I–II smooth, filiform; *hT* I–II only slightly barbed. Sclerotized lining of outer end of inseminatory canal shorter than 0.4 length of inseminatory canal. Copulatory tube absent 3

3(2) Inseminatory canal less than 3 times longer than its width at spermatheca (Fig. 9 *C*). Setae c_3 not reaching trochanters IV . . . . . . **Chaetodactylus zachvatkini**

- Inseminatory canal more than 5 times longer than its width at spermatheca (Fig. 9 *E*). Setae c_3 reaching trochanters IV but not extending beyond their posterior level . . . . **Chaetodactylus micheneri** (p. 127)

4(1) Inseminatory canal more than 2 times longer than its width at spermatheca (Fig. 9 *D*). Setae ps_3 usually anterior to *4a* level. Copulatory tube absent 6

- Inseminatory canal less than 2 times longer than its width at spermatheca. Short copulatory tube present 5

5(4) Inseminatory canal about 1.1–1.2 times longer than its width at spermatheca. Dorsal opisthosomal mammillae 1.0–2.0 (-) Setae ps_3 posterior to *4a* level . . . . **Chaetodactylus osmiae**

- Inseminatory canal about 1.7 times longer than its width at spermatheca. Dorsal opisthosomal mammillae 2.0–4.0 . . . . . **Chaetodactylus claudus** (p. 133)

6(4) Outer sclerotized ridge surrounding supracoxal gland opening distinctly longer than tibia II . . . . **Chaetodactylus krombeini** (p. 141)

- Outer sclerotized ridge surrounding supracoxal gland opening only as long as tibia II . . . . **Chaetodactylus hopliti** (p. 137)

Males***

1 Backward bend of aedeagus posterior to dorsal supporting sclerite. Transverse processes of dorsal supporting sclerite spirally twisted, band-like (Fig. 10 *F*). Genital valves with posterior bifurcated flaps (Fig. 10 *F*). Setae d_1 not extending beyond e_1. (-) Setae c_3 reaching trochanters IV but not extending beyond them. Central part of dorsal opisthosoma with mammillae or tubercles, diameter approximately 1.5. Basal widening of aedeagus not reaching level of ps_3, distance between them exceeding length of basal widening. Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite. Anterior end of genital capsule without distinct projection. Aedeagus distinctly extending beyond genital capsule. Setae *gT* and *hT* I–II smooth. Ratio of pretarsal sucker width/tarsus III width 0.34–0.35 . . . . **Chaetodactylus micheneri** (p. 127)

- Backward bend of aedeagus at level of dorsal supporting sclerite. Transverse processes of dorsal supporting sclerite not twisted, and not band-like (dorsal supporting sclerite shaped like a vertebra in superior or inferior view) (Fig. 12 *E*). Genital valves without posterior bifurcated flaps. Setae d_1 extending beyond e_1 2

2(1) Medial sclerite of genital capsule extending beyond posterior level of dorsal supporting sclerite (Fig. 12 *B*). Anterior end of genital capsule with distinct projection (Fig. 12 *B*). Anterior processes of dorsal supporting sclerite more than 2 times wider than posterior ones, forming anterior concavity that exceeds 1.6 of basal "body" (Fig. 12 *B*). (-) Setae d_1 not extending beyond h_1 (slightly extending beyond e_1). Setae c_3 reaching trochanters IV but not extending beyond them. Basal widening of aedeagus almost reaching level of ps_3. Aedeagus distinctly extending beyond genital capsule. Setae *gT* I–II smooth and *hT* I–II barbed. Ratio of pretarsal sucker width/tarsus III width 0.41–0.44. **Chaetodactylus reaumuri**

- Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite (Fig. 12 *C–E*). Anterior end of genital capsule without distinct projection (Fig. 12 *C–E*). Anterior processes of dorsal supporting sclerite usually less than 2 times wider than posterior ones; anterior concavity not exceeding 1.6 of basal "body" (Fig. 12 *C–E*). 3

3(2) Basal widening of aedeagus almost reaching or extending beyond level of ps_3, longer than distance between ps_3. Setae d_1 extending beyond posterior end of body. Central part of dorsal opisthosoma with distinct conical mammillae, diameter about 0.9. (-) Setae c_3 extending beyond trochanters IV. Aedeagus distinctly extending beyond genital capsule (Fig. 12 *E*). Setae *hT* I–II barbed 6

- Basal widening of aedeagus not reaching level of ps_3, shorter than distance between ps_3. Setae d_1 not extending beyond posterior end of body. Central part of dorsal opisthosoma with tubercles or somehow conical mammillae, diameter 1.5–2.2. Aedeagus not or slightly extending genital capsule (Fig. 12 *C–D*), or distinctly extending and reaching ps_3 level (*Ch. claudus*) 4

4(3) Setae c_3 not reaching trochanters IV. Setae *hT* I–II smooth. (-) Central part of dorsal opisthosoma with mammillae or tubercles, diameter 2.2. Ratio of pretarsal sucker width/tarsus III width 0.30–0.34. . . . . **Chaetodactylus zachvatkini**

- Setae c_3 reaching trochanters IV or extending beyond them. Setae *hT* I–II barbed 5

5(4) Aedeagus slightly extending beyond genital capsule, not reaching level of setae ps_3 (Fig. 12 *C*). Central part of dorsal opisthosoma with mammillae or tubercles, diameter 1.5. Ratio of pretarsal sucker width/tarsus III width 0.41–0.43 . . . . **Chaetodactylus osmiae**

- Aedeagus distinctly extending beyond genital capsule, almost reaching level of setae ps_3. Central part of dorsal opisthosoma with mammillae or tubercles, diameter about 2.0. Ratio of pretarsal sucker width/tarsus III width about 0.25 . . . . **Chaetodactylus claudus** (p. 133)

6(3) Distance d_1-d_1 (from outer edges) 46–56 (51 ± 3, n = 11) (1). Sclerotized area surrounding posterior supracoxal gland opening 36–45 (40 ± 3, n = 11) (2). (1)/(2) 1.1–1.4 (1.3 ± 0.1, n = 11). . . . . **Chaetodactylus krombeini** (p. 141)

- Distance d_1-d_1 (from outer edges) 54–67 (63 ± 6, n = 4) (1). Sclerotized area surrounding posterior supracoxal gland opening 34–36 (35 ± 1, n = 4) (2). (1)/(2) 1.6–1.9 (1.8 ± 0.1, n = 4) . . . . **Chaetodactylus hopliti** (p. 137)

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*Types of *Chaetodactylus poetae* were not studied. ** unknown for species other than included in the key; specimens of of *Ch. krombeini* and *Ch. ludwigi* were not studied. *** Because adults of many species are unknown, we give a descriptive key with additional characters after "(-)".

Chaetodactylus melitomae

Klimov & OConnor, 2007

Chaetodactylus sp. Linsley *et al*., 1980: 20 (specimens not examined, assigned to this species on basis of broad host range and geographic distribution of *C. melitomae*).

Chaetodactylus melitomae Klimov & OConnor, 2007: 821, Figs. 10–11; Klimov *et al*., 2007a: 1371.

Material. Holotype: HDN—**MEXICO: Tabasco**, Cardenas, ex *Melitoma* sp. (propodeum), on *Convolvulus* (Solanales: Convolvulaceae), 26 Sep 1979, C. Hoffman, CUIC, BMOC 95-0422-013. Paratypes: 7 HDNs, same data as holotype; 1 HDN—**Oaxaca**, Temascal, ex *Melitoma* sp. (metepisternum), 18 Oct 1963, D.H. Janzen, UCD, BMOC 95-0613-038; 9 HDNs—**Campeche,** Candelaria, 38 m, Nov 1944, No collector, AMNH, BMOC 04-0508-299; 4 HDNs—**Chiapas**, 3.5 mi N Ixtapa, Rio Blanco, ex pollen mass from cell of *Diadasia* sp., Mar 1953, R. Smith, EMEC, BMOC 04-0702-001; 4 HDNs—**HONDURAS**: **Yoro**, El Progreso, ex *Melitoma segmentaria* (propodeum), 14 Mar 1923, T.H. Hubbell, UMMZ, BMOC 95-0310-005. Holotype in CUIC; paratypes in AMNH, CUIC, OSAL, UCD, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 52, Fig. 53; Table 21, p. 201). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, separated by distinct space and diverging posteriorly (Fig. 52 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*. Prodorsal shield transversely striated. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield, longitudinally striated, except for anterio-lateral part; most lines long but shorter than half of hysterosomal shield. No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites dorsal, split into three small, separate sclerites, one of them posterior to cupule *im*, and two anterior. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Seta *cp* distinctly anterior to level of c_2. Setae *si* variable in length, either longer or shorter than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 slightly or distinctly shorter than e_1. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* more than 2 times shorter than *3a*. Sternal apodeme not bifurcate posteriorly. Posterior apodeme II absent, represented by short sclerite on middle of lateral edges of sternal shield. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) larger than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II present. Solenidion σ I from about 0.4–0.5 of genu I. Setae *mG* I shorter than combined length of genu and tibia I, *cG* I nearly equal to this. Genual setae *cG* I smooth. Genual setae *mG* I smooth. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II distinctly shorter than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, slightly longer or shorter than *mG* I, shorter or nearly equal to *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III at most reaching base of tarsus III. Seta *nG* III pectinate or smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV longer than than combined length of genu and tibia IV. Tarsal setae *s* IV present. Setae *w* or *s* IV longer than length of tarsus IV, uniform in length and width. Tarsal setae *f* and *e* IV longer than tarsus IV, symmetric, nearly equal in length. Tarsal setae *e* IV similar in length and width with *w* and *s* IV. Tarsus IV 2–1.5 times longer than its basal width.

Abnormalities. One c_2 is duplicated (95-0422-013#04); solenidion σ III developed (3.4) on one genu (95-0422-013#05); second posterior (external) solenidion σ' developed (2.3) on one genu I (95-0422-013#06).

Hosts. *Melitoma marginella*, *Melitoma segmentaria*, *Melitoma* sp. (type host) (Apidae: Emphorini) (Linsley *et al*., 1980; our data). Also known from *Diadasia* sp. (possibly host misidentification or secondary contamination; voucher specimens of the host were not available for study).

Distribution. Mexico: Campeche, Chiapas, Oaxaca, Tabasco (type locality); Honduras: Yoro.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20melitomae&-max=200&-find

Biology. Linsley *et al*. (1980) reported that 2.4% and 3.2% of the cells of *Melitoma marginella* examined at two sites in Chiapas, Mexico, contained heteromorphic deutonymphs of *Chaetodactylus* sp. nr. *ludwigi*. Given our collections of *C. melitomae* from *Melitoma* spp. from this region, we think Linsley *et al*. most likely observed this species. Those authors reported that most of these cells contained hundreds of mites, which appeared to have consumed all or substantial amounts of the pollen. The infested cells did not have fragments of bee eggs or larvae suggesting that the egg or young larva is also destroyed by the mites, or that the latter develop successfully only in cells in which oviposition did not take place. Since the deutonymphal stage is dependent upon phoretic transport from the cell in which it develops to a new cell where further development and reproduction occur, burrows of bees which arrange their cells in a series would seem to be suited to these mites. Bees emerging in cells lower down in the series would readily become contaminated if they pass through mite-infested cells (after Linsley *et al*., 1980).

Etymology. The specific epithet is derived from the host generic name and is a noun in the genitive case.

Chaetodactylus antillarum sp. n.

Material. Holotype: HDN—**JAMAICA**: **Parish of Saint Catherine**, Hellshire Hills, ex *Lithurgus antilleorum antilleorum* (propodeum), 8 Jun 1985, C. D. Michener, KU, BMOC 96-0916-190. Paratypes: 5 HDNs—same data as holotype; 2 + 3 + 6 HDNs—same data as holotype (propodeum + pronotum + metanotum), KU, BMOC 96-0916-189; 2 + 1 HDNs—**DOMINICAN**

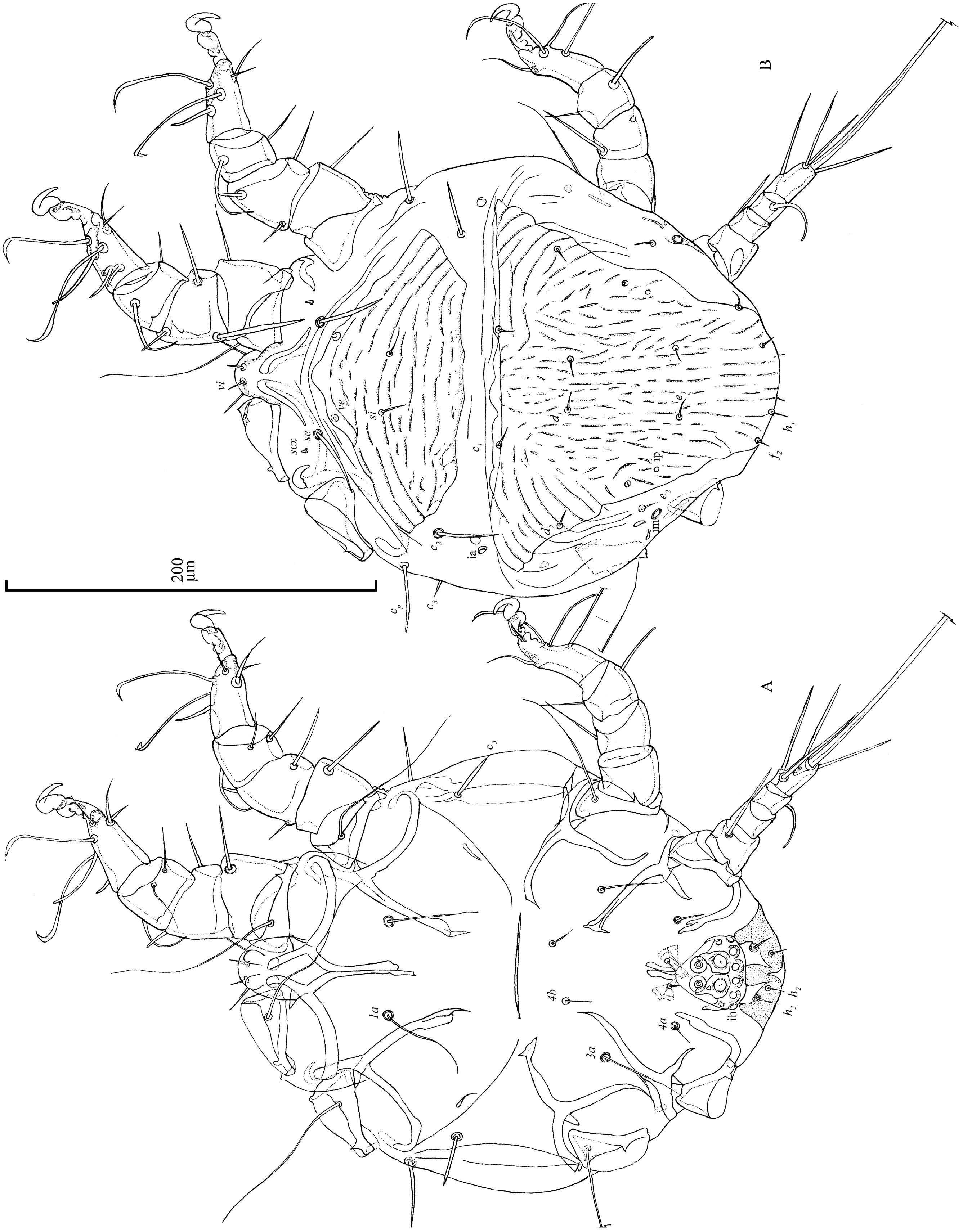

Fig. 52. *Chaetodactylus melitomae*, heteromorphic deutonymph (BMOC 95-0422-013, holotype). A, B - ventral and dorsal view.

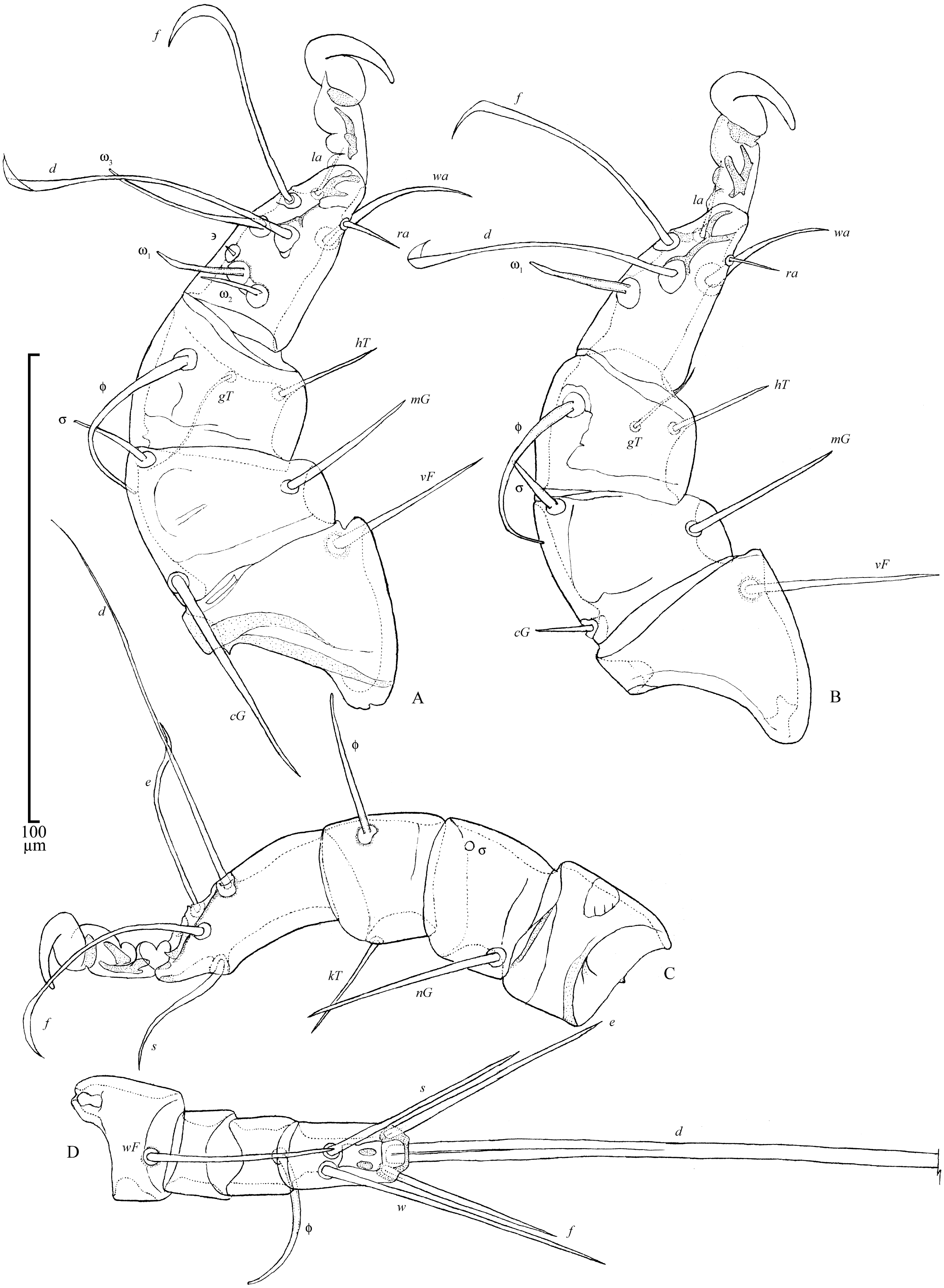

Fig. 53. *Chaetodactylus melitomae*, heteromorphic deutonymph (BMOC 95-0422-013, holotype). A–D - legs I–IV.

REPUBLIC: **Pedernales**, Cabo Rojo hdqtrs, 24 July 1985, ex *L. antilleorum antilleorum* (scrobe + propodeum), G. C. Eickwort, CUIC, BMOC 95-0422-097. Holotype in KU, paratypes in CUIC, KU, UMMZ.

Description. *Phoretic deutonymph* (Fig. 54, Fig. 55; Table 21, p. 201). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) weakly sclerotized, indistinct, separated by distinct space and diverging posteriorly (Fig. 54 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield with linear pattern indistinct because of reticulate pattern (except for anterio-lateral part). Lateral hysterosomal sclerites absent. Longest dorsal setae with slightly pectinate tips. Setae c_1 and d_2 situated outside hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae c_2 and c_p Seta c_p distinctly anterior to level of c_2. Setae *si* longer than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 slightly or distinctly shorter than e_1. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcate posteriorly. Posterior apodeme II absent. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II present. Solenidion σ I 0.9–1.0 of genu I. Setae *mG* and *cG* I shorter than combined length of genu and tibia I. Genual setae *cG* I and *mG* I pectinate. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II distinctly shorter than combined length of femur, genu and tibia II. Genual setae *mG* II pectinate, slightly longer or shorter than *mG* I, shorter or nearly equal to *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III not reaching base of tarsus III. Seta *nG* III pectinate or smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV longer than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV, uniform in length and width, shorter than 1.5 of maximum width of tarsus IV. Tarsal setae *f* and *e* IV, symmetric, nearly equal in length, shorter than tarsus IV. Tarsal setae *e* IV similar in length and width with *w* and *s* IV. Tarsus IV more than 2 times longer than its basal width.

Other instars unknown.

Abnormalities. Seta *w* IV shifted medially, *s* IV small (BMOC 96-0916-190#4). Setae *w* and *s* IV shifted: *w* medial, *s* posterior; there is only medial *w* on another tarsus IV (BMOC 96-0916-190#6). There is only one *w* IV and *s* IV alveolus on one tarsus (BMOC 96-0916-190#8). Only one seta (*w*) on each tarsus IV (BMOC 96-0916-190#9).

Hosts. *Lithurgus* (*Lithurgopsis*) *antilleorum antilleorum* (Megachilidae).

Distribution. Dominican Republic: Pedernales; Jamaica: Parish of Saint Catherine (type locality).

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20antillarum&-max=200&-find

Etymology. The specific epithet refers to the geographic region and is a noun in the genitive case.

Chaetodactylus furunculus sp. n.

Material. Holotype: HDN—**USA**: **California**, San Bernardino Co., Cedar Canyon, 4650', Sec 36 T13N R14E, *Lithurgus listrotus* (lateral mesosoma), 20 June 1980, T. Griswold, LACM, BMOC 04-1122-002. Paratypes: 21 HDNs—same data as holotype. Holotype in LACM, paratypes in LACM, OSAL, UMMZ.

Description. *Phoretic deutonymph* (Fig. 56, Fig. 57; Table 21, p. 201). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) weakly sclerotized, indistinct, separated by distinct space and diverging posteriorly (Fig. 56 *B*). Alveoli of *ve* absent. Prodorsal shield extends anterior of *se*. Prodorsal shield with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield with linear pattern indistinct because of reticulate pattern (except in anterio-lateral part). Lateral hysterosomal sclerites absent. Longest dorsal setae slightly pectinate at tips. Setae c_1 and d_2 situated outside hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae seta c_p distinctly anterior to level of c_2. Setae *si* shorter than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 h_1 slightly or distinctly shorter than e_1. Coxal setae *1a* filiform, *1a* situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* slightly shorter than *3a*. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II absent, or if present, interrupted anteriorly. Proximal acetabular extensions IV connected. Distal acetabular extensions of apodemes IV connected. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II. Solenidion σ I about 0.3 of genu I. Setae *mG* and usually *cG* I shorter or equal to combined length of genu and tibia I. Genual setae *cG* I pectinate. Genual setae *mG* I pectinate. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II distinctly shorter than combined length of femur, genu and tibia II. Genual setae *mG* II pectinate, slightly longer or shorter than *mG* I. Genual setae *mG* II shorter or nearly equal to *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III at most reaching base of

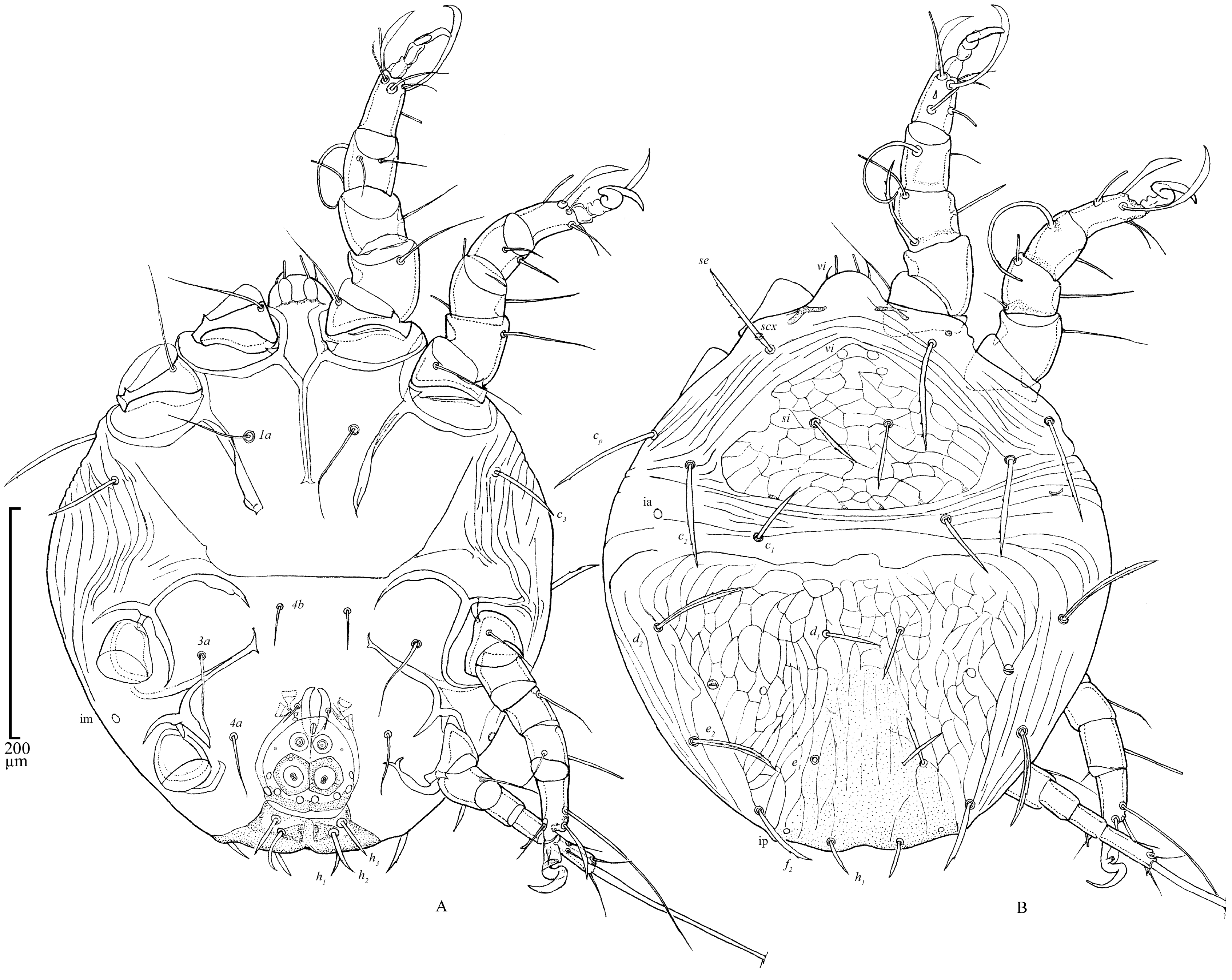

Fig. 54. *Chaetodactylus antillarum*, heteromorphic deutonymph (BMOC 96-0916-190, holotype). A, B - ventral and dorsal view.

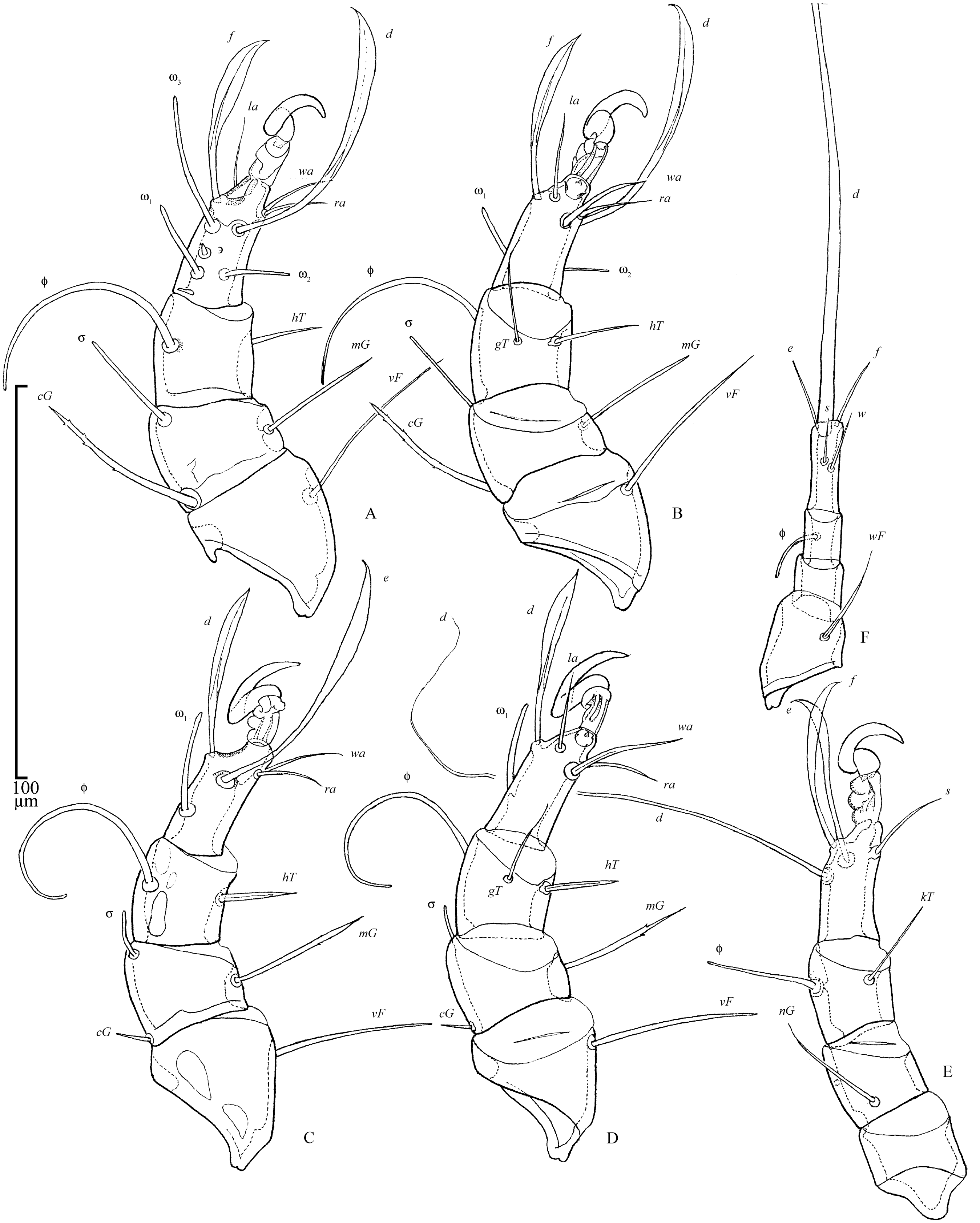

Fig. 55. *Chaetodactylus antillarum*, heteromorphic deutonymph (BMOC 96-0916-190). A, B - leg I, dorsal and ventral view; C, D - leg II, dorsal and ventral view; E - leg III; F - leg IV.

Fig. 56. *Chaetodactylus furunculus*, heteromorphic deutonymph (BMOC 04-1122-002, holotype). A, B - ventral and dorsal view.

Fig. 57. *Chaetodactylus furunculus*, heteromorphic deutonymph (BMOC 04-1122-002), A–D - legs I–IV, respectively; E–F - tarsi I–II, respectively.

tarsus III, smooth. Solenidion σ III present, vestigial. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV, uniform in length and width, shorter than 1.5 of maximum width of tarsus IV. Tarsal setae *f* and *e* IV, symmetric, nearly equal in length, shorter than tarsus IV. Tarsal setae *e* IV similar in length and width with *w* and *s* IV. Tarsus IV more than 2 times longer than its basal width.

Other instars unknown.

Hosts. *Lithurgus* (*Lithurgopsis*) *listrotus* (Megachilidae).

Distribution. USA: California.

Etymology. The species name, furunculus, is a Latin noun (sneak thief, pilferer) in apposition.

Chaetodactylus kouboy sp. n.

Material. Holotype: HDN—**USA**: **New Mexico**, Colfax Co., Cimarron Canyon, ex *Lithurgus apicalis* (pronotum), 12 Jun 1956, R. & K. Dreisbach, MSU, BMOC 95-0323-020. Paratypes: 20 + 27 + 5 HDNs—same data as holotype (propodeum + pronotum + wing bases). Holotype in MSU, paratypes in MSU, USNM, OSAL, UMMZ.

Description. *Phoretic deutonymph* (Fig. 58, Fig. 59; Table 21, p. 201). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, separated by distinct space and diverging posteriorly (Fig. 58 *B*). Alveoli *ve* situated on prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield with linear and reticular patterns present (except for anterio-lateral part). Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* shorter than 1/2 of distance between their bases. Setae h_3 microsetae, distinctly shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II interrupted anteriorly. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller or nearly equal to inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II present. Solenidion σ I from 0.3–0.4 of genu I. Setae *mG* and *cG* I shorter or equal to combined length of genu and tibia I. Genual setae *cG* I pectinate. Genual setae *mG* I smooth. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II distinctly shorter than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, slightly longer or shorter than *mG* I, shorter or nearly equal to *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III at most reaching base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV shorter than 1.5 of maximum width of tarsus IV, uniform in length and width. Tarsal setae *f* and *e* IV absent. Tarsus IV 2–1.5 times longer than its basal width.

Other instars unknown.

Abnormalities. One seta *4b* shifted anteriorly, touching posterior edge of sternal shield (BMOC 95-0323-020#7).

Hosts. *Lithurgus* (*Lithurgopsis*) *apicalis* (Megachilidae).

Distribution. USA: New Mexico.

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Etymology. The specific epithet, kouboy, is transliterated from the English noun cowboy (a man who rides on horseback and herds cattle in the western United States) and is a noun in apposition.

Notes. *Chaetodactylus kouboy* was found only once, on a host also harboring *C. lithurgi*. This suggests that the host association may be accidental.

Chaetodactylus lithurgi

Klimov & OConnor, 2004

Chaetodactylus lithurgi Klimov & OConnor, 2004: 173.

Material (USA). Holotype: HDN—**New Mexico**, Colfax Co., Cimarron Canyon, ex *Lithurgus apicalis* (propodeum/metepisternum), 12 Jun 1956, R. & K. Dreisbach, MSU, BMOC 95-0323-021. Paratypes: 14 + 5 + 5 + 4 HDN (propodeum/metepisternum + propodeum + wingbase + hindleg), other data as for holotype; 3+1 HDNs—same data (propodeum+pronotum), MSU, BMOC 95-0323-020; 2 + 1 HDNs—Cibola Co., El Malpais National Monument, North Pasture, T7N R10W S30 NOPA, ex *L. apicalis* (pronotum + 1st metasomal tergite), 26 Aug 1991, D.C. Lightfoot, USNM, BMOC 96-0510-008; 1 HDN—**Arizona**, Pima Co., Tucson, ex *L. apicalis* (1st metasomal tergite), on *Opuntia* (Caryophyllales: Cactaceae), 28 May 1953, G. D. Butler, USNM, BMOC 96-0510-007; 15 HDN'S—Santa Cruz Co., Santa Rita Mountains, ex *L. apicalis* (propodeum), 5 Sep 1937, W. Benedict, KU, BMOC 96-0916-191; 3 + 1 HDNs—**Colorado**, Fremont Co., Cañon City, ex *L. apicalis* (1st metasomal tergite/propodeum/midfemur + pronotum), 3 Jul 1949, L. D. Beamer, KU, BMOC 96-0916-192; 14 HDN'S—**Idaho**, Fremont Co., St. Anthony Sand Dunes, ex *L. apicalis* (ventral metasoma), 29 Jun 1977, W.F. Barr, USNM, BMOC 96-0510-009; 7 + 5 HDN'S—**Texas**, Big Bend National Park, Oak Canyon, 1400–1520m., ex *Lithurgus littoralis* (between hind coxae + propodeum), on *Prosopis juliflora* (Sw.) DC. (Fabales: Fabaceae), 11 Apr 1986, T. Griswold, USNM, BMOC 96-0510-011; 6 + 5 HDNs—Lee Co., Giddings, ex *Lithurgus gibbosus* (forewing base + propodeum), on *Opuntia*, 10 May 1953, L.D. Beamer, KU, BMOC 96-0916-199; 5 HDN'S—same locality and host, on *Opuntia* (around wing bases), 12 May 1953, R. H. Beamer KU, BMOC 96-0916-200; 6 HDNs—Maverick Co., Quemado, ex *L. littoralis* (proboscidial fossa) on *Opuntia*, 11 Apr 1950, Michener, Rozen, Beamer & Stephen, KU, BMOC 96-0916-204. Holotype in MSU, paratypes in IRSNB, KU, MSU, HNHM, UMMZ, USNM.

Additional material. 10 HDNs—Arizona, Cochise Co., Portal, ex *Lithurgus apicalis* on posterior mesosoma and 1st metasomal tergite, 6 Jun 1967, W. J. Gertsch, AMNH, BMOC 04-0508-145; 2HDNs—Pima Co., Continental, 31°50′32.3″N 110°57′17.1″W, elev. 936 m. *Opuntia*/cholla, ex *Diadasia* sp. wing base and middle trochanter, 19 May 2004, P. Klimov UMMZ BMOC 04-0524-

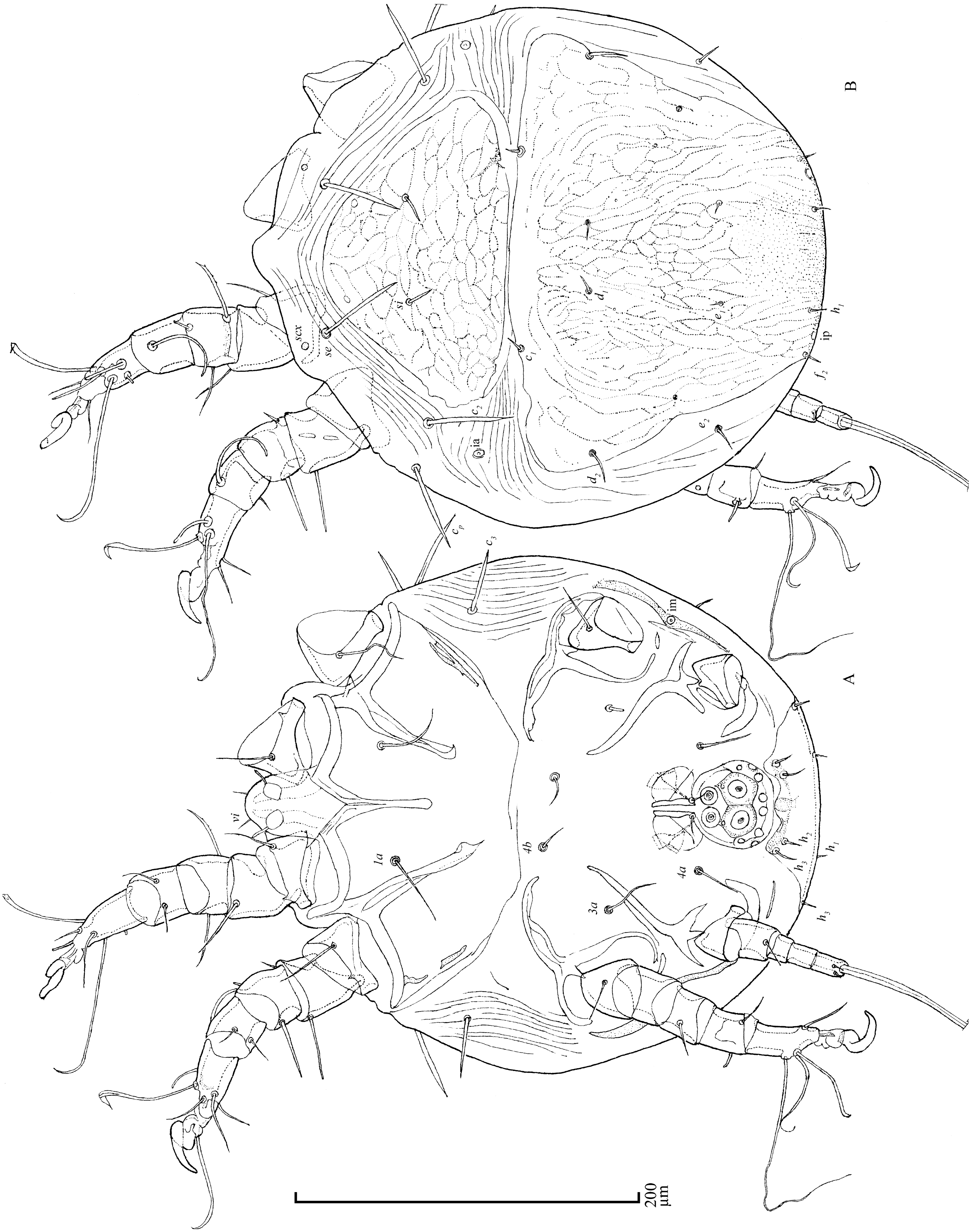

Fig. 58. *Chaetodactylus kouboy*, heteromorphic deutonymph (BMOC 95-0323-020, holotype). A, B - ventral and dorsal view.

Fig. 59. *Chaetodactylus kouboy*, heteromorphic deutonymph (BMOC 95-0323-020). A, B - leg I, dorsal and ventral view; C, D - leg II, dorsal and ventral view; E - leg III; F, G - leg IV, dorsal and ventral view.

012; 10HDNs—Pima Co., Continental, 31°50′32.3″N 110°57’17.1″W, elev. 936 m., *Opuntia*, ex *L. apicalis* on ventral mesosoma, 19 May 2004, P. Klimov, UMMZ BMOC 04-0524-013. Voucher specimens in OSAL, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Table 22, p. 203). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, separated by distinct space and diverging posteriorly. Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Ratio length of prodorsal shield/length of seta d_1 2.4–4.4 (3.2 ± 0.43). Hysterosomal shield with linear pattern indistinct because of reticulate pattern (except for anterio-lateral part). Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae slightly pectinate at tips. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Seta c_p distinctly anterior to level of c_2. Setae *si* longer than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II absent, or if present, interrupted anteriorly. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller to inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II. Solenidion σ I about 0.5 of genu I. Setae *mG* and *cG* I shorter or equal to combined length of genu and tibia I. Genual setae *cG* I pectinate. Genual setae *mG* I pectinate. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II distinctly shorter than combined length of femur, genu and tibia II. Genual setae *mG* II pectinate, slightly longer or shorter than *mG* I, shorter than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III at most reaching base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV shorter than 1.5 of maximum width of tarsus IV. Tarsal setae *w* and *s* IV uniform in length and width. Tarsal setae *f* and *e* IV shorter than tarsus IV, symmetric, nearly equal in length or both absent. Tarsal setae *e* IV nearly similar in length and width with *w* and *s* IV (slightly shorter). Tarsus IV 2–1.5 times longer than its basal width.

Other instars unknown.

Abnormalities. One ϕ IV elongated (17) and widened (BMOC 03-0127-001#66); two solenidia (σ) on one genu I (BMOC 03-0127-001#68); one c_1 missing, its alveolus located anterior to hysterosomal shield (BMOC 95-0323-021#48); one c_1 on unsclerotized cuticle, anterior to hysterosomal shield (BMOC 95-0323-021#50, 96-0510-011#07); one e_1 duplicated (96-0510-009#36); one h_1 duplicated (BMOC 95-0323-021#49); one h_1 very small, microseta (8), ω_1 on one tarsus I longer than on the other (35 and 25) (BMOC 96-0510-009#35).

Hosts. *Lithurgus* (*Lithurgopsis*) *apicalis* (type host), *Lithurgus* (*Lithurgopsis*) *littoralis*, *Lithurgus* (*Lithurgopsis*) *gibbosus* (Megachilidae).

Distribution. USA: Arizona, Colorado, Idaho, New Mexico (type locality), Texas.

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Chaetodactylus abditus
Klimov & OConnor, 2004

Chaetodactylus abditus Klimov & OConnor, 2004: 175, Figs 5, 6.

Material. Holotype: **USA: Arizona**, Pima Co., Continental, ex *Lithurgus planifrons* (ventral mesosoma), 8 Sep 1978, Knowlton & Hanson, USNM, BMOC 96-0510-012. Paratypes: 4 + 4 + 1 HDNs—same data as holotype (lateral mesosoma + ventral mesosoma + 1st metasomal tergite); 34 HDN’S—Pima Co., near Continental, elev. 1019 m., 10 am, 31°49.49’N 110°55.58’W, ex female of *Lithurgus echinocacti* (mostly pronotum) on *Ferocactus* (Caryophyllales: Cactaceae), 3 Sep 2003, P. Klimov, UMMZ, BMOC 03-0903-001; 5 HDN’S—**MEXICO: Colima**, Revillagigedo Arch., Socorro Is., ex male of *L. planifrons* (pronotum and posterior head), 1–5 May 1955, McDonald & Blodget, LACM, BMOC 03-0127-001; 3 HDN’S—same locality, Station 5, Elev. 900 ft. (274.3 m), ex female of *L. planifrons* (mesosoma, including propodeum), 8 Jun 1977, C. Hogue & A. Evans (Steele Exped.), LACM, BMOC 03-0127-002; 5 HDN’S—same data (metepisternum), LACM, BMOC 03-0127-003; 8 + 3 + 15 HDNs—same locality, Bahia Braithwaite, ex *L. planifrons* (propodeum + mesepisternum + ventral mesosoma), 7 May 1925, H. H. Keifer, CAS, BMOC 03-0604-003. Holotype in USNM, paratypes in CAS, HNHM, IRSNB, LACM, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 60, Fig. 61; Table 22, p. 203). Similar to *Chaetodactylus lithurgi* (see description on p. 121), diagnostic characters indicated in the key to *Chaetodactylus* species on p. 109. Measurements are given in Table 22.

Other instars unknown.

Abnormalities. Base of *wa* I wide, as wide as diameter of ω_3 (96-0510-012#56).

Hosts. *Lithurgus (Lithurgopsis) planifrons* (type host), *Lithurgus (Lithurgopsis) echinocacti* (Megachilidae).

Distribution. USA: Arizona (type locality), Mexico: Socorro Island.

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Chaetodactylus gibbosi
Klimov & OConnor, 2004

Chaetodactylus gibbosi Klimov & OConnor, 2004: 178, Fig 7.

Material (**USA**: **Florida**). Holotype: HDN—Liberty Co., T 2 N R7W, ex *Lithurgus gibbosus* (pronotum), 3 May 1924, T. H. Hubbell, UMMZ, BMOC 02-1205-006. Paratypes: 3 + 6 HDNs—same data as holotype (pronotum + ventral metasoma); 3 HDNs—Florida, Alachua Co., Gainesville, ex *L. gibbo-*

Fig. 60. *Chaetodactylus abditus*, heteromorphic deutonymph (BMOC 96-0510-012, holotype). A, B - ventral and dorsal view.

Fig. 61. *Chaetodactylus abditus*, heteromorphic deutonymph (BMOC 96-0510-012). A–D - legs I–IV, dorsal view, respectively; E-H - tarsi I–IV, ventral view, respectively.

sus (pronotum/hind femur/metasoma), 20 May 1929, "V. K. B. #113", UMMZ, BMOC 02-1205-007; 10 HDNs—Highlands Co., Highlands Hammock State Park, ex *Lithurgus* sp. (propodeum), 4 Apr 1974, G. C. Eickwort, CUIC, BMOC 95-0422-103; 14 HDNs—Highlands Co., Archbold Biological Station, ex *Lithurgus* sp. (metepisternum, posterior coxae III), 20 Apr 1969, L. L. Pechuman, CUIC, BMOC 95-0422-107; 5 + 11 + 20 HDNs—Miami-Dade Co., Coral Gables, ex *L. gibbosus* (propodeum + 1st metasomal tergite + pronotum), "19", no collector, USNM, BMOC 96-0510-010 UMMZ. Holotype in UMMZ, paratypes in CUIC, HNHM, IRSNB, FSCA, UMMZ, USNM.

Additional material. 15 HDNs—**Georgia**, Jefferson Co., Wadley, ex *Lithurgus gibbosus* on propodeum, 23 Apr 1938, F. E. Lutz, AMNH, BMOC 04-0508-149. Voucher specimens in AMNH, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 62; Table 22, p. 176). Similar to *Ch. abditus* and *Ch. lithurgi* (see description on p. 121). Differs from these two species by ratio length of prodorsal shield/length of seta d_1 (see key to *Chaetodactylus* species on p. 109).

Other instars unknown.

Abnormalities. *ih* and anterior cuticular sucker touching each other (BMOC 96-0510-010#08, 96-0510-010#09); pattern on anterior part of hysterosomal shield consists of short narrow strips, similar to those on posterior part but oriented transversely (BMOC 96-0510-010#16–19).

Hosts. *Lithurgus (Lithurgopsis) gibbosus* (Megachilidae).

Distribution. USA: Florida (type locality), Georgia.

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Chaetodactylus azteca sp. n.

Material (**MEXICO**). Holotype: HDN—**Hidalgo**, Tepeapulco, ex *Osmia* (*Diceratosmia*) *azteca* (propodeum), 18 Sep 1974, W. Hanson & G. Bohart, USNM, BMOC 96-0510-139. Paratypes: 4 HDNs—same data as holotype; 3 HDNs—**Chiapas**, Municipico Zinacantán, Parajé Vobits, 1158m, ex *O. azteca* (1st metasomal tergite), 28 Oct 1976, D. E. & J. A. Breedlove, USNM, BMOC 96-0510-140. Holotype in USNM, paratypes in UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 63, Fig. 64; Table 22, p. 203). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 63 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*. Prodorsal shield transversely striated. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield longitudinally striated, most lines long but shorter than half of hysterosomal shield (except for anterio-lateral part). No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae d_2 situated outside hysterosomal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* longer than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II present, equal or less than 1/2 of lateral edge of sternal shield. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites not reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller or nearly equal to inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I from about 0.6 of genu I. Setae *mG* and *cG* I shorter than combined length of genu and tibia I. Genual setae *cG* I pectinate. Genual setae *mG* I pectinate. Genual setae *mG* II shorter than combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer then combined length of femur, genu and tibia II. Genual setae *mG* II smooth, slightly longer or shorter than *mG* I, distinctly shorter than to *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III at most reaching base of tarsus III. Seta *nG* III pectinate. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV shorter than 1.5 of maximum width of tarsus IV, uniform in length and width. Tarsal setae *f* and *e* IV distinctly shorter than tarsus IV, symmetric, nearly equal in length. Tarsal setae *e* IV similar in length and width with *w* and *s* IV, or absent. Tarsus IV more than 2 times longer than its basal width.

Other instars unknown.

Hosts. *Osmia* (*Diceratosmia*) *azteca*.

Distribution. Mexico: Chiapas, Hidalgo (type locality).

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20azteca&-max=200&-find

Etymology. The specific epithet is derived from the species name of the host and also honors the indigenous people of central Mexico; the name is a noun in apposition.

Chaetodactylus micheneri sp. n.

Material. Holotype (form 1): HDN—**USA: California**, Fresno Co., Mt. Crocker, elev. 11800 ft., ex *Osmia subaustralis* (propodeum), 1 Jul 1974, T. Griswold, USNM, BMOC 96-0510-127.

Form 1 (All specimens from *O. subaustralis*, paratypes). **California**: 9+13 HDN—same data as holotype (propodeum+occiput); 5+5 HDN—Alpine Co., Dead Men Creek, Middle Fork Stanislaus River, 8000 ft., (occiput+between coxae I), 26 Jun 1937, C.D. Michener, KU, BMOC 03-0514-004; 11 HDN—same data (occiput), 26 Jun 1937, C.D. Michener, KU, BMOC 03-0514-007; 2 HDN—El Dorado Co., Tahoe, Mount Tallac, (propodeum), 27 Jul 1915, E.P. VanDuzee, KU, BMOC 03-0514-009; 3+1 HDN—Mariposa Co., Yosemite Valley, (1st metasomal tergite+propodeum), 10 Jul 1933, R.H. Beamer, KU, BMOC 03-0514-002; 12 HDN—Mono Co., Sardine Creek, Elev. 8500 ft., (1st metasomal tergite), 28 Jun 1951, J.W. MacSwain, KU, BMOC 03-0514-020; 12+3+1 HDN—Mono Co., Sonora Pass, on *Astragalus* (Fabales: Fabaceae) (occiput+propodeum+1st metasomal tergite), 27 Jun 1937, G.E. Bohart, KU,

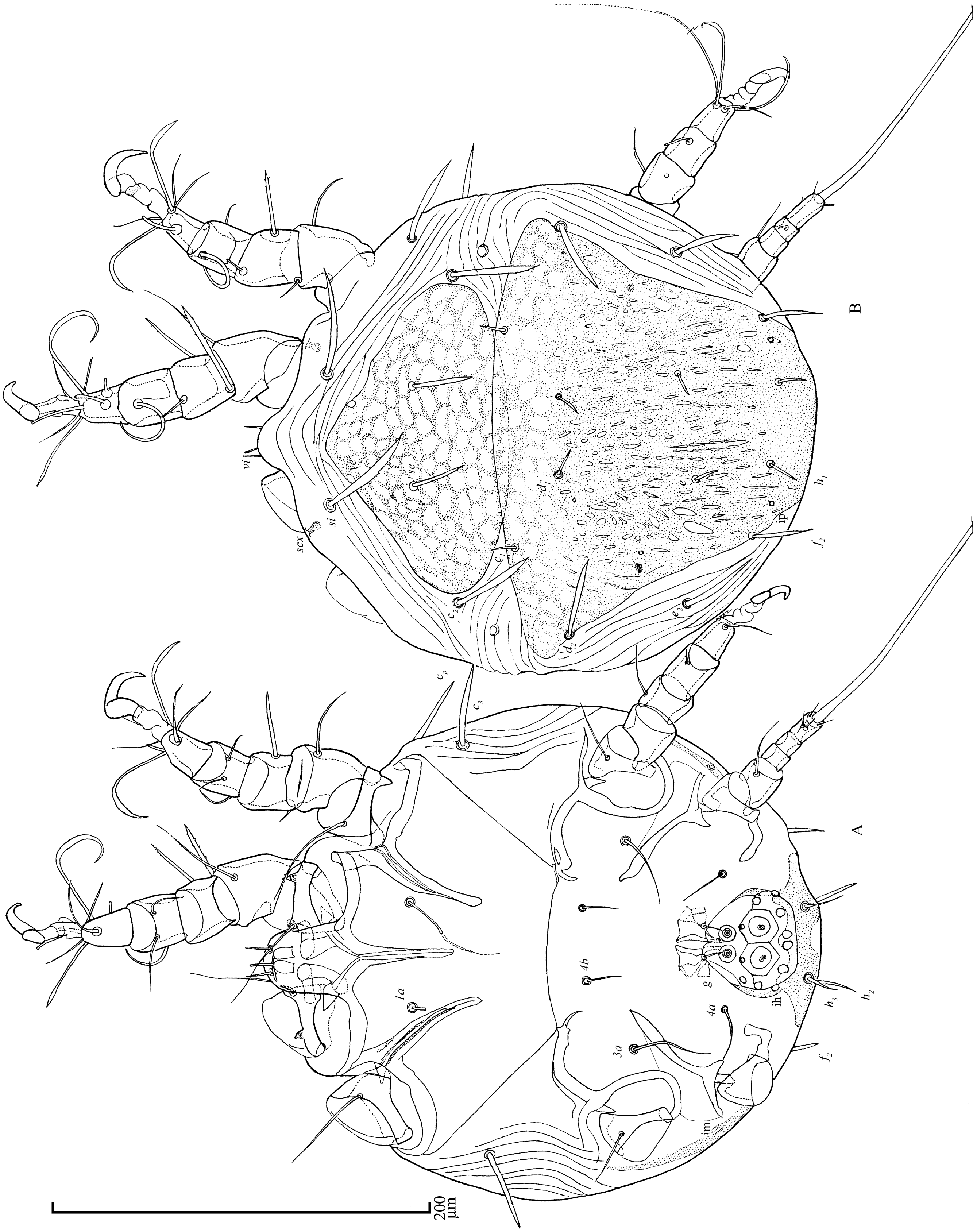

Fig. 62. *Chaetodactylus gibbosi*, heteromorphic deutonymph (BMOC 02-1205-006, holotype). A, B - ventral and dorsal view.

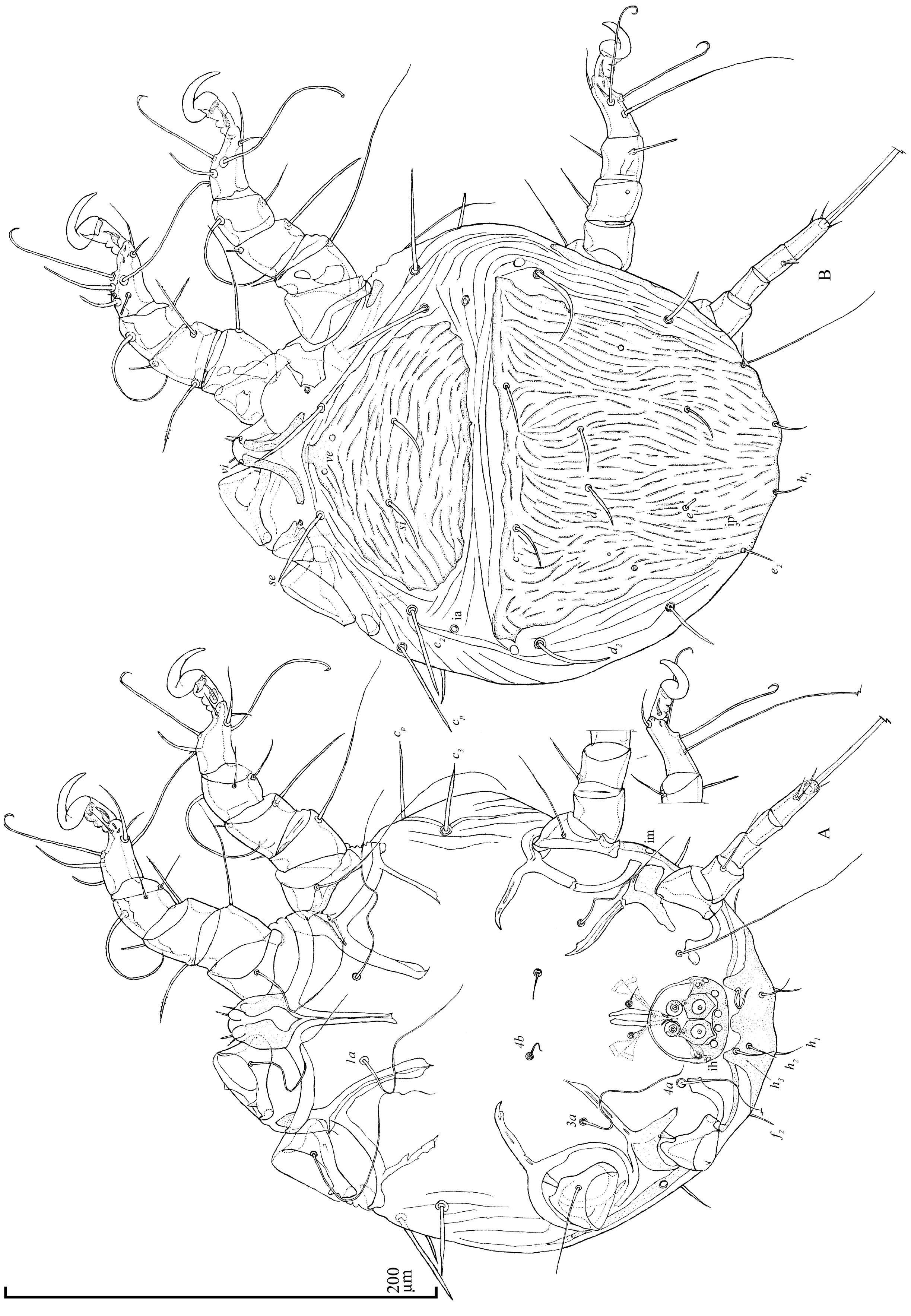

Fig. 63. *Chaetodactylus azteca*, heteromorphic deutonymph (BMOC 96-0510-139, holotype). A, B - ventral and dorsal view.

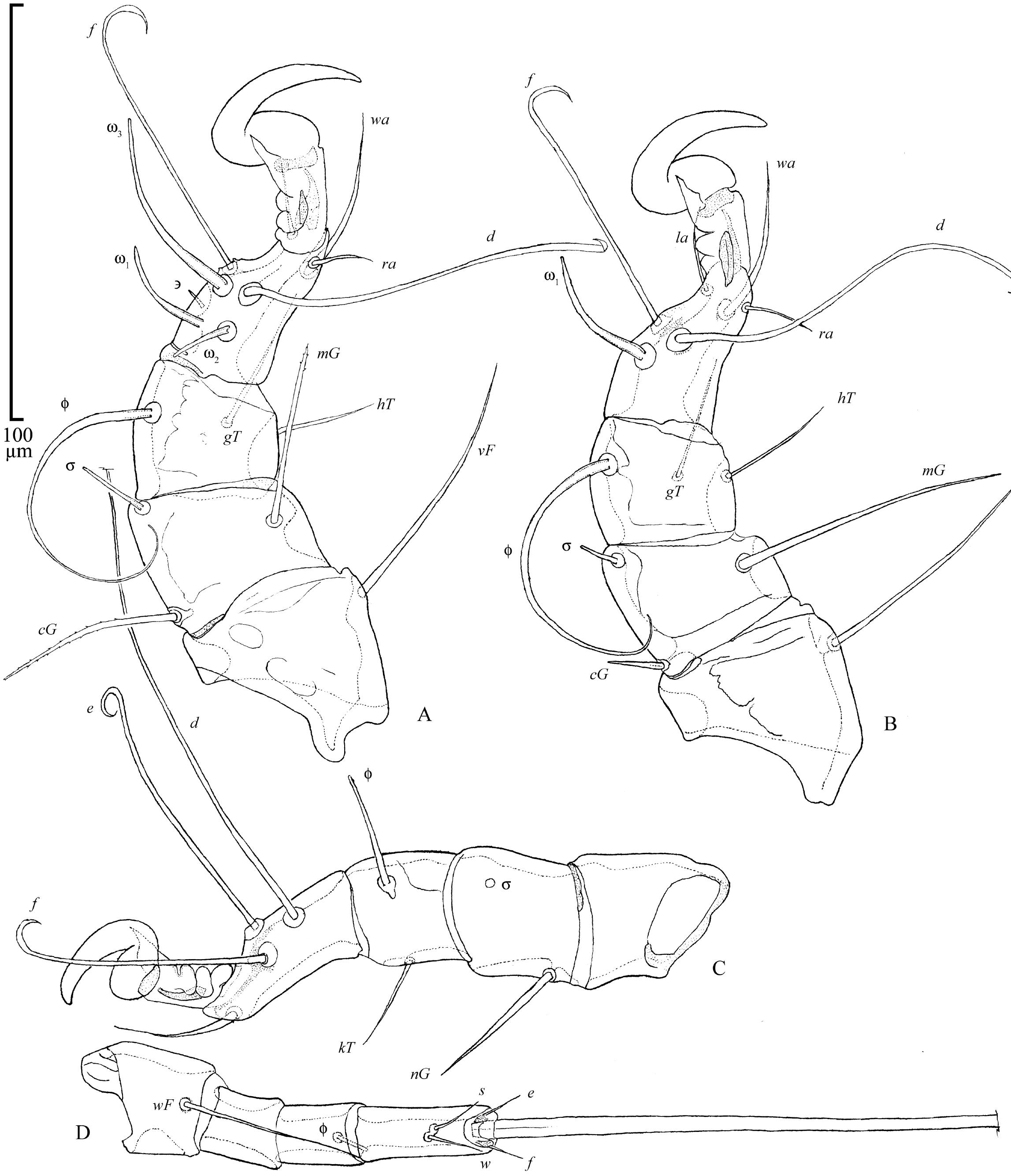

Fig. 64. *Chaetodactylus azteca*, heteromorphic deutonymph (BMOC 96-0510-139). A–D - legs I–IV.

BMOC 03-0514-003; 4+1 HDN—Mono Co., West Walker River, 7200 ft., on *Senecio* (Asterales: Asteraceae) (1st metasomal tergite+propodeum), 25 Jun 1937, C.D. Michener, KU, BMOC 03-0514-012; 1+1 HDN—San Diego Co., 4 mi S Mesa Grande (1st metasomal tergite+between coxae I), 9 Jul 1938, U. Lanham, USNM, BMOC 03-0501-003; 9 HDN—Sonoma Co., Cheney Gulch, (propodeum), 22 May 1958, no collector, USNM, BMOC 03-0501-001; 3+2 HDN—Tuolumne Co., Pinecrest, (1st metasomal tergite+propodeum), 27 Jun 1942, R.E. Beer, KU, BMOC 03-0514-001; 1 HDN—**Arizona**, Apache Co., near Alpine, (propodeum), 25 May 1947, H. & M. Townes, KU, BMOC 03-0514-008; **Colorado**: 11 HDN—Boulder Co., Longs Peak, elev. about 9000 ft., F 4774A, (1st metasomal tergite), 14–19 June 1922, no collector, AMNH, BMOC 03-0414-013; 2 HDN—Boulder Co., Nederland, on *Senecio perplexus* A. Nelson (Asterales: Asteraceae) (propodeum), 21 Jun 1950, C.D. Michener, KU, BMOC 03-0514-014; 4+8 HDN—same data (propodeum+1st metasomal tergite), 21 Jun 1950, C.D. Michener, KU, BMOC 03-0514-016; 1+1 HDN—Boulder Co., Nederland, (pronotum+1st metasomal tergite), 21 Jun 1950, C.D. Michener, KU, BMOC 03-0514-011; 24 HDN—Glacier Lake, (propodeum), 2 Jun 1913, M. [illegible] Ellis, AMNH, BMOC 03-0414-007; 5 HDN—Jackson Co., Camp Creek Research Station [41°00'N 106°12'W], F. 4730, (1st metasomal tergite), 19 Jun 1920, no collector, AMNH, BMOC 03-0414-008; 3 HDN—Jefferson Co., Golden, Green Mountain, (1st metasomal tergite), 24 May 1919, L.O. Jackson, AMNH, BMOC 03-0414-004; 2 HDN—Elbert Co., Elbert, elev. about 7400 ft., 4773, (ventral mesosoma), 9–11 June 1922, no collector, AMNH, BMOC 03-0414-012; 5+4 HDN—El Paso Co., (1st metasomal tergite+propodeum), 6–18 June 1937, W. Benedict, KU, BMOC 03-0514-017; 1 HDN—*La* Plata Co., Electra Lake, F.4367.14[or 11 or II], (lateral side of 1st metasomal tergite), 28 June-1 July 1919, no collector, AMNH, BMOC 03-0414-018; 12 HDN—Rio Grande Co., South Fork Rio Grande (37°33'N 106°47'W), elev. 9200 ft., F4357, (1st metasomal tergite), 18–19 June 1919, no collector, AMNH, BMOC 03-0414-011; 4 HDN—same locality, elev. 9250 ft., F4358, (1st metasomal tergite), 18–19 June 1919, no collector, AMNH, BMOC 03-0414-021; 2+4 HDN—same locality (37°36'N 106°43'W), elev. 8500 ft., F4357, (pronotum+1st metasomal tergite), 17 Jun 1919, no collector, AMNH, BMOC 03-0414-014; 2 HDN—San Miguel Co., Telluride, Cornet Creek, elev. about 11000 ft., 37°55'N 107°45'W F4375 II, (propodeum), 9 Jul 1919, no collector, AMNH, BMOC 03-0414-015; 9 HDN—Teller Co., Florissant, on *Senecio tridenticulatus* Rydb. (Asterales: Asteraceae) (1st metasomal tergite), 14 Jun 1907, S.A. Rohuer, USNM, BMOC 03-0501-006; 1+4 HDN—Ouray Co., Ouray, (propodeum+1st metasomal tergite), 1 Jul 1937, R.H. Beamer, KU, BMOC 03-0514-018; **Montana**: 12 HDN—Gallatin Co., Gallatin Range, elev. 5000 ft., (1st metasomal tergite), 7 Jul 1914, no collector, USNM, BMOC 03-0501-002; 5+3 HDN—Ravalli Co., Hamilton, Skalkaho Pass, on *Erigeron salsuginosus* (Richards) Gray (Asterales: Asteraceae) (1st metasomal tergite+pronotum), 19 Jul 1949, R.H. Beamer, KU, BMOC 03-0514-019; **Utah**: 2 HDN—Duchesne Co., along road Kamas Summit Co. to Mirror Lake, acc 35707, (propodeum), 17 Jul 1936, no collector, AMNH, BMOC 03-0414-020; 15 HDN—Cache Co., Tony Grove Lake, (propodeum), 14 Jul 1983, G.E. Bohart, USNM, BMOC 96-0510-128; **Washington**: 1 HDN—Yakima Co., Mount Adams, Signal Peak., 4500 ft., (pronotum), 10 Jul 1927, M.W. Stone, USNM, BMOC 03-0501-007; 2+4 HDN—same locality, West Klickitat, 3500 ft., (1st metasomal tergite+propodeum), 10 Jun 1925, L.A. Morley, USNM, BMOC 03-0501-009; **Wyoming**: 12 HDN—Crook Co., 5 mi N Sundance, Reuter Canyon Campground, 6100 ft., (1st metasomal tergite), 10 Jul 1959, F.P. & B. Rindge, AMNH, BMOC 03-0414-003; 21 HDN—Park Co., Yellowstone National Park, Camp Roosevelt, (metanotum & propodeum), no date, no collector, KU #Bc 24515, BMOC 03-0514-010; 5+2 HDN—Sheridan Co., Big Horn, (1st metasomal tergite+propodeum), 4 Jul 1953, P.B. Lawson, KU, BMOC 03-0514-015; 17+27 HDN—**CANADA**: **Alberta**, Banff, (pronotum+propodeum), May 21 1915, F.W.L. Sladen, KU 1019, BMOC 03-0514-005.

Form 2. **California:** 6 HDN—El Dorado Co., Fallen Leaf Lake, ex *O. montana* (1st metasomal & propodeum), 23 Jun 1955, P.Torchio, USNM, BMOC 96-0510-123; 1 HDN—ex *O. subaustralis* (propodeum), BMOC 03-0514-009; 19 HDN—Inyo Co., Westgard Pass, ex *Osmia grinnelli* (1st metasomal tergite & propodeum), 18 July 1942, R. Bohart, USDA, BMOC 03-1003-244; 2 HDN—Mono Co., Sonora Pass, ex *O. calcarata* (dorsal body), 29 Jun 1937, G.E. Bohart, USNM, BMOC 96-0510-147; 10 HDN—Mono Co., Sardine Creek, elev. 8500 ft., ex *O. montana* (pronotum), 28 Jun 1951, J.L. Mallars, USNM, BMOC 96-0510-125; 1+1 HDN—ex *O. subaustralis* (propodeum+1st metasomal tergite), BMOC 03-0514-003; 1 HDN—ex *O. subaustralis*, BMOC 03-0514-012; 1 HDN—ex *O. subaustralis* (1st metasomal tergite), BMOC 03-0514-020; 3 HDN—Nevada Co., Truckee, ex *O. marginipennis* (propodeum), 17 Jun 1927, E.P. VanDuzee, USNM, BMOC 96-0510-115; 1 HDN—ex *O. subaustralis* (propodeum), BMOC 03-0501-001; 2 HDN—ex *O. subaustralis* (1st metasomal tergite), BMOC 03-0514-001; 1 HDN—ex *O. subaustralis* (1st metasomal tergite), BMOC 03-0514-002; 1 HDN—ex *O. subaustralis* (pronotum), BMOC 03-0501-003; **Colorado**: 1 HDN—Boulder Co., Cairn Ponds, Roosevelt National Forest, Indian Peaks Wilderness, Niwot Ridge, elev. 3476 m., malaise trap, 23 Jul 1993, J. Cooley, BMOC 94-0125-003; 9 HDN—Boulder Co., Weather station C_1, Roosevelt National Forest, Indian Peaks Wilderness, 1.25 km NW of University of Colorado Mountain Research Station, elev. 3030m., malaise trap, 21 Jun 1993, J. Cooley, BMOC 94-0125-002; 1+1 HDN—ex *O. subaustralis* (propodeum+pronotum), BMOC 03-0514-011; 4 HDN—Jackson Co., Rabbit Ears Pass, ex *Hoplitis fulgida fulgida* (mesosoma), 13 Jul 1949, R.H. Beamer, KU, BMOC 96-0916-331; **Idaho**: 12 HDN—Oneida Co., Black Pine Mt., ex *O. marginipennis* (1st metasomal tergite), 11 May 1974, Bohart&Knowlton, USNM, BMOC 96-0510-119; 11 HDN—Oneida Co., Black Pine Canyon, ex *O. californica* (pronotum), 9 Jun 1982, Torchio/Bohart, USNM, BMOC 96-0510-112; 12 HDN—Franklin Co., Cub River Canyon, ex *O. montana* (propodeum), 8 May 1969, G.F. Knowlton, USNM, BMOC 96-0510-121; 5 HDN—Boise Co., Wilson Creek, ex *O. juxta* (scattered over body), 6 Mar 1975, C.W. Baker, USNM, BMOC 96-0510-129; 1+3 HDN—**Nevada**, Elko Co., Bear Creek Meadows, R575E-T45N, ex *O. californica* on *Hackelia* (Lamiales: Boraginaceae) (1st metasomal tergite+propodeum), 8 Jul 1979, R.W. Rust, USNM, BMOC 96-0510-114; **Utah**: 4 HDN—Cache Co., Birch Canyon, ex *O. californica* (pronotum), 23 May 1982, TL/RT Griswold, USNM, BMOC 96-0510-110; 13 HDN—same locality, ex *O. marginipennis* (propodeum), 23 May 1982, R.T. Griswold, USNM, BMOC 96-0510-116; 15 HDN—Cache Co., near Hyrum, Blacksmith Fork Canyon, ex *O. marginipennis* on *Salix* (Salicales: Salicaceae) (propodeum), 22 May 1948, G.E. Bohart, USNM, BMOC 96-0510-117; 16 HDN—Cache Co., Newton, ex *O. marginipennis* (propodeum), 25 Jun 1962, R. Brumley, USNM, BMOC 96-0510-118; 10 HDN—Rich Co., Bear Lake, S. Garden City, ex *O. californica* (pronotum), 19 May 1973, F.D. Parker, USNM, BMOC 96-0510-111; 12 HDN—Salt Lake Co., Emigration Canyon Mouth, ex *O. californica* (propodeum), 9 May 1938, Don M. Rees, USNM 23526, BMOC 96-0510-113; **Washington**: 4+5+2 HDN—ex *O. subaustralis* (1st metasomal tergite+pronotum+propodeum), BMOC 03-0501-007.

Form 3 (all from *O. subaustralis*). **CANADA**: **Northwest Territories**: 14 HDN—Great Slave Lake, Fort Resolution, on *Taraxacum* (Asterales: Asteraceae) (anterior scutum), 26 June 1903, Mer. Cary, USNM, BMOC 03-0501-005; 9 HDN—same data, USNM, BMOC 03-0501-004; **USA: Michigan**: 55 females, 41 males, 4 TNs, 1 immobile HDN, 82 PNs, 2 pharate PN, 23 L, 1 PL—Dickinson Co., nest (#CH-N-EW-S-3-9 cell 1, sample 2), 8 Sep 1984, M. Arduser, UMMZ, BMOC 03-0310-001; 2 PNs—Dickinson Co., nest, male cell, 22 May 1984, no collector, UMMZ BMOC 03-0310-002; 2 males, 5 females, 14 phoretic HDNs, 5 pharate HDNs, 1 immobile HDN, 3 pharate immobile HDNs (in PN skin), 26 PNs, 2 L—Dickinson Co., T43N R28W S14, nest (#FI-E-EW-S-4-4), on and among fecal pellets, 8 Sep 1984, M. Arduser, UMMZ, BMOC 03-0310-003; 18 HDN, 1 pharate HDN—same data, nest (#FORD-E-EW-S-4-9), cell 2, 27 Sep 1983, M. Arduser, UMMZ, BMOC 03-0310-004; 18 HDNs—Dickinson Co., same data, cell 5, UMMZ, BMOC 03-0310-005; 13+3 HDNs+pharate HDN—same data, nest (#FI-E-EW-S-4-4), cell 6, 8 Sep 1984, M. Arduser, UMMZ, BMOC 03-0310-006; 2 HDN—Cheboygan Co., University of Michigan Biological Station, (lateral mesosoma), 21 Jun 1986, J.T. Rotenberry, UMMZ, BMOC 87-0203-006.

Unclassified (all from USA). 10HDN's—**California**, Placer Co., Lake Tahoe, ex *Osmia montana quadriceps* (on dorsal mesosoma), 10 Jul 1952, M. Cazier, W. Gertach & R. Schrammel, AMNH, BMOC 04-0508-018; 4HDN's—**Colorado**, Boulder Co., Ward, alt. about 9300 ft, ex *Osmia montana montana*, on mesosoma, 25 Jun 1922, 4779A AMNH BMOC 04-0508-016; 4 HDNs—**Idaho**, Blaine Co., Carey, ex *O. californica* propodeum & pronotum, no date, A. C. Cole, OSU, OSUC 0066049, BMOC 03-1106-001; 6 HDNs—**Oregon**, Harney Co., "Blitzen River", ex *O. marginipennis* on propodeum, 1 Jun 1933, AMNH 33084, BMOC 04-0508-013; 2 HDNs—**Wyoming**, Sundance, ex *O. montana montana* propodeum+1st metasomal tergite, 10 Jul 1959, F. P. & B. Rindge, 9037 AMNH, BMOC 04-0508-014.

Holotype in USNM, paratypes in AMNH, CNC, KU, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 22, Fig. 23; Table 23, p. 205). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 22 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*. Prodorsal shield transversely striated. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield longitudinally striated, most lines longer than half of length of hysterosomal shield (except for anterio-lateral part). No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* shorter than 1/2 of distance between their bases. Setae h_3 longer than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II present, exceed 1/2 of lateral edge of sternal shield. Proximal acetabular extensions IV connected. Distal acetabular extensions of apodemes IV connected. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a* or equal or exceeds distance between *4a*. Lateral horns of attachment organ lateral sclerites reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I about 0.2 of genu I. Setae *mG* and *cG* I shorter or equal to combined length of genu and tibia I. Genual setae *cG* I smooth. Genual setae *mG* I smooth. Genual setae *mG* II exceed combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer then combined length of femur, genu and tibia II. Genual setae *mG* II smooth, distinctly longer than *mG* I, longer than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III clearly extending beyond base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV shorter than maximum width of tarsus IV, uniform in length and width. Tarsal setae *f* and *e* IV present or absent (usually absent in morph 2), shorter than tarsus IV, symmetric, nearly equal in length. Tarsal setae *e* IV (if present) similar in length and width with *w* and *s* IV. Tarsus IV 2–1.5 times longer than its basal width.

Inert deutonymph. Fig. 24, see also p. 103.

Female (Fig. 27, Fig. 28). Dorsal opisthosoma more or less uniformly covered with fleshy tubercles (diameter 2–3) that are smaller and sparser peripherally; tubercles not contiguous, usually with rounded, transparent tips. Setae c_3 not extending beyond posterior level of trochanters IV. Adanal setae ad_3 usually not or only slightly extending beyond level of *ih*. Setae ps_3 posterior to *4a* level. Inseminatory canal trumpet-shaped, more than 5 times longer than its width at spermatheca. Sclerotized lining layer of outer end of inseminatory canal shorter than 0.4 length of inseminatory canal. Setae *gT* I–II smooth, filiform; *hT* I smooth, *hT* II sparsely barbed to almost smooth.

Homeomorphic male (Fig. 29, Fig. 30). Setae d_1 not extending beyond e_1. Setae c_3 reaching trochanters IV but not extending beyond them. Central part of dorsal opisthosoma with mammillae or tubercles, diameter 1.5. Basal widening of aedeagus not reaching level of ps_3, distance between ps_3 exceeding length of basal widening. Aedeagus folds posterior to dorsal supporting sclerite. Transverse processes of dorsal supporting sclerite spirally twisted, band-like (Fig. 10 *F*). Genital valves with posterior cuticular flaps (Fig. 10 *F*). Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite (Fig. 10 *F*). Anterior end of genital capsule without distinct projection (Fig. 10 *F*). Anterior processes of dorsal supporting sclerite usually indistinctly wider than posterior ones, anterior concavity not exceeding 1.6 of basal "body". Aedeagus distinctly extending beyond genital capsule (Fig. 10 *F*). Ratio of pretarsal sucker width/tarsus III width 0.34–0.35. Setae *gT* and *hT* I–II smooth.

Abnormalities. Heteromorphic deutonymph: Form 1: *ra* I on one tarsus distinctly (26.5) longer than on the other (16.7) (BMOC 96-0510-127#1); *f* IV apparently absent; anterior cuticular conoids and *ih* touching each other (BMOC 96-0510-127#2); *e* and *f* IV not observed (BMOC 96-0510-127#1, 6, 10); one *vi* duplicated (BMOC 03-0514-010#1); one *vi* spiniform, short (6); one e_1 absent (a small alveolus in its place) (BMOC 03-0514-001-val25). Form 2: one *e* II swallowed (96-0510-118#2); free palpi touching each other (BMOC 96-0510-111-val9). Form 3: one e_1 duplicated (03-0310-003#5); σ'' present, small (2.7) on one genu (BMOC 03-0310-003#7); one *gT* I duplicated (BMOC 03-0310-003#8); one *ve* alveolus medial, shifted from edge of prodorsal shield; both *vi* absent (BMOC 87-0205-006#2)

Hosts. Form 1: *Osmia* (*Cephalosmia*) *subaustralis* (type host) (Megachilidae)

Form 2: *Hoplitis fulgida*; *O. (Cephalosmia) californica*; *O. (C.) grinnelli*; *O. (C.) marginipennis*; *O. (C.) montana*; *O. (C.) subaustralis*; *Osmia* (*Acanthosmioides*) *calcarata*; *Osmia* (*Melanosmia*) *juxta*.

Form 3: *O. subaustralis*.

Unclassified: *Osmia montana quadriceps*

Distribution. Form 1: USA: California (type locality), Arizona, Colorado, Montana, Utah, Washington, Wyoming; Canada: Alberta.

Form 2: USA: California, Colorado, Idaho, Nevada, Utah, Washington.

Form 3: USA: Michigan; Canada: Northwest Territories.

Unclassified: USA: Oregon.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20micheneri&-max=200&-find

Etymology. The new species is named after Charles D. Michener (KU), the world's leading authority on bee systematics.

Chaetodactylus rozeni sp. n.

?*Chaetodactylus* sp. Krombein, 1962: 248; Krombein, 1967: 310; Rust, 1974: 42.

Material (USA). Holotype: HDN—**North Carolina**, Swain Co., Bryson City, apple flowers, ex *Osmia georgica* on 1st metasomal tergite & propodeum, 27 Apr 1923, J. C. Crawford 5464, AMNH 33827, BMOC 04-0508-007. Paratypes: 10 HDNs—same data as holotype; 3 HDNs—**Texas**, Montague Co., ?Montague (label reads: "Monteagle Texas"), ex *O. georgica* on propodeum, 16 Apr 1946, C. D. Michener, AMNH, BMOC 04-0508-009; 4 HDNs—**Tennessee**, Burrville, ex *Chrysis coerulans* (Hymenoptera: Chrysididae) on dorsal and ventral mesosoma, 24 May 1953, B. Benesh, CUIC, BMOC 78-0417-003. Holotype in AMNH, paratypes in AMNH, CUIC, UMMZ.

Description. *Phoretic deutonymph* (Fig. 65; Table 24, p. 179). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 65 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*. Prodorsal shield transversely striated. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield longitudinally striated, most lines longer than half of length of hysterosomal shield (except for anterio-lateral part). No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventrolateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* shorter than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites.Ventral setae *4b* short, distinctly shorter than *3a*. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II present, exceed 1/2 of lateral edge of sternal shield. Proximal acetabular extensions IV connected. Distal acetabular extensions of apodemes IV connected. Attachment organ width (including transparent margin) equal or exceeds distance between *4a*. Lateral horns of attachment organ lateral sclerites reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases anterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I about 0.2–0.3 of genu I. Setae *mG* and usually *cG* I shorter or equal to combined length of genu and tibia I. Genual setae *cG* I smooth. Genual setae *mG* I smooth. Genual setae *mG* II exceed combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, distinctly longer than *mG* I, longer than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III clearly extending beyond base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* shorter than 1.5 of maximum width of tarsus IV. Tarsal setae *f* and *e* IV uniform in length and width with *w* and *s* IV, symmetric, nearly equal in length, or absent. Tarsal setae *e* IV similar in length and width with *w* and *s* IV, or absent. Tarsus IV 2–1.5 times longer than its basal width.

Other instars unknown.

Hosts. *Osmia* (*Helicosmia*) *georgica* (Megachilidae) (type host) (see also notes). Collected from *Chrysis coerulans* (Hymenoptera: Chrysididae), a polyxenous cleptoparasite of wasps and bees.

Distribution. USA: North Carolina (type locality), Tennessee (see also notes), Texas.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20rozeni&-max=200&-find

Etymology. The new species is named after Jerome G. Rozen (AMNH), the renowned authority on bee biology and systematics.

Notes. Krombein (1962) reported heteromorphic deutonymphs of *Chaetodactylus* associated with *Osmia caerulescens* from New York. The deutonymphs were similar to those of *Ch. krombeini* except for having slightly but consistently shorter body setae (Krombein, 1962). *Chaetodactylus rozeni*, sp. n. has dorsal setae that are distinctly shorter than in *Ch. krombeini*, however, these two species also differ in many other morphological details. Because *O. caerulescens* and *O. georgica* belong to the same subgenus, *Helicosmia*, and their ranges are overlapping, we believe that Krombein (1962, 1967) probably dealt with mites identical with *Ch. rozeni* sp. n.

Chaetodactylus claudus sp. n.

Material (**USA**). Holotype: HDN—**Utah**, Cache Co., Green Canyon, ex *Osmia* (*Osmia*) *ribifloris* (propodeum), 7–20 May 1983, No collector, USNM, BMOC 96-0510-092. Paratypes: 36 HDNs—same data as for holotype; 8 HDNs, 4 immobile HDNs, 4 pharate immobile HDNs, 16 PNs—**Texas**, Austin Co., Austin, CTM1, *O. ribifloris* nest 102, [illegible: prob] April 1987 [illegible: ope] Jan 1988 J.L. Neff, UMMZ, BMOC 03-0310-008; 2f, 2m, 28TNs, 3 mobile HDNs, 1PN—same locality, eggs+larvae, *Osmia ribifloris* nest, [illegible: 28 Aug 1988], J. L. Neff UMMZ BMOC 03-0310-009; 1TN—same locality, CTM1, *Osmia ribifloris* nest, Mar 88, J. L. Neff, UMMZ BMOC 03-0310-010. Holotype in USNM, paratypes in OSAL, UMMZ, USNM.

Description. *Phoretic deutonymph* (Fig. 66, Fig. 67; Table 24, p. 179). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 66 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield striated, most lines long but shorter than half of hysterosomal shield, except for anterio-lateral part longitudinally. No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated outside prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* longer than 1/2 of distance between their

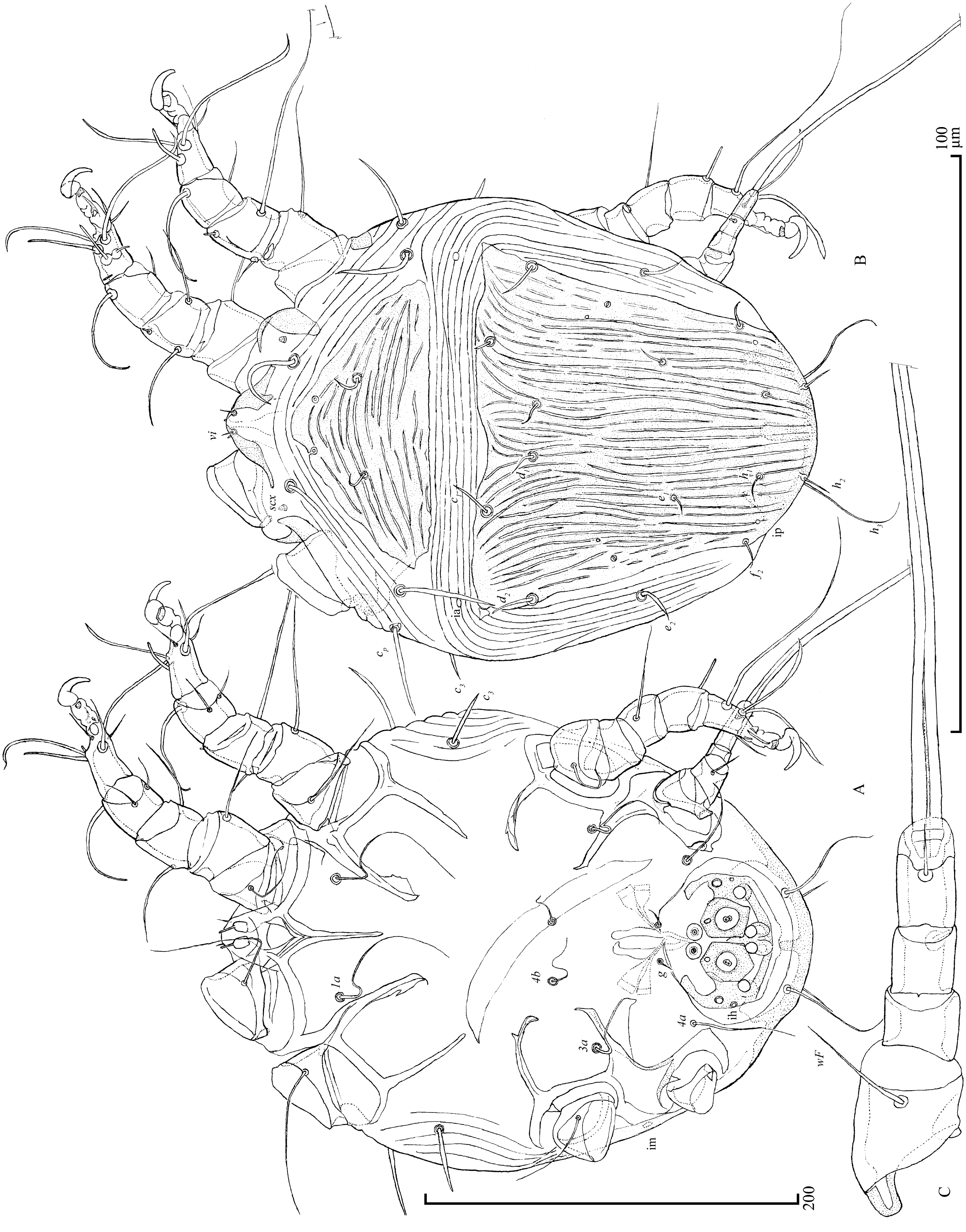

Fig. 65. *Chaetodactylus rozeni*, heteromorphic deutonymph (BMOC 04-0508-007, holotype). A,B - ventral and dorsal view; C - leg IV. Scale bars: left: A,B; bottom: C.

Fig. 66. *Chaetodactylus claudus*, heteromorphic deutonymph (BMOC 96-0510-092, holotype). A, B - ventral and dorsal view.

Fig. 67. *Chaetodactylus claudus*, heteromorphic deutonymph (BMOC 96-0510-092). A, B - leg I; C, D - leg II; E - leg III; F - leg IV.

bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 and e_1 nearly of same length. Coxal setae *1a* filiform, situated on soft cuticle. Coxal setae *3a* and *4b* situated on soft cuticle. Alveoli of *3a* and *4b* without surrounding sclerites. Ventral setae *4b* long, as long as *3a* or less than 2 times shorter. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II present, exceed 1/2 of lateral edge of sternal shield. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites reaching level of *4a*. Suckers ad_3 (excluding transparent margin) distinctly smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I from 0.5–0.6 of genu I. Setae *mG* and *cG* I longer than combined length of genu and tibia I. Genual setae *cG* I and *mG* I smooth. Genual setae *mG* II nearly equal or exceed combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, distinctly longer than *mG* I, longer than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base. Genual setae *nG* III clearly extending beyond base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV, uniform in length and width, shorter than 1.5 of maximum width of tarsus IV. Tarsal setae *f* and *e* IV slightly longer than tarsus IV, symmetric, nearly equal in length. Tarsus IV more than 2 times longer than its basal width.

Immobile deutonymph. See p. 103.

Female. Central part of dorsal opisthosoma more or less uniformly covered with large (2.0–4.0) mammillae, mammillae conical or subconical, with attenuated, darker tips. Setae c_3 almost reaching trochanters IV. Adanal setae ad_3 distinctly extending beyond *ih*. Copulatory tube present, short inseminatory canal about 1.7 times longer than its width at spermatheca. Sclerotized lining of outer end of inseminatory canal about 4 times shorter than length of inseminatory canal. Setae *gT* I–II smooth, filiform; *hT* I–II almost smooth.

Homeomorphic male. Central part of dorsal opisthosoma with mammillae or tubercles, diameter about 2.0. Setae c_3 reaching trochanters IV or extending beyond them. Setae d_1 extending beyond e_1. Aedeagus folds at level of dorsal supporting sclerite. Aedeagus distinctly extending beyond genital capsule, almost reaching level of setae ps_3. Transverse processes of dorsal supporting sclerite not twisted, and not band-like (dorsal supporting sclerite looks like a vertebra in superior or inferior view). Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite. Anterior end of genital capsule without distinct projection. Anterior processes of dorsal supporting sclerite usually less than 2 times wider than posterior ones, anterior concavity about as deep as length of "body". Genital valves without posterior bifurcated flaps. Setae *hT* I–II barbed. Ratio of pretarsal sucker width/tarsus III width about 0.25.

Abnormalities (phoretic deutonymphs). Both *g* spiniform (BMOC 96-0510-092#4)

Hosts. *Osmia* (*Osmia*) *ribifloris* (Megachilidae).

Distribution. USA: Texas, Utah.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20claudus&-max=200&-find

Etymology. Claudus (=limping, halting, lame) is a Latin adjective in reference to tarsus IV, which is usually slightly bent.

Chaetodactylus hopliti sp. n.

Chaetodactylus sp. A. OConnor, 1991: 319.
Chaetodactylus (*Spinodactylus*) sp. 1 OConnor, 1993a: 362.

Material (**USA**). Holotype: HDN—**New York**, Onondaga Co., Syracuse, ex female of *Hoplitis producta* (propodeum), 13 Jul 1978, M. O'Brien, UMMZ, BMOC 84-0409-001. Paratypes: 4 HDNs—same data as holotype; 16 females, 4 males—Albany Co., Rensselaerville, Huyck Preserve, ex nest of *H. producta*, 6 Jul 1975, K. Strickler 75-07-06A, UMMZ, BMOC 76-0113-001; 25 HDNs (7 slides)—Cattaraugus Co., Rock City, ex *H. producta* (dorsal and ventral mesosoma), 1 Jul 1916, No collector, CUIC, BMOC 79-0309-003; 2 HDNs—USA: Livingston Co., Tuxedo Park, ex *H. producta* mesosoma, 28 Jun 1928, AMNH, BMOC 04-0508-044; 6 HDNs—Rockland Co., Nyack, ex *Hoplitis pilosifrons* on propodeum, 27 Feb 1909, AMNH, BMOC 04-0508-041; 1 HDN—Rockland Co., Nyack, ex *H. producta* on propodeum, 27 Feb 1909, AMNH, BMOC 04-0508-042; 4 HDNs—Tompkins Co., Ithaca, bee nest in sumac (*Rhus*) twig, 2 Nov 1973, S. Vernoff, UMMZ, BMOC 73-1102-070; 21 HDNs (9 slides)—Tompkins Co., Ithaca, Fall Creek, ex *H. producta* (mesosoma), 28 Jun 1935, P.P. Babiy CUIC, BMOC 79-0309-002; 1 HDN—**Idaho**, Bear Lake Co., Bloomington Lake, ex female of *Osmia inermis* (propodeum & 1st metasomal tergite), 16 Jul 1950, G.E. Bohart, USNM, BMOC 96-0510-167; 5 HDNs—**Maine**, York Co., Saco, on *Rubus* (Rosales: Rosales), ex *Hoplitis spoliata* (pronotum), 7 Jun 1921, T.B. Mitchell, KU, BMOC 96-0916-334; 6 HDNs—**Michigan**, Cheboygan Co., Douglas Lake, *Osmia brevis*, on propodeum, July, C. H. Kennedy, OSU OSUC 0066119, BMOC 03-1106-022; 1HDN—Cheboygan Co., University of Michigan Biological Station, malaise trap residue, 29 Jun 1994, B. Scholtens, UMMZ, BMOC 94-0629-001; 15 HDNs—Kalamazoo Co., T2S, R12W sect. 7, ex *Isodontia mexicana* (Hymenoptera: Sphecidae) (mesosoma & propodeum), 4 Jul 1980, D. Cowan, UMMZ, BMOC 84-0409-005; 5 HDNs—Livingston Co., E. S. George Reserve, ex *H. spoliata* (mesosoma), 21 Jun 1980, L. Kirkendall, UMMZ, BMOC 84-0409-003; 5 HDNs—same locality and host (metasoma), 7 Jun 1972, F.C. Evans UMMZ, BMOC 91-1015-003; 3 HDNs—same locality and host, female (propodeum), 15 Jun 1971, F.C. Evans, UMMZ, BMOC 91-1015-004; 2 HDNs—same locality and host (head), 27 Jun 1972, F.C. Evans, UMMZ, BMOC 91-1015-005; 1HDN—same locality and host, female (mesosoma), 28 Jun 1972, F.C. Evans, UMMZ, BMOC 91-1015-006; 9 HDNs—same locality and host, female (propodeum), 3 Jul 1974, F.C. Evans, UMMZ, BMOC 91-1015-007; 3 HDNs—same locality and host, female (propodeum), 13 Jun 1980, F.C. Evans, UMMZ, BMOC 91-1015-008; 1 HDN—same locality, ex female of *H. producta* (head), 14 Jun 1972, F.C. Evans, UMMZ, BMOC 91-1015-009; 20 HDNs—Marquette Co., Huron Mountain Club, ex *H. spoliata* (ventral under head, few on mesosoma-metasoma), 26 Jun 1984, D. Gosling, UMMZ, BMOC 84-1121-001; 1 HDN—same locality, malaise trap residue, 21 Jun 1984, D.C.L. Gosling, UMMZ, BMOC 85-0719-001; 3HDN's—same locality, Hymenoptera in malaise trap 11 Jul 1985, D.C.L. Gosling, UMMZ, BMOC 85-0829-007; 1 HDN—same locality, ex *Megachile relativa* (ventral mesosoma), 23 Jun 1986, B. M. OConnor, UMMZ, BMOC 86-0623-011; 1HDN same locality, ex male of *M. relativa* (mesosoma), 25 Jun 1986, B. M. OConnor, UMMZ, BMOC 86-0625-007; 5 HDNs—Washtenaw Co., Pinckney State Recreation Area, near Halfmoon Lake, ex female of *H. pilosifrons* (head, pronotum—propodeum), 31 May 1982, M. & A. O'Brien, UMMZ, BMOC 84-0409-002; 10 HDNs—Washtenaw Co., Pinckney State Recreation Area, near Halfmoon Lake, ex *H. spoliata* (scattered over body), 31 May 1982, M. & A. O'Brien, UMMZ, BMOC 84-0409-004; 1 HDN—**North Carolina**, Buncombe Co., Black Mountain, *Amorpha fruticosa*, ex *H. spoliata* on propodeum, 19 May 1927, J. C. Crawford, AMNH 33827, BMOC 04-0508-046; 17 HDNs—Buncombe Co., Black Mountain, ex *H. spoliata* on propodeum, 26 Mar 1909, AMNH 33827 BMOC 04-0508-047; 11 + 2 HDNs—Swain Co., Great Smoky Mountains National Park, Forney Ridge & Andrews Bald, ex male of *H. spoliata* (ventral mesosoma + propodeum), 16 Jun 1946, R. R. Dreisbach ACC 980, GRSM 30589, BMOC 02-0525-013; 10 HDNs—**Ohio**, Hocking Co., ex *H. producta* (head), 1 Jun 1992, C. H. Kennedy OSU, OSU 0065821, BMOC 03-1106-037; 3 HDNs—**Oregon**, Curry Co., Illinois National Wild and Scenic River, *Amorpha*, ex *H. producta* on mesosoma, 20 Jun 1917, M. A. Cazier, AMNH, BMOC 04-0508-043; 20 HDNs—**Tennessee**, Sevier Co., Great Smoky Mountains National Park, Park Headquarters, ex *Osmia bucephala* (between coxae III), 20 Apr 1982, D. H. DeFoe, GRSM 30612, BMOC 02-0525-014; 10 HDNs—**Wisconsin**, Milwaukee Co., Milwaukee, ex *H. pilosifrons* on propodeum, 15 Jun 1902, S. Graenicher, AMNH, BMOC 04-0508-040; 4 HDNs—**CANADA**: **Quebec**, Hull, ex *H. producta* dorsal mesosoma and head, 14 Jun 1914, F. W. L. Sladen, AMNH, BMOC 04-0508-045. Holotype in UMMZ, paratypes in AMNH, GRSM, OSAL, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 68, Fig. 69; Table 24, p. 207). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 68 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield with pattern of short longitudinal lines (except for anteriolateral part). No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated on prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* longer than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 slightly or distinctly shorter than e_1. Coxal setae *1a* distinctly inflated at bases. Coxal setae *1a* situated on sclerite that fused with anterior apodemes II. Alveoli of *3a* and *4b* with small, ring-like surrounding sclerites, sclerite of *3a* not fused to anterior apodeme IV. Ventral setae *4b* long, as long as *3a* or less than 2 times shorter. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II present, exceed 1/2 of lateral edge of sternal shield. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) distinctly shorter than distance between *4a*. Lateral horns of attachment organ lateral sclerites reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I about 0.6–0.7 of genu I. Setae *mG* and *cG* I longer than combined length of genu and tibia I. Genual setae *cG* I and *mG* I smooth. Genual setae *mG* II exceed combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, distinctly longer than *mG* I, distinctly longer than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II filiform, slightly widened at base or spiniform. Genual setae *nG* III clearly extending beyond base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV longer than 1.5 of maximum width of tarsus IV, nearly uniform in length and width. Tarsal setae *f* and *e* IV several times longer than tarsus IV, symmetric, nearly equal in length. Tarsal setae *e* IV longer than legs IV. Tarsus IV more than 2 times longer than its basal width.

Female. Sclerotized area surrounding posterior supracoxal gland opening nearly as long as tibia II. Dorsal opisthosoma more or less uniformly covered with small conical or subconical mammillae (diameter 1.5–2.0), less dense pattern of these mammillae extending over rest of dorsal idiosoma; mammillae usually with attenuated, darker tips. Setae c_3 almost reaching or extending beyond trochanters IV. Setae ad_3 distinctly extending beyond level of *ih*. Setae ps_3 usually anterior to *4a* level. Inseminatory canal, trumpet-shaped, less than 5 times longer than its width at spermatheca. Sclerotized lining of outer end of inseminatory canal shorter than 0.4 length of inseminatory canal. Setae *gT* I–II smooth, filiform; *hT* I–II slightly barbed, *hT* I almost smooth.

Homeomorphic male (n = 4). Sclerotized area surrounding posterior supracoxal gland opening 34–36 (35 ± 1). Setae d_1 extending beyond posterior end of body. Distance d_1-d_1 (from outer edges) 54–67 (63 ± 6). Ratio d_1-d_1/sclerotized area surrounding posterior supracoxal gland opening 1.6–1.9 (1.8 ± 0.1). Setae c_3 extending beyond trochanters IV. Central part of dorsal opisthosoma with distinctly conical mammillae (diameter 0.9). Basal widening of aedeagus almost reaching level of ps_3. Aedeagus folds at level of dorsal supporting sclerite. Transverse processes of dorsal supporting sclerite not twisted, and not band-like (dorsal supporting sclerite looks like a vertebra in superior view). Genital valves without posterior bifurcated flaps. Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite. Anterior end of genital capsule without distinct projection. Anterior processes of dorsal supporting sclerite usually barely wider than posterior ones, anterior concavity not exceeding 1.6 of basal "body". Aedeagus distinctly extending beyond genital capsule. Setae *gT* I–II smooth and *hT* I–II barbed. Ratio of pretarsal sucker width/tarsus III width 0.26–0.33.

Abnormalities. *Phoretic deutonymph*: one ϕ IV inflated (1.9 in width); one f_2 slightly longer (43.7) than another (39.0) (84-0409-001#01).

Hosts. *Hoplitis* (*Alcidamea*) *producta* (type host); *Hoplitis* (*Alcidamea*) *pilosifrons*; *Hoplitis* (*Monumetha*) *spoliata*; *Mega-*

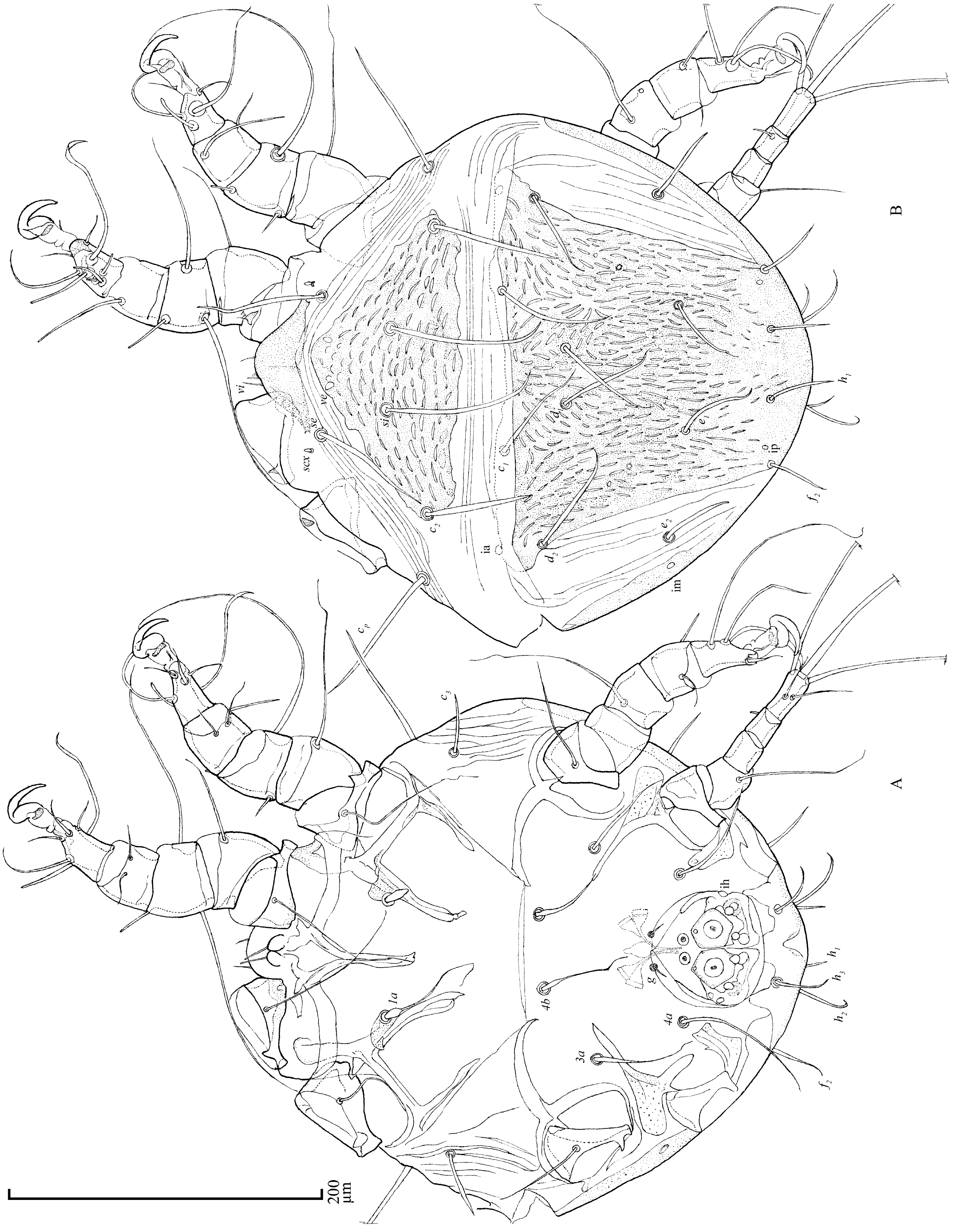

Fig. 68. *Chaetodactylus hoplitii*, heteromorphic deutonymph (BMOC 84-0409-001, holotype). A,B - ventral and dorsal view.

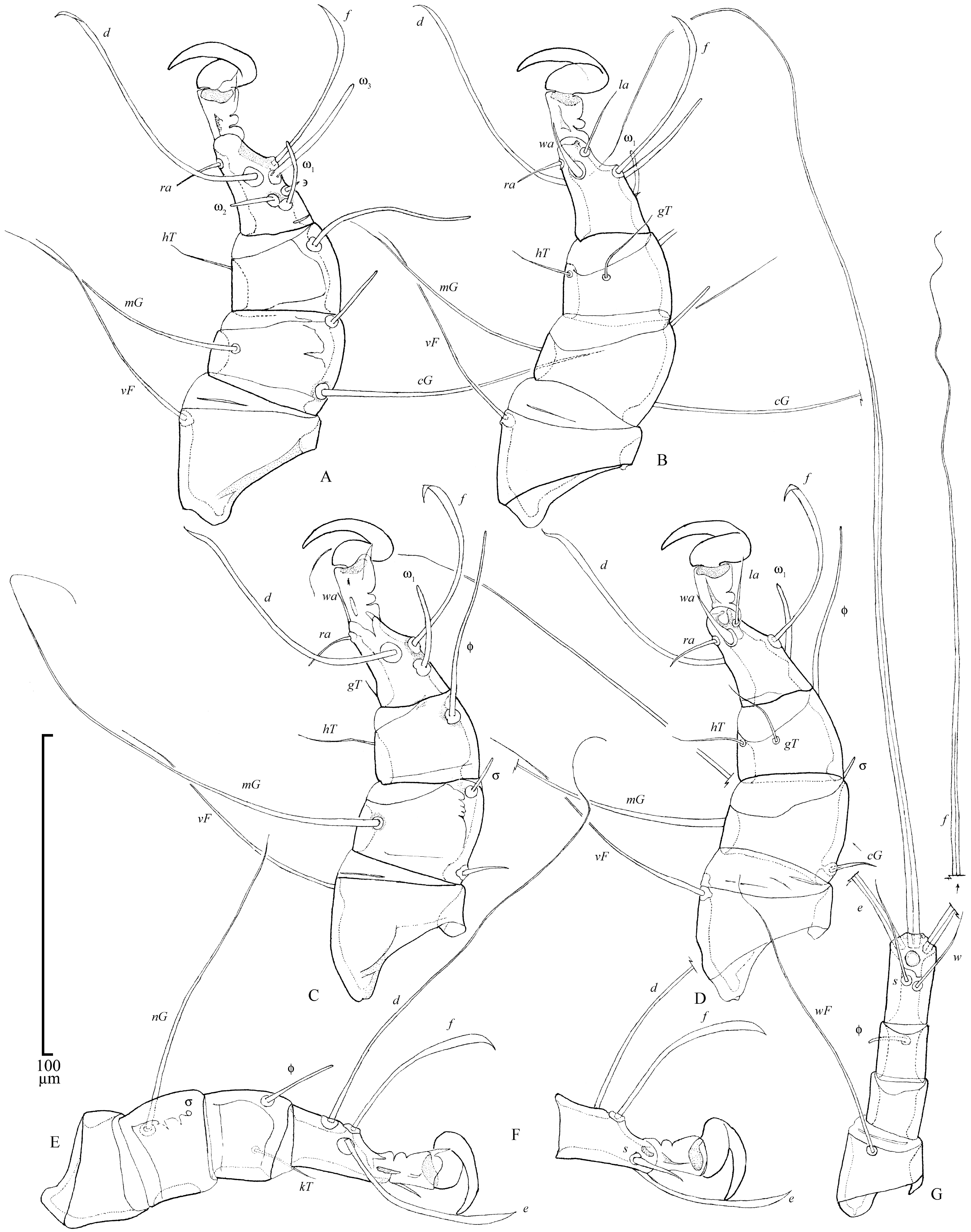

Fig. 69. *Chaetodactylus hopliti*, heteromorphic deutonymph (BMOC 84-0409-004). A, B - leg I; C, D - leg II; E - leg III; F - tarsus III; G - leg IV.

chile (*Megachile*) *relativa*; *Osmia* (*Melanosmia*) *brevis*; *Osmia* (*Centrosmia*) *bucephala*; *Osmia* (*Chenosmia*) *inermis* (Megachilidae); *Isodontia mexicana* (Hymenoptera: Sphecidae)

Distribution. USA: Idaho, Maine, Michigan, New York (type locality), North Carolina, Ohio, Oregon, Tennessee, Wisconsin; Canada: Quebec.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20hopliti&-max=200&-find

Etymology. The specific epithet is derived from the generic name of the host and is a noun in the genitive case.

Notes. The association of *Ch. hopliti* and the non-*Hoplitis* hosts (see above) is probably accidental. Because these insects construct their nests in the same habitat as *Hoplitis*, it seems possible that deutonymphs of *Ch. hopliti* may accidentally attach to them.

Chaetodactylus krombeini Baker, 1962

Chaetodactylus krombeini Baker, 1962a: 229, Figs 1–24 (holotype HDN (no. 2815), paratypes (10 HDNs, 3Ls, 45 PNs, 33 inert HDNs, 2TNs, 5 males, 6 females) in USNM); Krombein, 1962: 237 (observations on biology and development in nest); Fain, 1966: 252 (comparison of biology with *Chaetodactylus osmiae*); Krombein, 1967: 367, Figs 11–14 (observations on biology and development in nest); Elbadry, 1971: 88; Rust, 1974: 27; Baker *et al*., 1987: 65; OConnor, 1994: 149; Bosch & Kemp, 2001: 59, Fig. 52 (interaction with host); Qu *et al*., 2002: 137; Okabe & Makino, 2003: 658; Qu *et al*., 2003: 59; Van Asselt, 2003: 225; Klimov & OConnor, 2004: 158.

Chaetodactylus (*Spinodactylus*) *krombeini*: Fain, 1981b: 2 (as tentative junior synonym of *Chaetodactylus claviger*); OConnor, 1993a: 362 (genus-level character acquisition).

Chaetodactylus osmiae non Dufour, 1839: Krantz, 1978: 419, Figs. 211-1, 121-2 (species authorship attributed to Dujardin).

Chaetodactylus (*Spinodactylus*) *claviger* non Oudemans, 1928: Fain, 1981b: 2 (part.).

Chaetodactylus krambeini Abou Senna, 1997: 677 (*lapsus*)

Material (**USA**). 5HDN's—USA: **Arizona**, Cochise Co., 5mi W Portal, ex *Osmia ribifloris* on mesosoma, 15 Feb 1961, M. A. Cazier, AMNH, BMOC 04-0508-020; 5HDN's—Cochise Co., Ash Spring, 7mi SW Portal, 6400 ft., ex *Osmia ribifloris* over body, 31 Mar 1965, B. & C. Durden, AMNH, BMOC 04-0508-022; 5 HDNs—**California**, Napa Co., Angwin, ex *Osmia ribifloris biedermannii* (pronotum and propodeum), 15 Feb 1966, L. Eighme, USNM, BMOC 96-0510-103; 7 HDNs—Placer Co., Applegate, ex *O. ribifloris* (1st metasomal tergite), 22 Feb 1966, T.Griswold, USNM, BMOC 96-0510-104; 1 HDN—**Idaho**, Franklin Co., Cub River Canyon, ex male of *O. bucephala* on *Thermopsis montana* Nutt. (Fabales: Fabaceae), 1 Jun 1948, G.E. Bohart, USNM, BMOC 96-0510-144; 5 HDNs—**Maryland**, Prince George's Co., Beltsville, ex *O. bucephala* propodeum, 25 Apr 1978, F.D. Parker, USNM, BMOC 96-0510-145; 10 HDNs—**Michigan**, Livingston Co., E.S. George Reserve, ex *O. lignaria* mesosoma, 4 May 1972, T. Green, UMMZ, BMOC 91-1015-001; 20 HDNs—same locality and host, 25 Apr 1978, F.C. Evans, UMMZ, BMOC 91-1015-002; 11 HDN—**Nevada**, Elko Co., Lamoille Canyon, Ruby Mts., Elev. 9200', ex *O. grindeliae* (propodeum), 19 Jul 1975, T.L. Griswold, USNM, BMOC 96-0510-137; 3 HDNs—same locality and host, (propodeum), 19 Jul 1975, T. Griswold, USNM, BMOC 96-0510-138; 7 HDNs—Nye Co., Mt. Spring Pass, ex *O. ribifloris* (1st metasomal tergite) on *Berberis* (Ranunculales: Berberidaceae), 4 May 1963, G.E. Bohart, USNM, BMOC 96-0510-093; 1 larva, 2 protonymphs, 10 females—**New York**, Onondaga Co., Syracuse, ex *O. lignaria* nest, no date, M. O'Brien #0.22, BMOC 79-0312-001; 1 larva, 2 protonymphs, 7 tritonymphs, 4 females, 3 males—same data, BMOC 79-0312-002; 7 HDNs—Tompkins Co., Ithaca, ex male of *O. lignaria*, 30 Apr 1975, S. Jaronski, BMOC 75-0507-001; 2 HDNs—**Ohio**: Franklin Co., Worthington, ex *Osmia chalybea* over body, 17 May 1902, J. G. S. OSU OSUC 0065892, BMOC 03-1106-009; 19 HDNs—Licking Co., ex *Osmia lignaria* on pronotum, 10 May 1936, R. C. Osburn OSU OSUC 0066019, BMOC 03-1106-010; 1 HDN—Columbus, ex *Osmia simillima* on scutellum, May, Jas. S. Hine OSU OSUC 0066098 BMOC 03-1106-013; 5 HDNs—**Oregon**, Benton Co., Corvallis, ex *O. lignaria propinqua* (propodeum), 1 Apr 1957, R.F. Koontz, USNM, BMOC 96-0510-101; 3 HDNs—Benton Co., Corvallis, holes in fence post, 47-6186, ex *O. nigrifrons*, 17 Apr 1947, L. Wallace, USNM, BMOC 96-0510-146; 8 HDNs—**Utah**, Cache Co., Logan, USAC Campus, ex *O. lignaria propinqua* (propodeum) on *Prunus armeniaca* L. (Rosales: Rosaceae), 27 Apr 1948, G.E. Bohart, USNM, BMOC 96-0510-100; 3+6 HDNs—Cache Co., Cowley Canyon, ex *O. montana* (metasomal tergites I–II + propodeum), 13 May 1989, W.J. Hanson, USNM, BMOC 96-0510-122; 6 HDNs—Cache Co., W. Hodges Canyon, Malaise Trap, ex *O. bucephala* (propodeum), 13–20 June 1980, T.Griswold, USNM, BMOC 96-0510-143; 2 HDNs—Cache Co., Birch Canyon [label reads: Birch Creek Canyon], ex *O. californica* (pronotum), 23 May 1982, TL/RT Griswold, USNM, BMOC 96-0510-110; 6 HDNs—Cache Co., Logan Canyon, Tony Groove, ex *O. lignaria propinqua* (propodeum) on *Salix* (Salicales: Salicaceae), 20 May 1948, G.E. Bohart, USNM, BMOC 96-0510-102; 6 HDNs—Washington Co., Pintura, ex *O. ribifloris* (propodeum) on *Rhus ovata* S. Wats. (Sapindales: Anacardiaceae), 12 Apr 1970, G.E. Bohart, USNM, BMOC 96-0510-094; 1 HDN, 1 larva—Weber Co., S Monte Cristo Peak [label reads "S Monte Cristo"], ex *O. montana* (1st metasomal tergite), 23 Jun 1973, G.F. Knowlton, USNM, BMOC 96-0510-120; 6 females, 5 males, 3 HDNs, 2 tritonymphs, 1 protonymph, 3 larvae—**Washington**, King Co., Bothell, *O. lignaria* nest, 17 Jun 1998, E.A. Sugden, UMMZ BMOC 98-1202-001. Voucher specimens in AMNH, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 70, Fig. 71; Table 24, p. 207). Longitudinal sclerites on rostral projection (extensions of coxal apodemes I) well sclerotized, distinct, touching or almost touching each other medially, here not diverging (Fig. 70 *B*). Alveoli *ve* situated on or contiguous with prodorsal shield. Prodorsal shield extends anterior of *se*, with pattern of short transverse lines. Lateral angles of prodorsal shield not attenuated. Setae *si* situated on prodorsal shield. Hysterosomal shield with pattern of short longitudinal lines (except for anteriolateral part). No reticulate pattern on hysterosomal shield. Lateral hysterosomal sclerites ventro-lateral, with anterior end situated at anterior level coxal apodemes III and posterior end at attachment organ. Longest dorsal setae smooth. Setae c_1 and d_2 situated on hysterosomal shield. Setae c_2 situated on prodorsal shield. Setae c_p and c_2 almost on same transverse level (distance between them usually not exceeds 2 diameters of bases of c_2). Setae *si* longer than 1/2 of distance between their bases. Setae h_3 shorter than combined length of femur, genu, and tibia I. Setae h_1 slightly or distinctly shorter than e_1. Coxal setae *1a* distinctly inflated at bases. Coxal setae *1a* situated on sclerite that fused with anterior apodemes II. Coxal setae *3a* and *4b* situated on sclerites. Sclerites surrounding coxal setae *3a* and *4b* large, irregular in shape, sclerite *3a* fused to anterior apodeme IV. Ventral setae *4b* long, as long as *3a* or less than 2 times shorter. Coxal setae *4a* almost as long as *3a*, or slightly shorter. Sternal apodeme not bifurcated posteriorly or bifurcated posteriorly. Posterior apodeme II present, exceed 1/2 of lateral edge of sternal shield. Proximal and distal acetabular extensions of apodemes IV disjunct. Attachment organ width (including transparent margin) equal or exceeds distance between *4a*. Lateral horns of attachment organ lateral sclerites reaching level of *4a*. Suckers ad_3 (excluding transparent margin) smaller

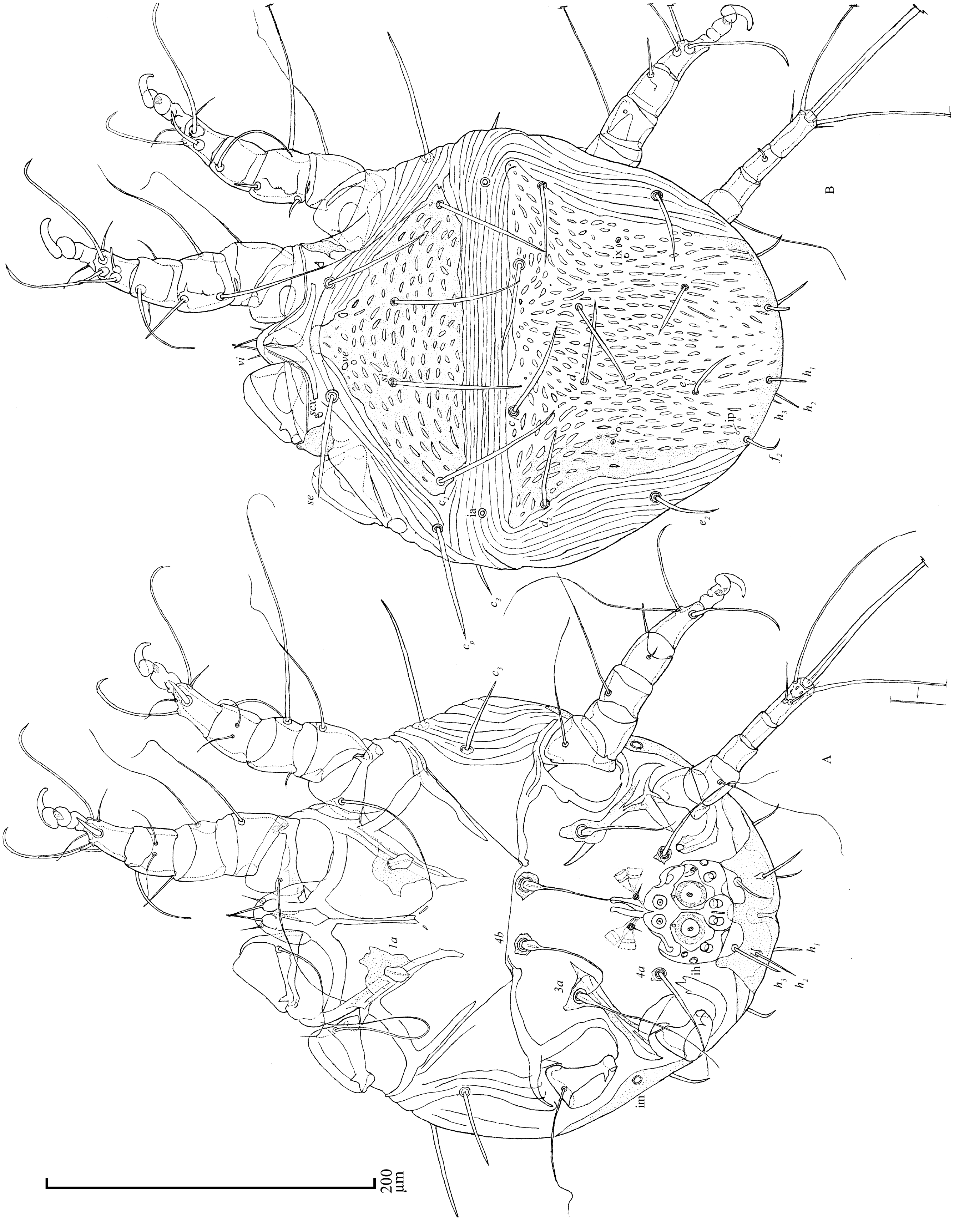

Fig. 70. *Chaetodactylus krombeini*, heteromorphic deutonymph (BMOC 91-1015-001). A, B - ventral and dorsal view.

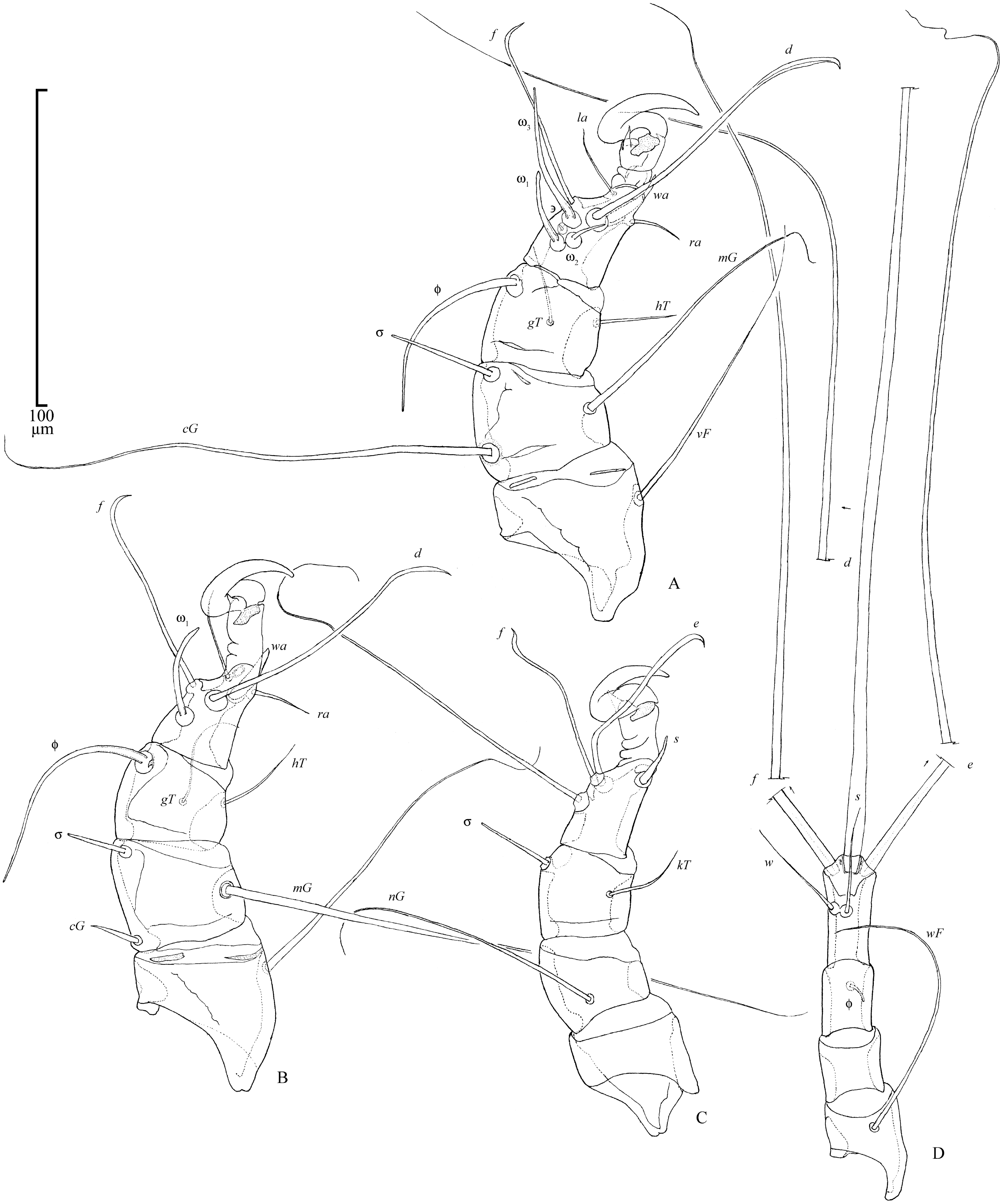

Fig. 71. *Chaetodactylus krombeini*, heteromorphic deutonymph (BMOC 91-1015-001). A–D - legs I–IV, respectively.

than inner unsclerotized area of suckers ad_{1+2}. Anterior edge of ps_2 bases posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}. Legs with semicircular sclerite distal to base of *wa* I–II absent. Solenidion σ I about 0.7 of genu I. of genu I. Setae *mG* and *cG* I longer than combined length of genu and tibia I. Genual setae *cG* I smooth. Genual setae *mG* I smooth. Genual setae *mG* II distinctly exceed combined length of femur, genu and tibia II. Femoral setae *vF* II nearly equal or longer than combined length of femur, genu and tibia II. Genual setae *mG* II smooth, distinctly longer than *mG* I, longer than *vF* II. Tarsal setae *la* I–II filiform. Tarsal setae *wa* I–II spiniform. Genual setae *nG* III clearly extending beyond base of tarsus III. Seta *nG* III smooth. Solenidion σ III absent. Seta *s* III subapical. Solenidion ϕ IV shorter than genu IV. Tarsal seta *s* IV present. Setae *w* or *s* IV longer than 1.5 of maximum width of tarsus IV, uniform in length and width. Tarsal setae *f* and *e* IV several times longer than tarsus IV, symmetric, nearly equal in length. Tarsal setae *e* IV distinctly longer than legs IV. Tarsus IV more than 2 times longer than its basal width.

Immobile deutonymph. See p. 103.

Female. Sclerotized area surrounding posterior supracoxal gland opening distinctly longer than tibia II. Dorsal opisthosoma more or less uniformly covered with small conical or subconical mammillae (diameter 1.5–2.0), less dense pattern of mammillae covering remaining dorsal idiosoma; mammillae usually with attenuated, darker tips. Setae c_3 almost reaching or extending beyond trochanters IV. Setae ad_3 distinctly extending beyond level of *ih*. Setae ps_3 usually anterior to *4a* level. Inseminatory canal, trumpet-shaped, less than 5 times longer than its width at spermatheca. Sclerotized lining of outer end of inseminatory canal shorter than 0.4 length of inseminatory canal. Setae *gT* I–II smooth, filiform; *hT* I–II sparsely barbed, *hT* I almost smooth.

Homeomorphic male. Sclerotized area surrounding posterior supracoxal gland opening 36–45 (40 ± 3, n = 11). Setae d_1 extending beyond posterior end of body. Distance d_1-d_1 (from outer edges) 46–56 (51 ± 3, n = 11). Ratio d_1-d_1/sclerotized area surrounding posterior supracoxal gland opening 1.1–1.4 (1.3 ± 0.1, n = 11). Setae c_3 extending beyond trochanters IV. Central part of dorsal opisthosoma with distinctly conical mammillae, diameter 0.9. Basal widening of aedeagus almost reaching level of ps_3. Aedeagus folds at level of dorsal supporting sclerite. Transverse processes of dorsal supporting sclerite not twisted, and not band-like (dorsal supporting sclerite looks like a vertebra in superior view) (Fig. 12 *E*). Genital valves without posterior bifurcate flaps (Fig. 12 *E*). Medial sclerite of genital capsule not reaching posterior level of dorsal supporting sclerite (Fig. 12 *E*). Anterior end of genital capsule without distinct projection (Fig. 12 *E*). Anterior processes of dorsal supporting sclerite barely wider than posterior ones, anterior concavity not exceeding 1.6 of basal "body". Aedeagus distinctly extending beyond genital capsule (Fig. 12 *E*). Setae *gT* I–II smooth and *hT* I–II barbed. Ratio of pretarsal sucker width/tarsus III width 0.34.

Hosts. *Osmia* (*Osmia*) *lignaria* (type host); *Osmia* (*O.*) *lignaria propinqua*; *Osmia* (*O.*) *ribifloris*; *Osmia* (*O.*) *ribifloris biedermannii*; *Osmia* (*Acanthosmioides*) *nigrifrons*; *Osmia* (*Centrosmia*) *bucephala*; *Osmia* (*Cephalosmia*) *californica*; *Osmia* (*Cephalosmia*) *montana*; *Osmia* (*Helicosmia*) *chalybea*; *Osmia* (*Melanosmia*) *grindeliae*; *Osmia* (*M.*) *simillima*.

Distribution. USA: Arizona, California, Idaho, Maryland (type locality), Michigan, Nevada, New York, Ohio, Oregon, Utah, Washington.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=chaetodactylus%20krombeini&-max=200&-find

Biology. *Chaetodactylus krombeini* is primarily associated with the megachilid bee *Osmia lignaria*. Life cycles of both bee and mite were studied by Krombein (1962). He observed deutonymphs disposed in a random fashion over the bee's body, although the majority were attached to setae on the propodeum or anterior part of the metasoma. One or more of these deutonymphs were observed to crawl off the body of the female bee while she provisioned the cell with pollen and nectar. Presumably they then transformed into tritonymphs. Adult mites of both sexes were present in infested cells 3 to 4 days after the cell was provisioned. In an attempt to explain this phenomenon, Krombein speculates that the phoretic deutonymphs transform into tritonymphs and females, each of which lays a single egg that develops very rapidly into an adult male. This male mates with its mother, or with another female that may be in the same cell, and the female then proceeds to lay fertilized eggs.

Male bees were more commonly infested with phoretic deutonymphs, and also had more mites per bee. This phenomenon is possibly a consequence of the skewed sex ratio and of the prior emergence of male bees in the spring.

Chaetodactylus krombeini may attack and kill the egg or young larva in a newly provisioned cell or in newly infested cells. Occasionally the mites do not kill the host but feed on the provisioned pollen, and the young bee larva is nutritionally deprived (Bosch & Kemp, 2001). In this case a smaller than normal adult bee may develop, along with some mites. Ordinarily, the mites are unable to gain access to uninfested cells once the infested cell is capped, and they are confined to the original cell until the partition is broken down the following spring by emergence of an adult bee from one of the earlier constructed cells. Mites frequently move into adjacent cells when partitions break during nest manipulation in managed colonies of *Osmia lignaria* (Bosch & Kemp, 2001).

After killing and feeding on the bee egg or young larva, the female mite deposits her eggs principally on the cell walls beyond the pollen-nectar mass. The eggs hatch in 4 to 5 days into larvae. The larvae feed on nectar from the pollen-nectar mass and transform into protonymphs, which also continue to feed on the nectar. There is some doubt as to what happens next, but it seems probable that the protonymphs occurring early in the season transform directly into tritonymphs, bypassing the deutonymphal stage completely. However, *Chaetodactylus* deutonymphs were never found in nests early in the spring. The tritonymphs transform into adults, which in turn repeat the cycle, within the infested cell until all the provisioned food has been consumed. The number of generations and duration of breeding is dependent on the volume of the pollen-nectar mass.

Formation of the immobile deutonymph in *Chaetodactylus* may be due to insufficient food or to decreased humidity caused by the use of all of the nectar, or to a combination of both factors. It is not possible to state what factors determine whether immobile and/or phoretic deutonymphs will develop in an individual nest. Formation of the latter was never observed in the laboratory. In an undisturbed nest, both forms of deutonymphs are probably confined to the originally infested cells because of the presumed inability of the mites to break through the mud partitions separating the cells.

Very early in the spring the phoretic deutonymph presumably attaches to an adult bee as the latter chews its way through the mud seal capping its cell. In an undisturbed nest the mites in the innermost cell or cells would possibly die *in situ* because of their inability to mount an adult bee. The mites would need to infest some cells in the middle or near the outer end of the nest, so that bees would develop in the innermost cells and provide the necessary vehicle for migration of the mites as the bees chewed their way out of the nest. Mites trapped in the innermost cell might be released by a female bee chewing through the closing partition during her efforts to clean out the debris from an old nest for re-use.

The role of the immobile deutonymph in initiating a new infestation requires additional investigation. Some of the immobile deutonymphs transformed to tritonymphs several days after the bees left the nest in the spring. Theoretically, it would be possible for the immobile deutonymphs to remain in that stage in an old nest for some length of time. If this nest was then re-used by another bee, the capping of cells by that bee would increase the humidity to the point where the heteromorphic deutonymphs could transform into tritonymphs, which would then infest the cells provisioned by that bee.

Obviously, the presence of both immobile and phoretic deutonymphs in a mite species may be of profound evolutionary significance. The phoretic deutonymphs, which attach to the body of the host bee and then drop off in a new nest of that same bee species, insure only the continuation of the same host relationship. But the occurrence of immobile deutonymphs, which remain in the old nest, gives the mite species an opportunity to colonize other species of bees that also nest in abandoned borings.

Parasitism by *Ch. krombeini* can attain high levels, especially in humid areas of the United States (Bosch & Kemp, 2001).

Control. Inspection of *Osmia lignaria* nests in semi-translucent paper straws and removal of infested cells is a time-consuming, but effective method to prevent damaging *Ch. krombeini* infestations in managed colonies. Stripping cocoons out of the nesting materials and managing loose cocoons, instead of whole nests, reduces initial infestation because emerging bees are not forced to walk through infested cells. However, releasing *O. lignaria* populations as loose cocoons increases dispersal of prenesting females (Bosch & Kemp, 2001).

Studies on the Japanese species *Chaetodactylus nipponicus*, associated with the hornfaced bee, *Osmia cornifrons*, showed significant reductions of mite infestation in nesting materials treated with endosulfan (60–600 ppm). These same studies indicated that exposure of hornfaced bee nests to high temperatures (e.g., 60 days at 30°C, or three days at 40°C) effectively kills *Ch. nipponicus* mites without harming hornfaced bees, as long as the bees are in the prepupal stage (Yamada, 1990; Sekita & Yamada, 1993). Similarly, treating cocoons of *O. cornuta* and *O. rufa* during the winter period with a 0.007% solution of endosulfan for a period of 3 min is a very effective method of controlling *Ch. osmiae* in Europe. It was found that such treatment of cocoons had no negative effect on the bees inside (Krunić *et al*., 2005). The potential utility of these or similar methods to control *Ch. krombeini* in *Osmia lignaria* populations is being tested.

Notes. Specimens from *Osmia pumila* (8 HDNs, 4 females—USA: New York, mixed sample from 5 localities from Suffolk (4) and Nassau Co. (1), *Osmia pumila* nest cell V-VI 1998, K. Goodell UMMZ BMOC 98-1110-001) probably belong to a closely related species. In three well mounted females, the dorsal opisthosoma has a pattern of large tubercles (1.9–2.5 in diameter) (versus conical or subconical mammillae (1.5–2.0) in *Ch. krombeini*) and the outer ridge of the supracoxal sclerite is shorter than tibia II (longer in *Ch. krombeini*). Deutonymphs from *O. pumila* do not have any distinct differences from those of *Ch. krombeini*, but all have slightly thinner *s* III and longer e_1. Since mites from *O. pumila* originated from mixed samples with small sample size, and all characters of phoretic deutonymphs overlap with *Ch. krombeini*, we refrain from specifically determining these specimens at this time.

Genus *Sennertia* Oudemans, 1905

Pediculus (non Linnaeus): Scopoli, 1763: 381 (part.)

Trichodactylus (nom. preocc. Latreille, 1828 in Decapoda): Gervais, 1844: 266 (part.); Berlese, 1884b: 12 (synonymized with *Homopus* Koch, 1841 and *Dermacarus* Haller, 1880; only *Trichodactylus xylocopae* mentioned; part.); Berlese, 1885: XVIII; Canestrini & Berlese, 1885: 207; Murray, 1877: 251 (part); Mégnin, 1880: 146 (part.).

Trichotarsus Canestrini, 1888b: 7 (nom. n. pro *Trichodactylus* "Dugès" (=*Trichodactyle* Donnadieu, 1868); Donnadieu, 1868: 70 (also as *Trichodactyle*, French vernacular form of *Trichodactylus* Dufour, 1839), part.; Donnadieu (1868) recognized *Trichodactylus* Dufour, 1839 proposed for *Trichodactylus osmiae*; part.); Canestrini, 1888a: 394 (part.); Berlese, 1897: 105 (part., with genus *Eutarsus* Hessling, 1852 as junior synonym); Banks, 1902: 176 (part.); Berlese, 1898: fasc. 89, n. 12 (part); Canestrini & Kramer, 1899: 148 (part.); Tietze in Canestrini, 1899: 938 (part., also includes *Scutacarus* and Winterschmidtiidae gen.); Giard, 1900: 377 (part.); Oudemans, 1900: 115 (part); Oudemans, 1901: 82 (part.); Michael, 1903: 13 (part.); Oudemans, 1903a: 144 (part.); Oudemans, 1903b: 13 (part.); Oudemans, 1903c: 138; Trägårdh, 1904: 156; Trägårdh, 1907: 12; Vitzthum, 1912c: 231; Vitzthum, 1912d: 289 (part.); LeVeque, 1928: 1; LeVeque, 1930: 2.

Acarus (non Linnaeus); Perkins, 1899: 38 (part. also incules *Dinogamasus* and Winterschmidtiidae).

Trichotarsus group D Oudemans, 1903a: 147.

Sennertia Oudemans, 1905a: 21 (type species *Pediculus cerambycinus* Scopoli, 1763, by original designation); Oudemans, 1911a: 168; Vitzthum, 1919:

38; Vitzthum, 1929: 76; Womersley, 1941: 479; Vitzthum, 1933: 152; Vitzthum, 1943: 886; Vitzthum, 1941: 307; Baker & Wharton, 1952: 351; Türk & Türk, 1957: 210; Elbadry, 1971: 89; Fain, 1974a: 215; Sherbef & Duweini, 1980: 245; Lombert *et al*., 1987: 113; OConnor, 1993a: 345; Fain & Pauly, 2001: 131; Klimov *et al*., 2007a: 1369; Klimov *et al*., 2007b: 120.
Chaetodactylus: Pugh, 1993: 373 (misidentification).
Hericia (non Robin): Oudemans, 1917: 345 (part.).
Sonnertia Delfinado & Baker, 1976: 87 (lapsus).
Sennertai Baker & Delfinado-Baker, 1983: 119 (lapsus).
Seneria Ramaraju & Mohanasundaram, 2001: 107 (lapsus).
Senertia Ramaraju & Mohanasundaram, 2001: 107 (lapsus).

Biology and host associations. Species of this genus are associated with xylocopine bees *Ceratina* and *Xylocopa* (Apidae). Sometimes monophyletic groups of mites occur on monophyletic groups of hosts, indicating their close biological relationships and possible codivergence. Host associations of major groups of *Sennertia* are recorded on p. 73.

The majority of *Sennertia* disperse as heteromorphic deutonymphs on adult bees, however the *Sennertia vaga* group does not form deutonymphs and disperses as feeding instars. Reproduction and feeding also probably occur during dispersal.

The interactions of *Sennertia* with their hosts remain largely unknown. There are conflicting accounts suggesting either negative or neutral effect of the mite presence (p. 55). In the former case, the damage to developing bees was marginal and always substantially lesser than that of *Chaetodactylus*. Some species are phoretic inside special pouches (acarinaria) on the body of certain *Ceratina* and *Sennertia*, suggesting mutualistic relationships (p. 58). Unfortunately, the biology of such species has not been studied.

Distribution. Worldwide, except for Antarctica. In contrast to *Chaetodactylus*, there is a clear division between New and Old World lineages (see p. 73).

Description. *Phoretic deutonymph*. Gnathosomal solenidion present *and* setae on free palpi absent *and* free palpi absent. Alveoli *ve* dorsal, approximately at level of *se*. Prodorsal shield absent. Setae *se* situated on soft cuticle. Setae c_2 situated distinctly anterior to level of c_1. Setae e_2 situated outside hysterosomal shield or touch it. Setae *1a* and *3a* not touching posterior borders of respective coxal fields, if touching then inflated and elongated. Cupules *ia* situated outside hysterosomal shield. Cupules *im* situated at level of bases of legs III, approximately at middle of line connecting d_2 and e_2 (*surinamensis*-group) or distinctly posterior to basesof legs III, laterad of line connecting d_2 and e_2. Cupules *ip* are posterior to setae f_2. Cupules *ih* situated on sides of attachment organ. Posterior part of posterior apodemes of coxal fields II displaced posteriorly to anterior apodemes III. Coxal fields III open. Coxal fields IV open. Transverse medial extension of posterior apodemes IV absent. Anterior extension of posterior apodemes IV absent or not connecting or present, connecting with anterior apodeme III (*surinamensis*-group). Ventral longitudinal sclerites of progenital chamber at posterior part conspicuous. Ventral longitudinal sclerites of progenital chamber at anterior part inconspicuous. Posterior and lateral cuticular suckers (*e.g.*, Fig. 8 *A*) absent. Anterior cuticular suckers vestigial or absent (Fig. 8 *D*). Bases of anterior cuticular suckers incorporated to the border (Fig. 8 *D*). Apodemes of ps_1 completely fused. Setae *wa* and *f* I–II *wa* I–II apical or subapical, *f* I–II at level or proximal to *wa* I–II and far from tarsal apices. Solenidion ω_2 present. Empodial claws I–III twisted. Dorsal cuticular folds of ambulacra I–III well-developed, with distal part distinctly larger than any of proximal folds (Fig. 17 *C*). Condylophores of tarsi I–III well-developed, distinctly asymmetrical—anterior longer, posterior shorter, incorporated into posterio-lateral lobe. Supporting sclerites of condylophores (latero-apical sclerites of tarsus) distinct from the tarsus, connected by dorsal bridge (Fig. 17 *C*). Disto-dorsal lobe of distal part of the caruncle (Fig. 17 *B*) present, well developed. Dorsal condylar plate of femur-tibia joint (Fig. 14 *A*) absent or indistinct. Tarsi I–II with 5 setae (*p* and *q* absent). Tarsal setae *ra* and *la* I–II simple or spiniform. Genual seta *cG* I distinctly shorter than genu I and unmodified. Genual setae *cG* I–II subequal. Tarsal setae *q* III absent. Tarsal setae *w*, *r*, and *p* III absent. Tarsal seta *s* III simple. Sigma III present. Tarsus IV with maximum 5 setae (*s*, *p*, *q* always absent). Tarsal setae *e*, *f* IV simple or absent. Tarsal setae *w* IV distinctly shorter than leg IV or absent. Tibial setae *kT* IV absent. Solenidion ϕ IV absent, represented by alveolus.

Immobile deutonymph absent.

Adults. Second anterior tooth of fixed digit (*tf2″*) forms long, blade-shaped crown long, extending to posterior group of teeth (Fig. 1 *A*). Anterior paraxial process of cheliceral body absent (Fig. 1 *A*). Fenestrate area *fe1* of cheliceral body not striated (Fig. 1 *A*). Paraxial and antiaxial rutellar lobes (*rlp* and *rpa*) free, paraxial lobe separate ventrally and dorsally (Fig. 4 *A,B*). Supracoxal seta filiform, situated on supracoxal sclerite or outside supracoxal sclerite (*Sennertia vaga*) lateral to outer ridge of supracoxal sclerite or anterior to outer ridge of supracoxal sclerite (*S. vaga*). Anterio-lateral ridge of supracoxal sclerite (Fig. 6 *D*) present. Setae h_3 external to h_2. Cupules *im* dorsal (correlated with HDN). Cupules *ip* posterior to setae f_2 (correlated with HDN). Disto-dorsal lobe of distal part of the caruncle present, well developed (correlated with HDN). Dorsal condylar plate of femur-tibia joint broad, sometimes medially incised, submedial. Solenidion ω_2 I proximal to *d* I. Solenidion ω_2 II absent. Setae *w* III absent (correlated with HDN). Tarsal setae *r* III–IV absent. Setae *kT* IV absent (correlated with HDN).

Female. Proximal ends of anterior apodemes I and pregenital sclerite fused. Proximal ends of anterior apodemes I separated from each other by large pregenital sclerite. Spermatophores absent. Inseminatory canal trumpet-shaped or funnel shaped, weakly sclerotized, not protruding inside spermatheca. Posterior ends of supporting sclerite of preoviporal canal situated near area of genital papillae or near posterior edges of the progenital folds. Condylophores with long sclerotized portion, distinct proximal unsclerotized portion absent.

Male. Main part of progenital sclerites lateral to genital capsule (Fig. 10 *A-E*). Progenital sclerites not touching each other (Fig. 10 *A-E*). Lateral processes (horns) of dorsal supporting sclerite simple, long or short. Body of dorsal supporting sclerite, posterior to base of aedeagus absent. Genital setae slightly (about on their diameter at base) anterior to progenital fold or on progenital folds. Genital setae short, transparent mammillae or filiform or spiniform. Tarsal setae *q* II absent. Tarsal setae *e* III–IV present. Tarsal setae *q* III–IV absent. Setae *s* and *w* IV both subapical, close to each other. Tarsi I–IV as thick as in females. Sclerotized portions of condylophores separate, anterior condylophore modified to a bilobed sucker. Pretarsal suckers present. Distinct anterio-dorsal protuberance on tarsi I–IV absent.

Larva. Claparède's organs absent.

Notes. Although the monophyly of *Sennertia* is well supported (see above, p. 76), the internal relationships among different lineages and, especially their early divergence, are not clear. *Sennertia zhelochovtsevi* represents a mixture of advanced (the shape of hysterosomal shield) and plesiomorphic characters (relative length of *si* and c_1), and the latter indicate its early divergence. Several characters (length of setae c_1 and the reduction of hysterosomal sclerotization) suggest its possible sister-group relationship with the New World clades associated with *Xylocopa*.

With the extremely conservative and variable morphology in several distant lineages, the question about the monophyly of some *Ceratina* and *Xylocopa* associated lineages remains unsolved. The high rate of convergent morphological changes probably occurred because of correlated increase of the lengths of setae situated off the hysterosomal shield following its reduction. A preliminary phylogenetic analysis of several putative groups is given on p. 73.

Different groups of *Sennertia* phoretic deutonymphs are diagnosed in the following key (see also diagnosis of the *vaga*-group based on adults on p. 130):

Key to Subgenera and Species-Groups of *Sennertia* (Heteromorphic Deutonymphs)

1 Setae c_1 long, nearly as long as *se*. Setae *si* nearly as long as *se* 2

\- Setae c_1 shorter than *se*, microsetae. Setae *si* variable 8

2(1) Hysterosomal shield triangle. Opisthosomal gland openings outside shield. Tarsal setae *w* IV short. Posterior apodeme IV absent. *Xylocopa* (*Proxylocopa*). Mediterranean, Middle Asia . . . . ***zhelochovtsevi***-group (new)

\- Hysterosomal shield not triangle. Position of opisthosomal gland openings, length of tarsal setae *w* IV, and presence/absence of posterior apodeme IV variable. New World. (*Amsennertia* s. l.). 3

3(2) Tarsal ventral setae *w* IV long, distinctly longer than leg IV. Posterior apodeme IV present. Setae *1a*, *3a*, *4b* conoidal; *c3*, *4a*, and *g* inflated at bases. Setae *wa* I–II bifid . . . . ***devincta***-group

\- Tarsal ventral setae *w* IV distinctly shorter than leg IV. Posterior apodeme IV absent. Setae *1a*, *3a*, *4b*, c_3, *4a*, *g*, and *wa* I–II simple. Associated with *Xylocopa*. (**Amsennertia** s. str.) 4

4(3) Setae d_1, e_1, and h_1 nearly uniform in length, microsetae, d_1 and e_1 distinctly shorter than respective 1/2 of distance between them. (-) Setae c_1 situated on anterior margin of hysterosomal shield (*frontalis*-, *loricata*-groups) or anterior to it (*americana*-group). Opisthosomal gland openings on (*frontalis*-group) or outside hysterosomal shield (*loricata*-group, *americana*-group). 6

\- Setae d_1 and e_1 distinctly longer than h_1, at least one of them longer than 1/2 of distance between bases. Setae c_1 anterior to hysterosomal shield. Opisthosomal gland openings outside hysterosomal shield. 5

5(4) Setae *mG* II almost as long as leg II, distinctly longer than *vF* II. Tarsal setae *ra* I–II simple . . . . ***ignota***-group

\- Setae *mG* II distinctly shorter than leg II and setae *vF* II. Tarsal setae *ra* I–II bifid . . . . ***faini***-group

6(4)Setae c_1 anterior to hysterosomal shield . . . . ***americana***-group

\- Setae c_1 situated on anterior margin of hysterosomal shield 7

7(6) Opisthosomal gland openings outside hysterosomal shield. Usual striate pattern of hysterosoma accompanied by sclerotization . . . . ***loricata***-group

\- Opisthosomal gland openings on hysterosomal shield. Striate pattern of hysterosoma without sclerotization . . . . ***frontalis***-group

8(1) Caruncle I–III with 2 distinct transparent lobes. Setae *si* distinctly longer than *se*. Tarsal setae *e* and *f* I–II strongly asymmetrical, *f* about 2 times shorter and filiform, *e* longer and lanceolate. (-) Hysterosomal shield triangle in outline. Setae *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II spiniform. Associated with *Xylocopa* in the Neotropics . . . . **Spinosennertia** Fain

\- Caruncle I–III with 1, usually sclerotized lobe (distal lobe absent). Tarsal setae *e* and *f* I–II slightly asymmetrical, *f* maximum 1.5 shorter than *e*. Other characters variable 9

9(8) Setae c_1 anterior to hysterosomal shield. Associated with *Xylocopa*. Afrotropical, Oriental, Eastern Palaearctic . . . . **Afrosennertia** Fain (=*Asiosennertia* Fain, **syn. n.**)

\- Setae c_1 situated on hysterosomal shield. Associated with *Xylocopa* and *Ceratina*. Old World (**Sennertia**) 10

10(9) Setae *si* of medium length, not microsetae 11

\- Setae *si* microsetae 12

11(10) Ventral tarsal seta *w* IV long, distinctly longer than tarsus IV. Setae *si* and *se* on same transverse level (*si* distinctly posterior in one undescribed species). Associated with *Xylocopa*. Oriental region and Madagascar . . . . ***horrida***-group

\- Ventral tarsal seta *w* IV short, usually shorter than tarsus IV. Setae *si* posterior to *se*. Associated with *Ceratina*. Neotropics . . . . ***surinamensis***-group

12(10) Ventral tarsal seta *w* IV elongated. Afrotropic and Oriental, Eastern Palaearctic. Associated with *Xylocopa* (placement of the African clade here is questionable) . . . . ***japonica***-group

\- Ventral tarsal seta *wa* IV not elongated. Associated with *Xylocopa* or *Ceratina*. Old World. (probably paraphyletic) . . . . ***cerambycina***-group (including *Eosennertia* Kurosa)

Artificial Key to Species of the Genus *Sennertia* of the New World

Phoretic deutonymphs

1 Setae c_1 longer, nearly as long as *se*. Posterior apodeme IV absent (present in one species). 8

\- Setae c_1 microsetae, distinctly shorter than *se*. Posterior apodeme IV present 2

2(1) Hysterosomal shield triangle in outline, setae f_2 on edge and opisthosomal gland openings and setae c_1 outside hysterosomal shield. Supracoxal setae *scx* situated on small sclerite separate from dorsal part of apodeme I. Posterior apodeme IV not connected to anterior apodeme IV. Setae *mG* I–II filiform. Suckers ad_3 enlarged, exceed central suckers (ad_{1+2}). Conoids ps_2 at transverse level of central suckers. Tarsal setae *e* and *f* I–II strongly asymmetrical, *f* about 2 times shorter and filiform, *e* longer and lanceolate. Caruncle I–III with 2 distinct transparent lobes. Setae *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II spiniform. Associated with *Xylocopa*. (Subgenus *Spinosennertia*) 3

- Hysterosomal shield not triangle in outlines, distinctly expanded beyond lateral gland opening and bases of setae c_1 and f_2. Supracoxal setae *scx* situated on dorsal extension of posterior apodeme I. Posterior apodeme IV connected to anterior apodeme IV. Setae *mG* I–II bifid at tips. Suckers ad_3 not enlarged, smaller than central suckers (ad_{1+2}). Conoids ps_2 anterior to anterior transverse level of central suckers. Tarsal setae *e* and *f* I–II slightly asymmetrical. Caruncle I–III with 1 distinct, usually sclerotized lobe. Setae *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Associated with *Ceratina*. (*surinamensis*-group) 4

3(1) Setae h_3 shorter or nearly equal to legs IV. *1a*, *3a*, *4a* attenuated. Argentina (type locality), Brazil, Costa Rica, Guatemala, Mexico, Nicaragua, Peru, Suriname. Genital capsules of males and oviducts of females of *Xylocopa (Neoxylocopa)*: *X. frontalis* (type host), *X. fimbriata*, *X. mexicanorum*, *X. nasica*, and *X. nautlana* . . . . **Sennertia argentina** Vitzthum, 1941 (p. 156)

- Setae h_3 distinctly longer than legs IV. *1a*, *3a*, *4a* slightly rounded at tips. Trinidad and Tobago (type locality), Brazil, Venezuela. *Xylocopa frontalis* (type host), *X. fimbriata*. . . . . . **Sennertia donaldi** F. Turk, 1948 (p. 228)

4(2) Setae c_3 nearly spiniform, situated on soft cuticle; *4b* filiform. Transparent margin of anterior suckers (ad_3) without rough sclerotization 5

- Setae c_3 conoidal, situated on large triangle sclerite touching posterior apodemes II and anterior apodemes III; *4b* conoidal. Transparent margin of anterior suckers (ad_3) with rough sclerotization 7

5(4) 5–7 lines between setae *se* and *si*. Additional posterior sclerite of posterior apodeme IV absent. Gnathosomal solenidia distinctly shorter than half of setae *vi*. *Ceratina* sp. (type host), *Ceratina eximia*. Mexico (type locality), Costa Rica, Panama . . . . **Sennertia sodalis** sp. n. (p. 156)

- 10–14 lines between setae *se* and *si*. Additional posterior sclerite of posterior apodeme IV present. Gnathosomal solenidia exceeding half of setae *vi* 6

6(5) Setae c_3 about 1.3 wider than *si*. Setae d_2 usually reaching or slightly protruding transverse level of *im*. Posterior apodeme IV and its additional posterior sclerite not separated by transparent grove, latter porous. *Ceratina eximia*. Mexico: Quintana Roo (type locality), Belize . . . . **Sennertia recondita** sp. n. (p. 151)

- Setae c_3 and *si* nearly of same width. Setae d_2 not reaching transverse level of *im*. Posterior apodeme IV and its additional posterior sclerite separated by transparent grove, usually latter not porous. *Ceratina* (*Calloceratina*) *chloris*. Suriname (type locality), French Guiana, Panama. . . . . **Sennertia surinamensis** Fain & Lukoschus, 1971 (p. 237)

7(4) Maximal length of rough sclerotization on transparent margin of anterior suckers (ad_3) distinctly shorter than two diameters of anterior suckers. *Ceratina capitosa*. Mexico. . . . . **Sennertia haustrifera** sp. n. (p. 151)

- Maximal length of rough sclerotization on transparent margin of anterior suckers (ad_3) as long as two diameters of anterior suckers. *Ceratina* sp. Guatemala . . . . **Sennertia** sp.

8(1) Tarsal ventral setae *w* IV distinctly shorter than leg IV. Posterior apodeme IV absent. Setae *1a*, *3a*, *4b*, c_3, *4a*, *g*, and *wa* I–II simple (*Amsennertia* s. str.) 10

- Tarsal ventral setae *w* IV long, distinctly longer than leg IV. Posterior apodeme IV present. Setae *1a*, *3a*, *4b* conoidal; c_3, *4a*, and *g* inflated at bases. Setae *wa* I–II bifid. *Ceratina*. Neotropics. (*devincta*-group) 9

9(8) Striate pattern at posterior end of hysterosomal shield nearly uniformly parallel. Setae c_p not reaching *im* and setae e_2. Setae *sR* III not protruding femur III. Costa Rica. *Ceratina laticeps* . . . . **Sennertia sayutara** Klimov & OConnor, 2007 (p. 137)

- Striate pattern at posterior end of hysterosomal shield not uniform, with two distinct areas. Setae c_p protruding bases of e_2. Setae *sR* III protruding femur III. Peru. *Ceratina* sp . . . . **Sennertia devincta** Klimov & OConnor, 2007

10(8) Setae d_1, e_1, and h_1 nearly uniform in length, microsetae, d_1 and e_1 distinctly shorter than respective 1/2 of distance between them. (-) Setae c_1 situated on anterior margin of hysterosomal shield (*frontalis*-, *loricata*-groups) or anterior to it (*americana*-group). Opisthosomal gland openings on (*frontalis*-group) or outside hysterosomal shield (*loricata*-group, *americana*-group) 17

- Setae d_1 and e_1 distinctly longer than h_1, at least one of them longer than 1/2 of distance between bases. Setae c_1 anterior to hysterosomal shield. Opisthosomal gland openings outside hysterosomal shield 11

11(10) Setae *mG* II almost as long as leg II, distinctly longer than *vF* II. Tarsal setae *ra* I–II simple (*ignota*-group) 14

- Setae *mG* II distinctly shorter than leg II and setae *vF* II. Tarsal setae *ra* I–II bifid (*faini*-group). 12

12(11) Seta *wF* IV reaching base of tarsus IV. On *Xylocopa* (*Xylocopoides*) *californica*, *Xylocopa* (*Xylocopoides*) *cyanea*, *Xylocopa* (*Notoxylocopa*) *tabaniformis orpifex*. USA: California, Arizona; Mexico . . . . **Sennertia segnis** sp. n. (p. 170)

- Setae *wF* IV at most reaching middle of tibia IV 13

13(12) Ratio tarsus IV/anterior suckers 1.2–2.1 (1.6 ± 0.19, n = 72); ratio tarsus IV/*hT* II 0.7–1.3 (0.9 ± 0.11, n = 72). On *Xylocopa* (*Neoxylocopa*) *varipuncta* and other species of subgenera *Neoxylocopa*, *Xylocopoides*, and *Notoxylocopa*. USA: Arizona, California, Texas; Mexico. . . . . **Sennertia lucrosa** sp. n. (p. 164)

- Ratio tarsus IV/anterior suckers 2.1–2.6 (2.3 ± 0.18, n = 6); ratio tarsus IV/*hT* II 1.3–1.4 (1.4 ± 0.07, n = 6). *Apis mellifera*. Guatemala . . . . **Sennertia faini** Baker & Delfinado-Baker, 1983 (p. 170)

14(11) Setae h_3 less than 110, 82–95 (89 ± 4, n = 10). Posterior processes of anterior coxal apodemes IV not reaching level of anterior cuticular suckers rudiments. Mexico: Oaxaca. *Xylocopa* (*Notoxylocopa*) *tabaniformis tabaniformis*, *Xylocopa t. azteca* . . . . **Sennertia hurdi** sp. n. (p. 164)

- Setae h_3 exceeding 110. Posterior processes of anterior coxal apodemes IV almost reaching level of anterior cuticular suckers rudiments (in normally mounted specimens) 15

15(14) Setae *4a* reaching transverse level of pores *ih* (not studied). Argentina. *Xylocopa* (*Schonnherria*) *splendidula* . . . . **Sennertia longipilis** Alzuet & Abrahamovich, 1987 (p. 232)

- Setae *4a* not reaching transverse level of pores *ih* 16

16(15) Tarsal setae *w* about 2 times longer than *s* IV, 7–9. Lateral gland openings reduced, do not look like usual distinct transverse slit. Peru. *Xylocopa* (*Xylocopsis*) *funesta* . . . . **Sennertia** sp.

- Tarsal setae *w* and *s* IV subequal, very short (3–5). Lateral gland openings with usual distinct transverse slit. Peru. *Xylocopa* sp. . . . . **Sennertia ignota** Delfinado & Baker, 1976 (p. 211)

17(10) Setae c_1 situated on anterior margin of hysterosomal shield 19

- Setae c_1 anterior to hysterosomal shield (*americana*-group) 18

18(17) Setae *wF* distinctly protruding apex of tarsus IV. Setae d_1 usually longer than 1/4 of distance between them. *Xylocopa* (*Xylocopoides*) *virginica*. USA . . . . **Sennertia americana** Delfinado & Baker, 1976 (p. 230)

- Setae *wF* slightly protruding apex of tarsus IV. Setae d_1 shorter or equal 1/4 of distance between them. *Xylocopa* (*Schonnherria*) *splendidula* (type host). *Xylocopa* (*Neoxylocopa*) *mendozana*. Argentina . . . . **Sennertia splendidulae** Alzuet & Abrahamovich, 1989 (=*S. brevipilis* Alzuet and Abrahamovich, 1987, nom. preocc.) (p. 235)

19(17) Opisthosomal gland openings outside hysterosomal shield. Usual striate pattern of hysterosoma accompanied by sclerotization (*loricata*-group) 23

- Opisthosomal gland openings on hysterosomal shield. Striate pattern of hysterosoma without sclerotization (*frontalis*-group) 20

20(19) Setae *4b*, *g*, and *4a* without distinct subbasal dense layer. Setae *wa* I–II and *s* III filiform, not widened. Setae *ra* I–II blade-like. *Xylocopa* (*Stenoxylocopa*) *artifex*. Brazil, Argentina. . . . . **Sennertia** sp.

- At least some of *4b*, *g*, and *4a* with distinct subbasal dense layer. Setae *s* I–III distinctly widened or spiniform (-) Setae *ra* I–II blade-like or filiform 21

21(20) Setae *wa* I–II and *s* III filiform, slightly widened, *s* III with pointed tips. *Xylocopa* (*Neoxylocopa*) *darwini* (Ecuador: Galapagos Is.), *Xylocopa* (*Neoxylocopa*) *bruesi* (Peru) . . . . **Sennertia** sp.

- Setae *wa* I–II and *s* III spiniform or almost spiniform, at least *s* III with blunt tips 22

22(21) Ventral hysterosoma distinctly and densely striated. Setae *ra* I–II blade-like. *Xylocopa* (*Neoxylocopa*) *mordax* (USA: Puerto Rico, Virgin Islands of the United States, British Virgin Islands), *Xylocopa* (*Neoxylocopa*) *cubaecola* (Cuba), *Xylocopa* sp. (Bahamas) . . . . **Sennertia pirata** sp. n. (p. 176)

- Ventral hysterosoma smooth. Setae *ra* I–II filiform. Continental North and South America. . . . . **Sennertia frontalis, Sennertia shimanukii, Sennertia augustii** (see p. 94)

23(19) Sclerotization bands accompanying usual striate pattern wide, in area of d_1 wider than space between them. Setae c_1 shorter than distance between them. *Xylocopa* (*Schonnherria*) *muscaria*. Venezuela . . . . . **Sennertia** sp.

- Sclerotization bands accompanying usual striate pattern narrow, in area of d_1 narrower than space between them. Setae c_1 usually longer than distance between them. 24

24(23) *wF* IV not protruding or slightly protruding apex of tarsus IV. Setae c_1 almost reaching level of d_1. *Xylocopa* (*Schonnherria*) *viridis*. Guyana . . . . **Sennertia** sp.

- *wF* IV distinctly protruding apex of tarsus IV. Setae c_1 not reaching level of d_1. Mainly on *Xylocopa* (*Schonnherria*) *micans*, *Xylocopa* (*Schonnherria*) *barbatella barbatella*, *Xylocopa* (*Schonnherria*) *muscaria*. USA: Florida, Louisiana, Puerto Rico, Texas, Virginia; Mexico. . . . . **Sennertia loricata** sp. n. (p. 181)

Adults*

1 Idiosoma without mammillae. Supracoxal seta situated outside supracoxal sclerite; lateral to its outer ridge. Coxal fields III closed. Opisthosomal gland openings distinctly anterior to setae e_2. (Neotropics, phoretic as adults on *Xylocopa* and *Centris*, heteromorphic deutonymphs probably absent *vaga*-group, new). Proximal acetabular extensions of *ap′* III partially border antiaxial margins of coxal fields III. Proximal acetabular extensions of *ap′* IV partially border antiaxial margins of coxal fields IV. Tarsal setae *ra* and *la* II absent. Solenidion ω_2 I intermediate between subapical and submedial. Famulus (ε) lanceolate. Setae *ba* I as long as famulus (ε) or shorter. *Female*: Pseudanal seta ps_3 posterior to *4a* level. *Male*: Genital setae slightly (about on their diameter at base) anterior to progenital fold. Setae *p* II present. *Xylocopa* (*Notoxylocopa*) *tabaniformis orpifex*, *Xylocopa* (*Notoxylocopa*) *tabaniformis androleuca*, *Xylocopa* (*Xylocopoides*) *californica*. USA: Arizona, California; Mexico . . . . **Sennertia vaga** sp. n. (p. 132)

- Idiosoma with mammillae. Supracoxal seta situated on supracoxal sclerite; anterior to its outer ridge. Coxal fields III opened. Opisthosomal gland openings approximately at level of e_2 or distinctly posterior to e_2 (*S. splendidulae*). Proximal acetabular extensions of *ap′* III completely border antiaxial margins of coxal fields III. Proximal acetabular extensions of *ap′* IV completely border antiaxial margins of coxal fields IV. Tarsal setae *ra* and *la* II present. Solenidion ω_2 I subapical. Famulus (ε) spiniform or almost cylindrical (**). Setae *ba* I longer than famulus ε (**). *Female*: Pseudanal seta ps_3 anterior to *4a* level. External copulatory tube absent. *Male*: Genital setae situated on progenital folds. Setae *p* II absent (**). Worldwide. Usually in nests of *Xylocopa* and *Ceratina*, heteromorphic deutonymphs present . . 2

2(1) Prodorsal shield length/width 1.4. **(-)** Dorsal idiosomal cuticle striate, striae with small tubercles. Microtuberculate pattern absent. Dorsal idiosomal setae c_1-h_1 filiform and long, reaching at least half of distance to next posterior pair of setae. Dorsal idiosomal setae c_p, c_3, h_3 narrowing distally, not compressed dorso-ventrally, usually evenly barbed. Dorsal setae e_2 and f_2 filiform. Dorsal setae e_2 and f_2 nearly as long as h_3. Prodorsal shield without falsifoveate pattern. Coxal fields III opened. Distal acetabular extensions of ap′ III and ap″ III separate or not developed. Distal acetabular extensions of *ap′* IV and *ap″* IV separate. Opisthosomal gland openings approximately at level of e_2. *Female*: Setae ps_3 short, distinctly shorter than ps_2. Setae h_3 anterior to h_2. Posterio-medial part of dorsal opisthosoma without distinct longitudinal linear pattern. *Male*: Setae ad_1 absent. Genital setae and pseudanal setae ps_3 filiform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base or shorter. Leg and some other characters unknown. . . . . **Sennertia augustii** (p. 223)

- Prodorsal shield distinctly elongated, length/width 1.7–2.4 3

3(1) Dorsal idiosomal setae c_1-h_1 elongated, reaching at least half of distance to next posterior pair of setae. Dorsal idiosomal setae c_p, c_3, and h_3 long, filiform, narrowing and not compressed distally, more or less evenly barbed. *Male*: Pseudanal setae ps_3 on progenital sclerites. Setae *q* I absent. Pretarsal suckers IV distinctly smaller than those on tarsi I–III. **(-)** Alveoli of setae *ve* present. Dorsal idiosomal cuticle uniformly striate, striae with small tubercles. Dorsal setae e_2 and f_2 filiform. Dorsal setae e_2 and f_2 nearly as long as h_3. Prodorsal shield without falsifoveate pattern. Coxal fields III opened. Distal acetabular extensions of *ap′* III and *ap″* III separate or not developed. Distal acetabular extensions of *ap′* IV and *ap″* IV separate or not developed. Opisthosomal gland openings approximately at level of e_2. Famulus ε almost cylindrical. Setae *ba* II as long as famulus or shorter. *Female*: Setae ad_1 absent. Setae ad_2 absent. Setae ps_3 long, nearly as long as ps_2. Setae h_3 anterior to h_2. Posterio-medial part of dorsal opisthosoma without distinct longitudinal linear pattern. *Male*: Setae ad_1 absent. Genital setae and pseudanal setae ps_3 filiform. Dorsal supporting sclerites distinctly longer than 2 diameters of aedeagus at base. *Protonymph*. Tarsal setae *e* IV and *f* IV present . . . . **Sennertia scutata** (p. 234)

- Dorsal idiosomal setae c_1-h_1 short (not reaching half of distance to next posterior pair of setae). Dorsal idiosomal setae c_p, c_3, h_3 either short and spiniform or long and feather-like. *Male*: Pseudanal setae ps_3 outside progenital sclerites. Setae *q* I present. Pretarsal suckers IV similar to those on tarsi I–III 4

4(3) Setae e_2 and f_2 feather-like, flattened, with distinct apical rachis and barbs. Famulus ε almost cylindrical (**). Distal acetabular extensions of *ap′* III and *ap″* III separate (unknown for *S. leei* and *S. splendidulae*). Tarsal setae *ba* II present. Setae h_3 anterior to h_2 6

- Setae e_2 and f_2 spiniform, scarcely barbed, if flattened then not feather-like. Distal acetabular extensions of *ap′* III and *ap″* III fused. Famulus ε spiniform. Tarsal setae *ba* II absent. Setae h_3 at level of h_2. 5

5(4) Setae h_3 distinctly longer than e_2 and f_2. Dorsal idiosomal setae c_p, c_3, h_3 long (several times longer than c_1-e_1) and feather-like. Dorsal cuticle with tuberculate (mammillate). Prodorsal shield without large cuticular “windows”. *Female:* setae ad_1-ad_2 absent. Setae ps_3 short, distinctly shorter than ps_2. Posterio-medial part of dorsal opisthosoma with distinct longitudinal linear pattern. *Male*: Genital setae short, transparent mammillae. Pseudanal setae ps_3 spiniform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base. Aedeagus Fig. 10 *B,C* . . . . . . **Sennertia americana** (p. 173)

- Setae h_3 as long as e_2 and f_2. Dorsal idiosomal setae c_p, c_3, h_3 short (less than 1 time longer than c_1-e_1) and spiniform. Dorsal cuticle with two distinct patterns, tuberculate (mammillate) and scarce microtuberculate. Prodorsal shield with large cuticular “windows”. *Female:* setae ad_1-ad_2 present. Setae

ps_3 long, as long as ps_2. Posterio-medial part of dorsal opisthosoma without longitudinal linear pattern. *Male*: Genital and pseudanal setae ps_3 filiform. Dorsal supporting sclerites distinctly longer than 2 diameters of aedeagus at base. Aedeagus Fig. 10 *E* (-) Alveoli of setae *ve* absent. Coxal fields III opened. Distal acetabular extensions of *ap′* IV and *ap″* IV separate or not developed. Opisthosomal gland openings approximately at level of e_2. Setae *ba* II absent. *Male*: Setae ad_1 absent ...... **Sennertia koptorthosomae** (p. 212)

6(4) Opisthosomal gland openings distinctly posterior to e_2. *Female*: Setae ps_3 short, distinctly shorter than ps_2. **(-)** Dorsal idiosomal cuticle striate (striae may be with small tubercles). Dorsal cuticular pattern more or less uniform. Dorsal setae e_2 and f_2 distinctly shorter than h_3. Prodorsal shield without falsifoveate pattern. Coxal fields III opened. Distal acetabular extensions of *ap′* IV and *ap″* IV separate or not developed. *Female*: Posterio-medial part of dorsal opisthosoma without distinct longitudinal linear pattern. *Male*: Setae ad_1 absent. Genital setae filiform. Pseudanal setae ps_3 filiform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base or shorter. Leg and some other characters unknown.. **Sennertia splendidulae** (p. 219)

\- Opisthosomal gland openings approximately at level of e_2. *Female*: Setae ps_3 long, nearly as long as ps_2 (-) Alveoli of setae *ve* absent. Dorsal idiosomal cuticle tuberculate or mammillate. Dorsal cuticular pattern more or less uniform. Dorsal setae e_2 and f_2 nearly as long as h_3. Prodorsal shield without falsifoveate pattern. Coxal fields III opened. Setae *ba* II as long as famulus ε or shorter. *Female*: Posterio-medial part of dorsal opisthosoma without distinct longitudinal linear pattern. *Male*: Setae ad_1 present. Genital setae filiform. Pseudanal setae ps_3 filiform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base or shorter ...... **Sennertia leei**

Sennertia vaga sp. n.

Material. Holotype: f—**USA: California**, Los Angeles Co., Rustic Canyon, SM, on *Lotus* (Fabales: Fabaceae) (no 671), ex *Xylocopa tabaniformis orpifex* on mesosoma, 11 Apr 1955, R. S. Erdmann, LACM 208287, BMOC 04-1122-025; Paratypes: 1m, 6 TNs, 4PN's, 1L (same data as for holotype); 2f, 3m, 6TN, 5PN (on 11 slides)—Los Angeles Co., Claremont, ex *Xylocopa t. orpifex* on pronotum, no date, Baker, USNM, BMOC 05-0420-389; 6TNs, 8PNs—**Arizona**, Santa Cruz Co., Patagonia Mountains, ex *X. californica* on propodeum & posterior wing bases, 1 Jun 1917, Oslar, INHS Insect Collection 62340, BMOC 04-1222-003; 5 TNs—Santa Cruz Mts., Felton, 15–19 May 1907, J. C. Bradley, ex *X. tabaniformis orpifex*, CUIC HK 84-1217-002; 1m, 1f, 1TNs, 2PNs—**MEXICO**: **Baja California Sur**, 2 mi S La Paz, ex *X. tabaniformis androleuca* on dorsal mesosoma, 6 Aug 1966, J. A. Chemsak, P. D. Hurd & E. G. Linsley, USNM, BMOC 05-0420-387; 2m, 1f, 2TNs, 8PNs—**Sinaloa**, 15 mi N Los Mochis, ex *X. t. androleuca* on dorsal mesosoma, 28 Jul 1966, J. A. Chemsak, E. G. & J. M. Linsley, USNM, BMOC 05-0420-386. Holotype in LACM, paratypes in CUIC, INHS, LACM, UMMZ, UNAM, USNM.

Description. *Phoretic and immobile deutonymph* unknown, probably absent (see notes).

Adults (Fig. 36, Fig. 37, Fig. 38, Fig. 39). Supracoxal seta *scx* situated outside supracoxal sclerite, lateral to outer ridge of supracoxal sclerite. Alveoli of setae *ve* present. Dorsal idiosomal cuticle uniformly striate (striae may be with small tubercles). Dorsal cuticular pattern more or less uniform. Dorsal idiosomal setae c_1-h_1 filiform and long, reaching at least half of distance to next posterior pair of setae). Dorsal idiosomal setae c_p, c_3, h_3 narrowing distally, not compressed dorsoventrally, usually evenly barbed. Dorsal setae e_2 and f_2 filiform, nearly as long as h_3. Prodorsal shield subquadrate, length/width 0.8–1.4. Prodorsal shield without falsifoveate pattern. Coxal fields III closed. Proximal acetabular extensions of *ap′* I partially border antiaxial margins of coxal fields I. Proximal acetabular extensions of *ap′* II partially border antiaxial margins of coxal fields II. Distal acetabular extensions of *ap′* II and *ap″* II separate. Proximal acetabular extensions of *ap′* III partially border antiaxial margins of coxal fields III. Distal acetabular extensions of *ap′* III and *ap″* III separate or not developed. Proximal acetabular extensions of *ap′* IV partially border antiaxial margins of coxal fields IV. Distal acetabular extensions of *ap′* IV and *ap″* IV separate or not developed. Opisthosomal gland openings distinctly anterior to setae e_2. Tarsal setae *ra* and *la* II absent. Solenidion ω_2 I intermediate between subapical and submedial. Famulus ε lanceolate. Setae *ba* I as long as famulus ε or shorter. Setae *ba* II as long as famulus ε or shorter.

Female. Setae ad_1 and ad_2 present. Setae ps_3 short, distinctly shorter than ps_2; posterior to *4a* level. External copulatory tube present. Setae h_3 anterior to h_2. Posterio-medial part of dorsal opisthosoma without distinct longitudinal linear pattern.

Male. Setae ad_1 present. Genital setae spiniform; slightly (about on their diameter at base) anterior to progenital fold. Pseudanal setae ps_3 outside progenital sclerites, filiform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base or shorter. Setae *q* I and *p* II present. Pretarsal suckers IV same as pretarsal suckers I–III.

Tritonymphs (Fig. 34, Fig. 35).

Protonymph (Fig. 32, Fig. 33). Tarsal setae *e* IV absent; *f* IV present.

Larva (Fig. 31, Fig. 32). Proportional length of dorsal idiosomal setae as in other instars.

Hosts. *Xylocopa* (*Notoxylocopa*) *tabaniformis orpifex*, *Xylocopa* (*Notoxylocopa*) *tabaniformis androleuca*, *Xylocopa* (*Xylocopoides*) *californica*.

Distribution. USA: Arizona, California; Mexico: Baja California Sur, Sinaloa.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20vaga&-max=200&-find

Etymology. Vagus is a Latin adjective (roving, wandering, doubtful).

Notes. This species probably does not form phoretic deutonymphs. In the southern Nearctic, it is associated with hosts that also harbor *S. lucrosa* and *S. shimanukii* and sometimes may be found with the former on the same bee specimen. A single pharate tritonymph of *S. lucrosa* (BMOC 05-0420-076) is substantially distinct from tritonymphs of *S. vaga* in having *la* and *ra* II developed and coxal fields III opened. Feeding instars of *S. augustii* (deutonymphs virtually undistinguishable

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*Because many adult *Sennertia* are poorly described, we give a descriptive key to species of the World with supplemental characters separated by the "(-)". Descriptions of North American taxa are given below and omitted here. The following inadequately described species are not included: *S. bifilis* (Canestrini, 1897), *S. caffra* Vitzthum, 1919, *S. cantabrica* Zachvatkin, 1941, *S. cerambycina* (Scopoli, 1763), *S. flabellifera* Oudemans, 1924, *S. greeni* (Oudemans, 1917), *S. morstatti* (Vitzthum, 1914), *S. perturbans* Vitzthum, 1919, *S. roepkei* Oudemans, 1924.

**unknown for *S. augustii* and *S. splendidulae* from *S. shimanukii*) also have opened coxal fields III. The same situation was also detected for some Neotropic *Centris* that have phoretic feeding instars of a similar species and heteromorphic deutonymphs of *Centriacarus turbator*.

Sennertia haustrifera sp. n.

Material (**MEXICO**). Holotype: HDN—**Jalisco**, Estación de Biología Chamela, UNAM, 19°32′N 105°05′W, 8 Sep 1983, S.H. Bullock, ex *Ceratina capitosa*, LACM BMOC 97-0331-035. Paratypes: 9 HDNs—same data as holotype; 6 HDNs—same data, 18 Apr 1980, BMOC 97-0331-036; 5 HDNs—same data, BMOC 97-0331-039; 6 HDNs—same data, 31 May 1983, BMOC 97-0331-037; 10 HDNs—same data, 31 Aug 1982, BMOC 97-0331-034; 2 HDNs—**Chiapas**, 20 km N Acala on road along Rio Grijalva, 548 m., 30 Jul 1981, D. E. & P. M. Breedlove, ex *Ceratina* sp. (propodeum), CAS BMOC 03-0604-019. Holotype in LACM, paratypes in CAS, LACM, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 72, Fig. 73; Table 25, p. 209). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on dorsal extension of posterior apodeme I. Hysterosomal shield distinctly expanded beyond lateral gland opening and bases of setae f_2. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield formed by long striae, with sclerotization, sclerotization shifted to posterior striae. Distinct rudiments of *vi* absent. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 and d_1-h_1 uniform in length, microsetae. Setae c_1 microsetae; situated posterior to anterior margin of hysterosomal shield. Setae c_3 conoidal, situated on large triangle sclerite touching posterior apodemes II and anterior apodemes III. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated on hysterosomal shield. Setae *4b* conoidal. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening (*4b* pear-shaped, *4a* and *g* filiform). Setae *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV present, connected to anterior apodeme III. Conoids ps_2 anterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) with rough sclerotization, maximal length of rough sclerotization distinctly shorter than two diameters of anterior suckers. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers absent. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II bifid at tips, *mG* II shorter than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, filiform. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II foliate. Tarsal setae *d* and *f* I–II almost symmetrical, *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated shifted from tarsal base, distance distinctly exceeding diameter of *d* III alveolus. Leg IV not protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV not protruding tibia IV.

Other instars unknown.

Hosts. *Ceratina capitosa* (Apidae).

Distribution. Mexico: Jalisco (type locality), Chiapas.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20haustrifera&-max=200&-find

Etymology. The specific epithet is formed from the Latin noun haustrum (=pump) and the verb fero (=to carry, bear), considered as an adjective.

Sennertia recondita sp. n.

Material. Holotype: HDN—**MEXICO**: **Quintana Roo**, Vallarta, 17 km. W Pto. Morelos, 20°30’N 87°00’W, 6 Oct 1986, T. Griswold, ex *Ceratina eximia* (propodeum), USNM, BMOC 96-0510-231. Paratypes: 10 HDNs—same data as holotype; 5 HDNs—same data, BMOC 96-0510-230; 7 HDNs—**BELIZE**: **Cayo**, 7 mi N of Blancaneaux Lodge, ex *C. eximia* (orig: *C. aurata*) (propodeum), 11 Jul 1973, Y. Sedman, AMNH BMOC 04-0508-276. Holotype in USNM, paratypes in AMNH, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 74, Fig. 75; Table 25, p. 181). Gnathosomal solenidia shorter than 1/3 of femur I width, gnathosomal solenidia exceeding half of setae *vi*. Supracoxal setae *scx* situated on dorsal extension of posterior apodeme I. Hysterosomal shield distinctly expanded beyond lateral gland opening and bases of setae f_2. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield formed by long striae, with sclerotization, sclerotization shifted to posterior striae. 10–14 lines between setae *se* and *si*. Distinct rudiments of *vi* absent. Setae *si* distinctly posterior *se*; exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 and d_1-h_1 uniform in length, microsetae. Setae c_1 microsetae; situated posterior to anterior margin of hysterosomal shield. Setae c_3 nearly spiniform, situated on soft cuticle. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated on hysterosomal shield. Setae *4b* filiform. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme

Fig. 72. *Sennertia haustrifera*, heteromorphic deutonymph (BMOC 97-0331-035, holotype). A, B - ventral and dorsal view.

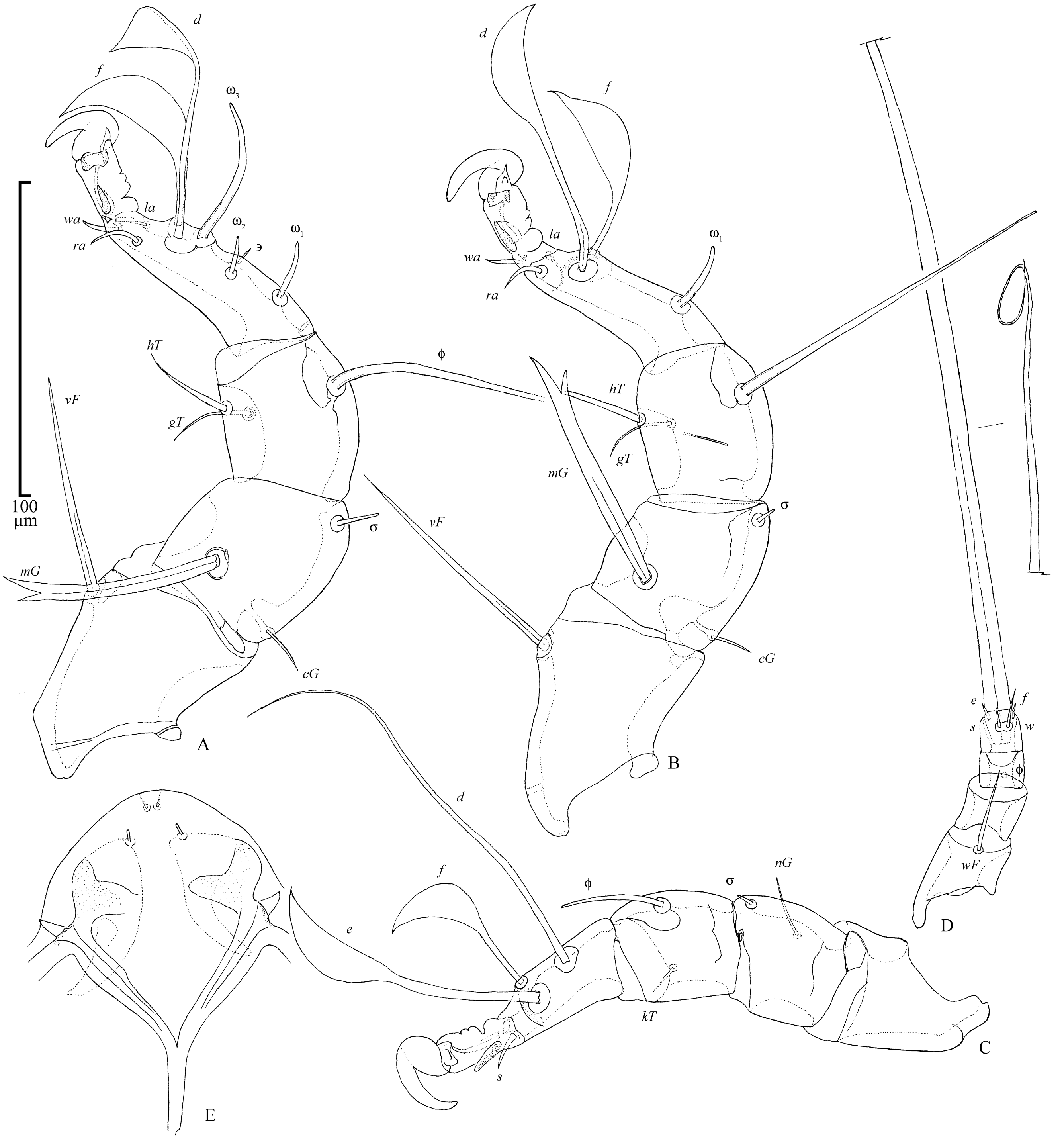

Fig. 73. *Sennertia haustrifera*, heteromorphic deutonymph (BMOC 97-0331-034, holotype). A–D - legs IV, E - rostral projection and anterior apodemes I, ventral view.

IV present, connected to anterior apodeme III. Additional posterior sclerite of posterior apodeme IV present. Conoids ps_2 anterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II bifid at tips, *mG* II shorter than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, filiform. Tarsal

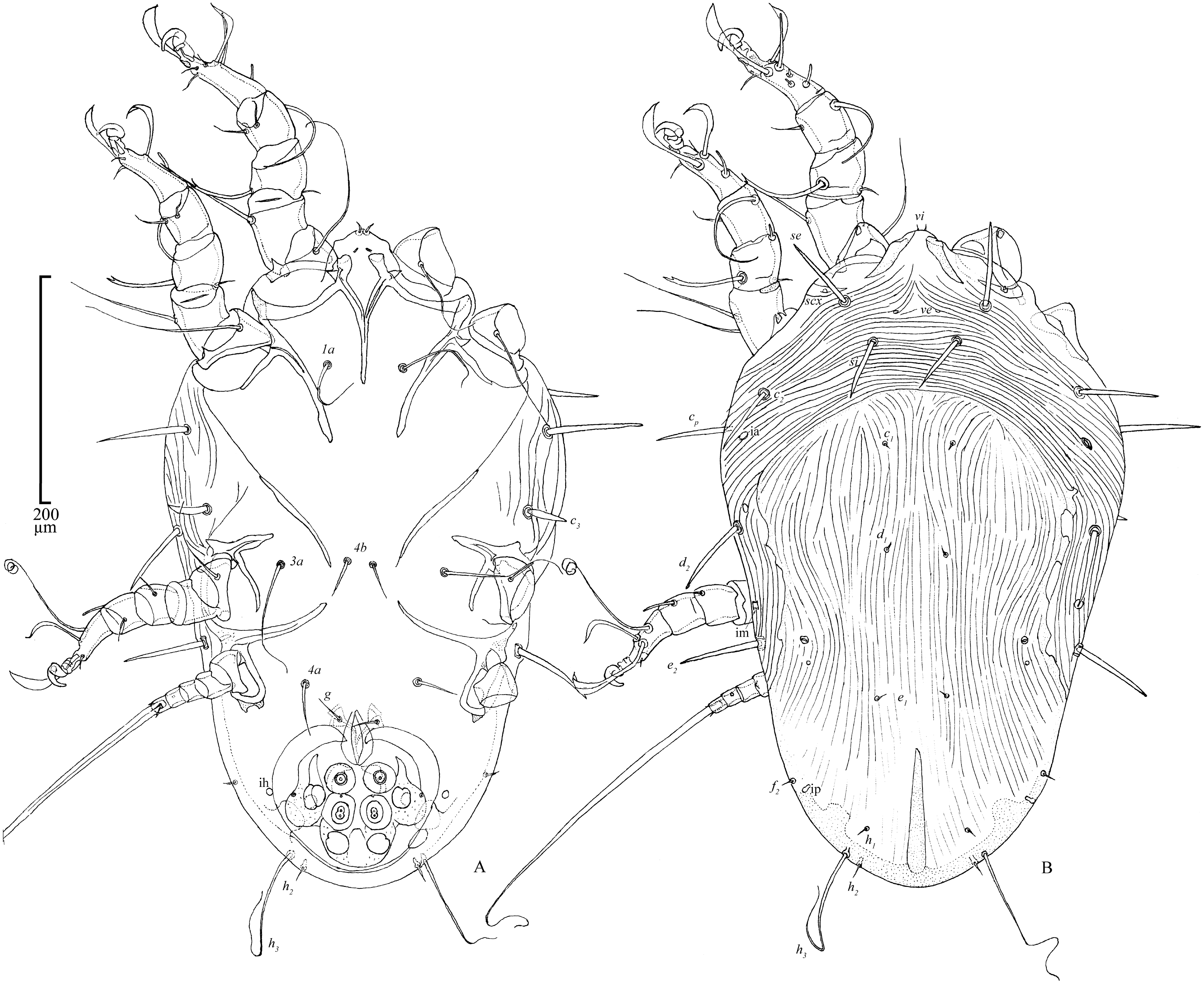

Fig. 74. *Sennertia recondita*, heteromorphic deutonymph (BMOC 96-0510-231, holotype). A, B - ventral and dorsal view.

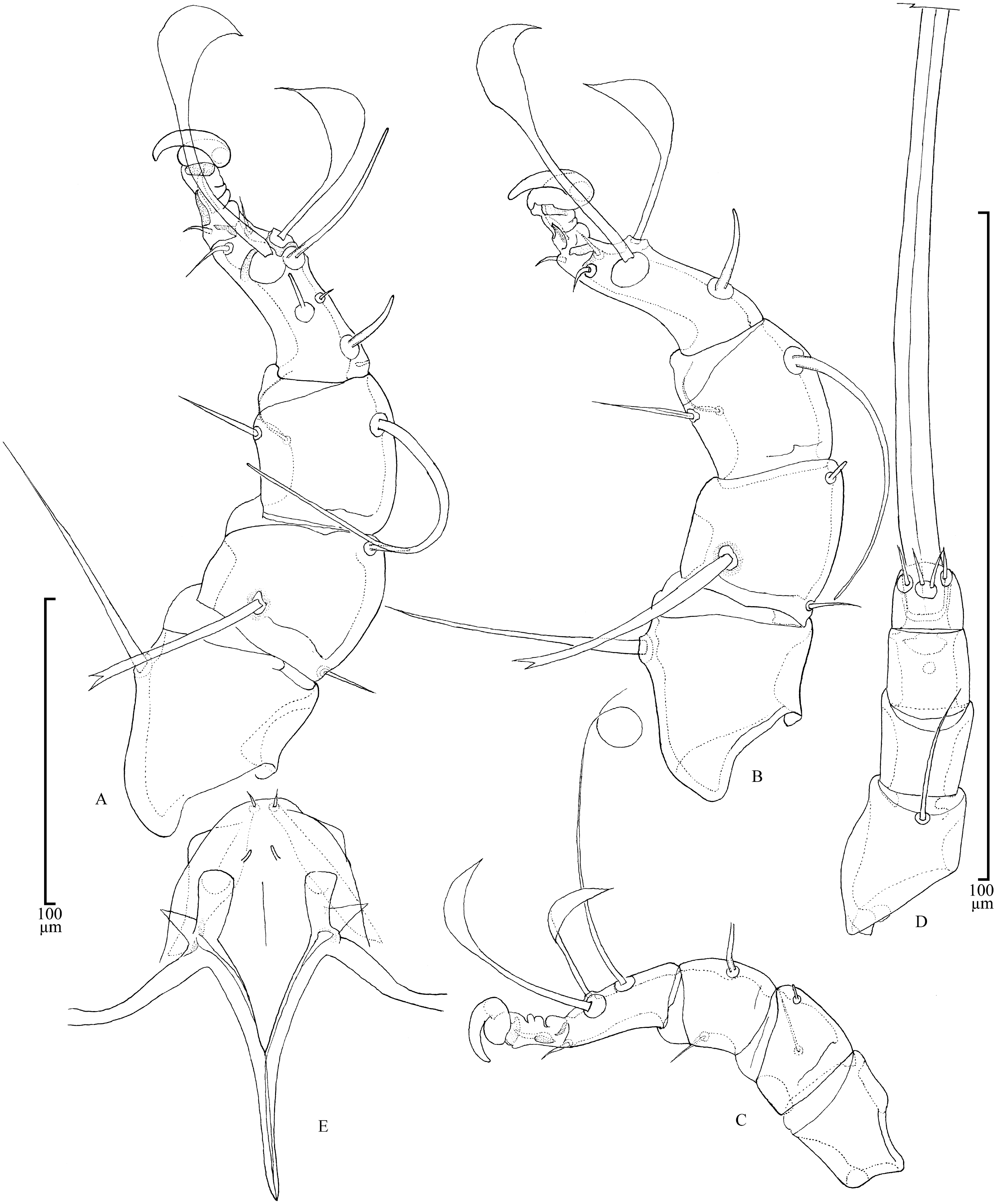

Fig. 75. *Sennertia recondita*, heteromorphic deutonymph (BMOC 04-0508-276). A–D - legs IV, E - rostral projection and anterior apodemes I, ventral view. Scale bars: left: A–C, E; right: D.

setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II foliate. Tarsal setae *d* and *f* I–II almost symmetrical, *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated shifted from tarsal base, distance distinctly exceeding diameter of *d* III alveolus. Leg IV not protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV not protruding tibia IV.

Other instars unknown.

Hosts. *Ceratina* (*Calloceratina*) *eximia*.

Distribution. Mexico: Quintana Roo (type locality), Belize: Cayo.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20recondita&-max=200&-find

Etymology. Recondita (put away, concealed) is a Latin adjective in the feminine gender.

Notes. Similar to *S. surinamensis* and *S. sodalis*, sp. n. See key above for the diagnostic characters.

Sennertia sodalis sp. n.

Material. Holotype: HDN—**MEXICO**: **Veracruz**, San Juan de la Punta, ex *Ceratina* sp. (propodeum), 18 Jul 1941, H. S. Dybas, BMOC 03-1008-055, FMNH. Paratypes: 3 HDNs—same data as holotype; 4 HDNs—**Oaxaca**, 5 mi E Temascal, on *Acacia cornigera* (Fabales: Fabaceae), ex *Ceratina* sp. (propodeum), 6 Sep 1964, D. H. Janzen, CAS BMOC 03-0604-020; 7 HDNs—**San Luis Potosí**, Tamazunchale, on *Cucurbita ?mixta* (Violales: Cucurbitaceae), ex *Ceratina* sp. (propodeum), 26 Jul 1964, H. V. Daly, CAS BMOC 03-0604-021; 4 HDNs—**Yucatán**, Ruinas Chichén-Itzá, ex *Ceratina* sp. propodeum, no date, E. Thompson, FMNH BMOC 03-1008-053; 9 HDNs—same data, FMNH BMOC 03-1008-054; 2 HDNs—**COSTA RICA**: **Alajuela**, La Garita, ex *Ceratina* sp. (propodeum), 29 Jun 1971, A. Avila, CUIC BMOC 80-0722-001; 5 HDNs—**Guanacaste**, Finca Montezuma, 3 km SE Rio Naranjo, ex *Ceratina eximia* propodeum, 1 Apr 1992, F. Parker, USNM BMOC 96-0510-229; 5 HDNs—same data, 5 Apr 1992, USNM BMOC 96-0510-232; **PANAMA**: **Panamá**, Pueblo Nuevo, ex *Ceratina eximia* (propodeum+metasoma), 13 Mar 1945, C. D. Michener, BMOC 04-0508-280 AMNH. Holotype in FMNH, paratypes in AMNH, CAS, CUIC, FMNH, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 76, Fig. 77; Table 25, p. 209). Gnathosomal solenidia shorter than 1/3 of femur I width, distinctly shorter than half of setae *vi*. Supracoxal setae *scx* situated on dorsal extension of posterior apodeme I. Hysterosomal shield distinctly expanded beyond lateral gland opening and bases of setae f_2. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield formed by long striae, with sclerotization, sclerotization shifted to posterior striae. 5–7 lines between setae *se* and *si*. Distinct rudiments of *vi* absent. Setae *si* distinctly posterior *se*; exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 and d_1-h_1 uniform in length, microsetae. Setae c_1 microsetae; situated posterior to anterior margin of hysterosomal shield. Setae c_3 nearly spiniform, situated on soft cuticle. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated on hysterosomal shield. Setae *4b* filiform. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV present, connected to anterior apodeme III. Additional posterior sclerite of posterior apodeme IV absent. Conoids ps_2 anterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II bifid at tips, *mG* II shorter than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, filiform. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II foliate. Tarsal setae *d* and *f* I–II almost symmetrical, *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated shifted from tarsal base, distance distinctly exceeding diameter of *d* III alveolus. Leg IV not protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV not protruding genu IV.

Other instars unknown.

Hosts. *Ceratina* sp., *Ceratina* (*Calloceratina*) *eximia* (Apidae).

Distribution. Mexico: Oaxaca, San Luis Potosí, Veracruz (type locality), Yucatán; Costa Rica, Panama.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20sodalis&-max=200&-find

Etymology. Sodalis (=companious, friendly) is a Latin adjective.

Sennertia argentina Vitzthum, 1941

Sennertia argentina Vitzthum, 1941: 309, Fig. 2 (Lectotype HDN A20031417-18, 2 paralectotype HDNs labeled as *Sennertia argentina* in ZSMC A20031417, A20032894 (Jürgen *et al*., 2005)).

Sennertia (*Spinosennertia*) *argentina*: Fain, 1981a: 176, Figs 49, 51 (lectotype designation, synonymized with *Sennertia donaldi* F. Turk, 1948) (part.); Alzuet & Abrahamovich, 1987: 350 (part.); OConnor, 1993a: 362 (part.); ?Haitlinger, 1999: 59 (part., record from Guatemala, ex Passalidae); Klimov *et al*., 2007b: 129 (diagnosis, included in key).

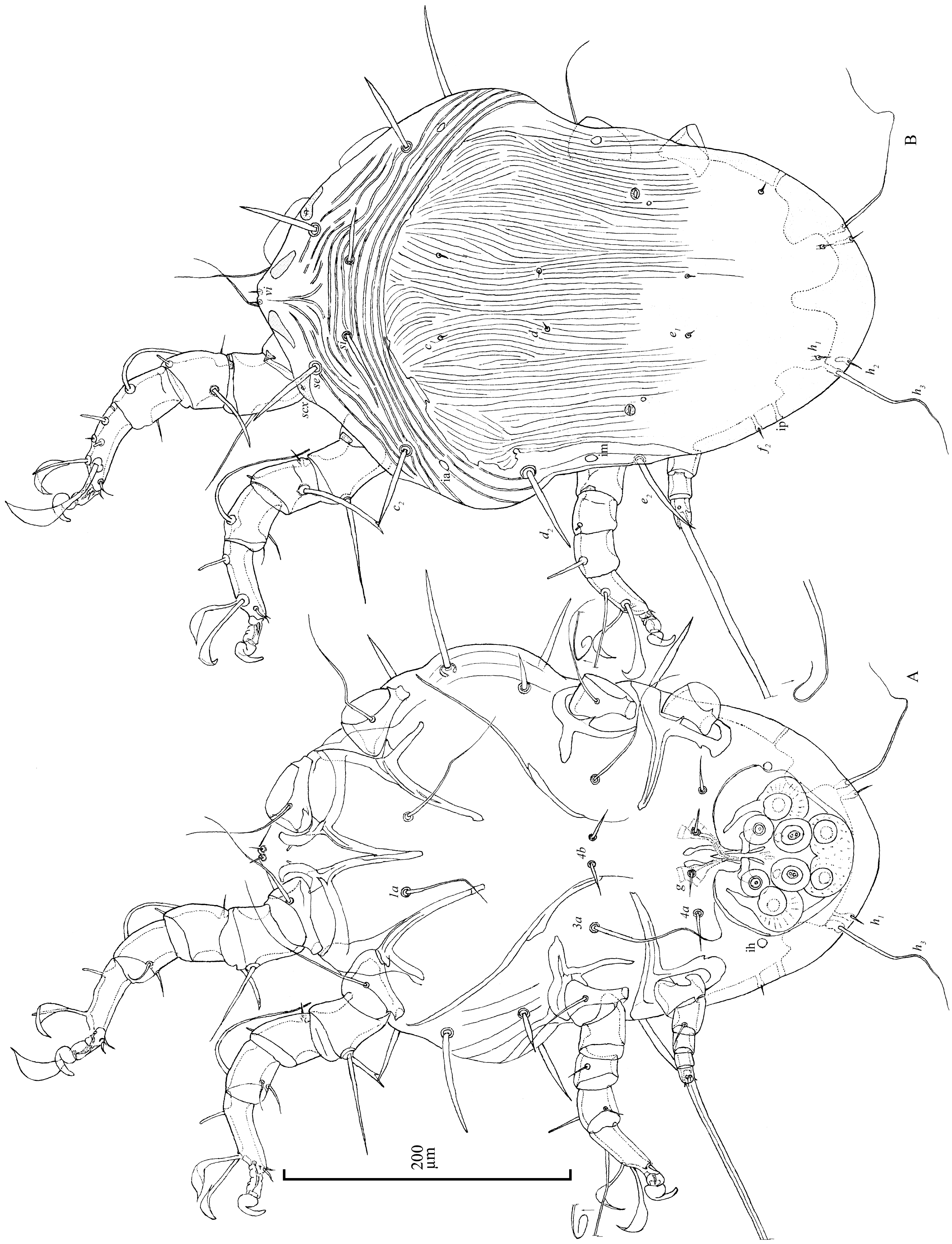

Fig. 76. *Sennertia sodalis*, heteromorphic deutonymph (BMOC 03-1008-055, holotype). A, B - ventral and dorsal view.

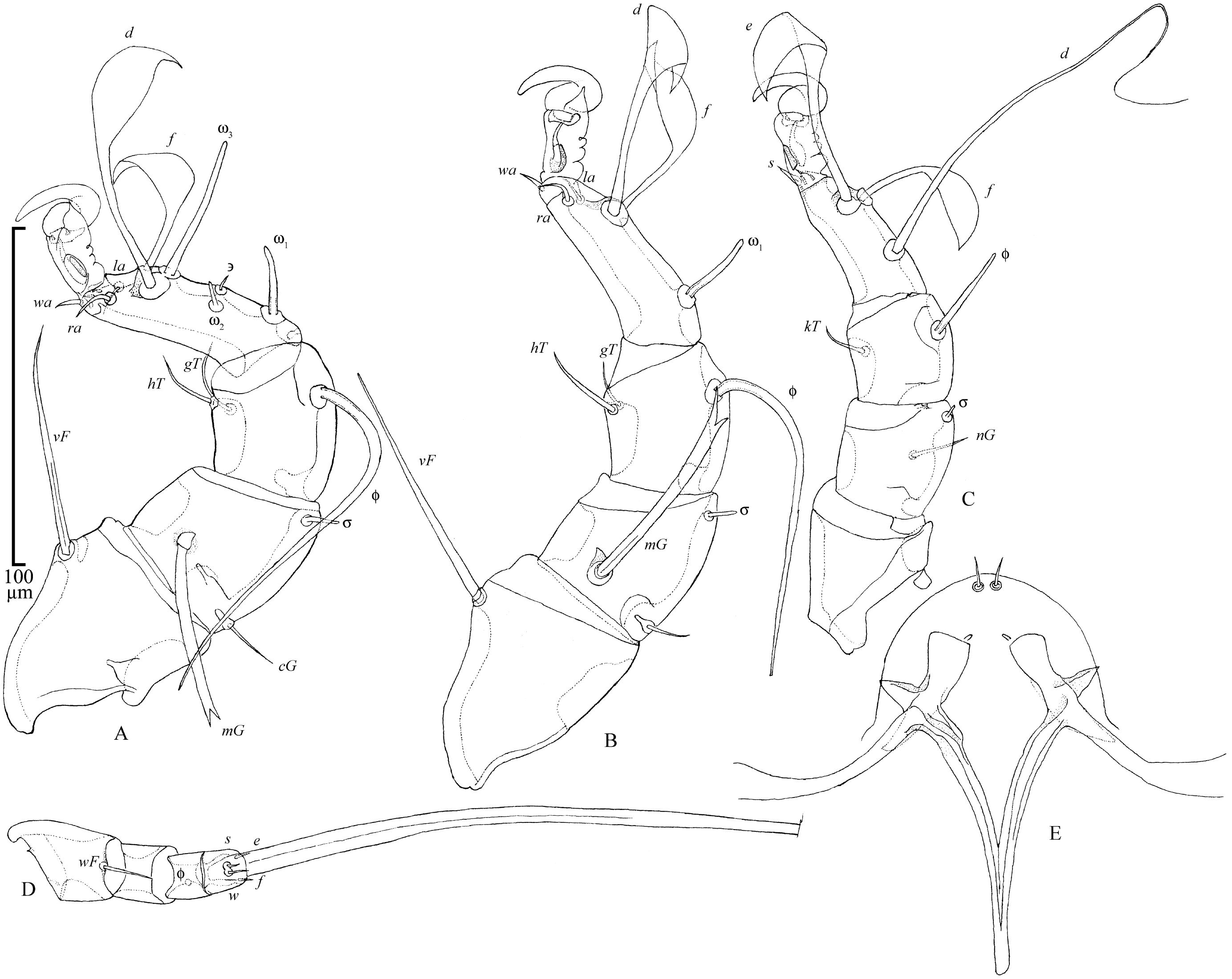

Fig. 77. *Sennertia sodalis*, heteromorphic deutonymph (BMOC 03-0604-021). A–D - legs IV, E - rostral projection and anterior apodemes I, ventral view.

Material. HDN—**Amazonas**, Tapuruquára (Santa Isabel do Rio Negro), ex *Xylocopa frontalis* on propodeum, 1 Jun 1963, L. Guindani, USNM, BMOC 05-0420-197; 1 HDN—**BRAZIL**: **Mato Grosso do Sul**, Aquidauana, 11 Dec 1919, Cornell University Expedition, ex *X. frontalis*, CUIC, BMOC 74-0812-001; 4 HDNs—R. Putamayo, Pto. America, 30 Aug-2 Sep 1920, Cornell University Expedition lot#569, ex *X. frontalis*, UMMZ, BMOC 04-0914-001; 6 HDNs—**Goiás**, 24 km E Formosa, 16 May 1956, F. S. Truxal, ex f *X. frontalis* (over body) LACM ENT 208600 BMOC 05-0102-036; 2 HDNs—same data, LACM ENT 208601, BMOC 05-0102-037; 5 HDNs—**COSTA RICA**: **Cartago**, Cartago, no date and collector, ex *X. fimbriata* (male) CUIC, HK 84-0827-004; 24 HDNs (6 slides)—Cartago, 2.5 km E 4 km N Chitaría, ex *X. frontalis* on propodeum, 13 Aug 1965, R. D. Sage, USNM, BMOC 05-0420-198; 6 HDNs—**Guanacaste**, Lomas Barbudal Biological Reserve, area B, ex *X. fimbriata* (female reproductive tract), Feb. 1988, 1989, S. B. Vinson, UMMZ, BMOC 80-1215-001; 2 HDNs—**GUATEMALA**: **Suchitepéquez**, Variedades, Finca, 500 ft., 27 Aug 1947, F. Johnson, ex *X. frontalis* (mesosoma), AMNH, BMOC 04-0508-318; 3 HDNs—**MEXICO**: **Sinaloa**, Escuinapa de Hidalgo, no date, J. H. Batty, ex *X. frontalis* (mesosoma), AMNH, BMOC 04-0508-316; 13 HDNs—**Chiapas**, Simojovel de Allende, 12 Aug 1958, J. A. Chemsak ex *X. nautlana* (male, ventral metasoma, including genital area), FMNH, BMOC 03-1008-056; 5HDNs—**Jalisco**, Chamela, ex *X. mexicanorum* genital area, 18 Jun 1981, S. Bullock, LACM ENT 208591, BMOC 05-0102-027; 16 HDNs—**NICARAGUA**: **Rivas**, San Juan del Sur, 10 Jan 1936, Zaca Exped 37483, ex *X. frontalis*, AMNH, BMOC 04-0508-317; 18HDNs—**PANAMA**: Albrook Field, Canal Zone, ex *X. frontalis* (orig: *frontalis viridimicans*), on 1st metasomal tergite, 20 Mar 1938, L. Stannard, Jr., INHS Insect Collection 62497, BMOC 04-1222-157; 2 HDNs—same locality, *X. frontalis*, on 1st metasomal tergite, 20 Mar 1938 L. J. Stannard INHS Insect Collection 62341, BMOC 04-1222-004; 18HDNs—Lake Alajuela, ex *X. nasica* all on 1st metasomal tergite, 29 May 1912, A. Busck, USNM, BMOC 05-0420-292; 4 HDNs—**PERU**: **Loreto**, Iquitos/San Roque, Jan 1929, Klug, ex *X. frontalis* (male) CUIC, HK 84-0820-004; 10 HDNs—Pucallpa, 200 m., ex m *X. frontalis* on 1st metasomal tergite, 1 Jan 1965, J. Schunke, LACM 208298, BMOC 04-1122-027; 6 HDNs—**SURINAME**: Marowijne Cottica R., Moengo, 12 May 1927, no collector *X. frontalis* (male) CUIC, HK 84-0820-001; 15 HDNs—**UNKNOWN [?COLOMBIA]**: El Reposo, ex *X. fimbriata* genital area, no date, Champion, INHS Insect Collection 62496, BMOC 04-1222-156.

Description. *Phoretic deutonymph* (Fig. 78, Fig. 79; Table 25, p. 209). Gnathosomal solenidia shorter than 1/3 of femur I

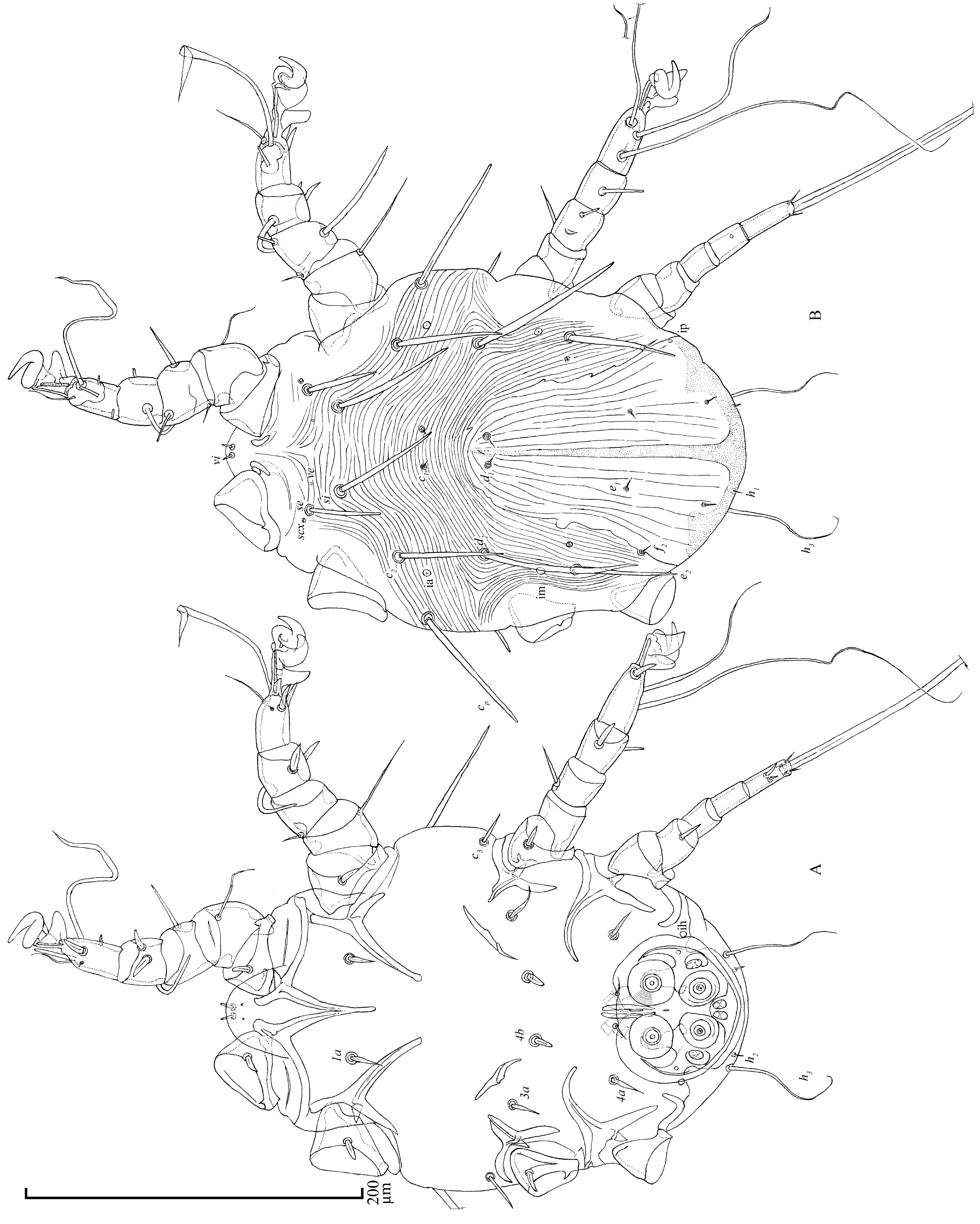

Fig. 78. *Sennertia argentina*, heteromorphic deutonymph (BMOC 04-0508-316). A, B - ventral and dorsal view.

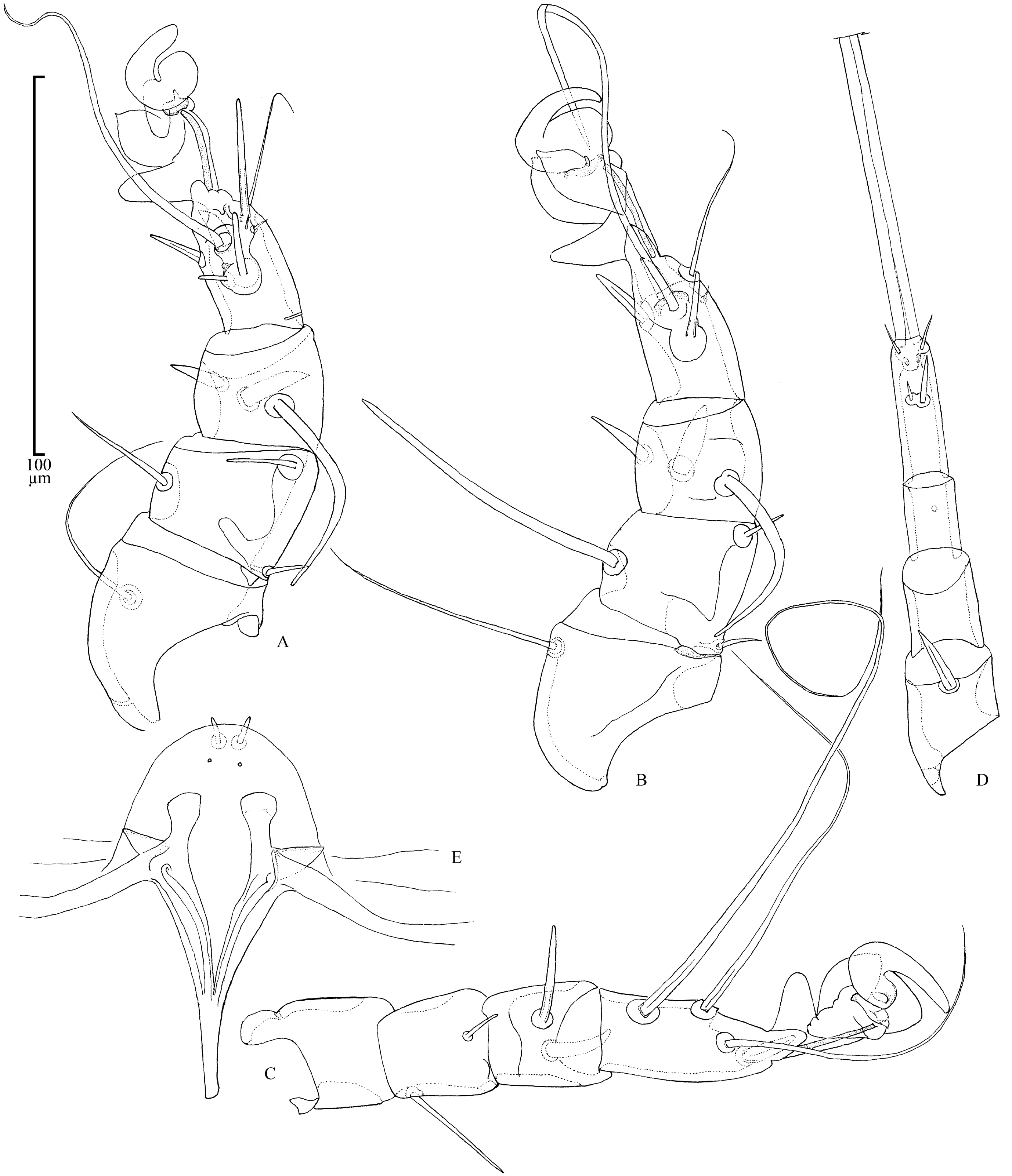

Fig. 79. *Sennertia argentina*, heteromorphic deutonymph (BMOC 04-0508-316). A–D - legs I–IV, respectively; E - rostral projection and anterior apodemes I, ventral view.

width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part distinctly narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 and d_1-h_1 uniform in length, microsetae. Setae c_1 microsetae, situated anterior to hysterosomal shield. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2; not touching hysterosomal shield. Setae h_3 shorter or nearly equal to legs IV. Lateral gland openings situated outside hysterosomal shield. Setae *1a*, *3a*, *4a* attenuated. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening but widened otherwise (spiniform or nearly spiniform). Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II spiniform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, arc-like. Posterior apodeme IV present, not connected to anterior apodeme III. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 enlarged. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, *mG* II distinctly shorter than leg II, but longer than femur II. Tarsal setae *la* I–II microsetae, as long as famulus ε. Tarsal setae *ra* I–II not bifid, spiniform. Tarsal setae *wa* I–II and *s* III spiniform (at least *s* III with rounded apices). Tarsal setae *d* I–II distinctly widened, lanceolate. Tarsal setae *d* and *f* I–II strongly asymmetrical, *f* about 2 times shorter and filiform, *e* longer and lanceolate; *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore absent. Anterior condylophore I–II without distal bending. Seta *d* III situated shifted from tarsal base, distance distinctly exceeding diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV shorter than femur IV.

Other instars unknown.

Hosts. *Xylocopa* (*Neoxylocopa*) *frontalis* (type host), *Xylocopa* (*Neoxylocopa*) *fimbriata*, *Xylocopa* (*Neoxylocopa*) *nautlana*, *Xylocopa* (*Neoxylocopa*) *nasica*, *Xylocopa* (*Neoxylocopa*) *mexicanorum* (Apidae).

Distribution. Argentina (type locality); Brazil; Costa Rica; Guatemala; Mexico: Jalisco, Sinaloa, Chiapas; Nicaragua; Peru; Panama; Suriname.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20argentina&-max=200&-find

Biology. Frequently found phoretic in and around genital capsules of host males, numerous deutonymphs were also found in a special pouch (genital acarinarium) of the female genital system (Klimov *et al.*, 2007b).

Sennertia sayutara
Klimov & OConnor, 2007

Sennertia sayutara Klimov & OConnor in Klimov *et al.*, 2007b: 122, Figs. 9, 10 (holotype in AMNH, paratypes in AMNH, UMMZ).

Material. Holotype: HDN—**COSTA RICA**: **San José**, San José, 28 Mar 1909, no collector, ex *Ceratina laticeps*, in metasomal acarinarium, AMNH 25499, BMOC 04-0508-284. Paratypes: 2 HDNs, same data; 2 HDNs—same data, AMNH 24499, BMOC 04-0508-283. Holotype in AMNH, paratypes in AMNH, UMMZ.

Description. *Phoretic deutonymph* (Fig. 80, Fig. 81). Gnathosomal solenidia distinctly shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield distinctly expanded beyond lateral gland opening and bases of setae f_2. Lateral edges of hysterosomal shield in anterior part not narrowing, rounded. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae *si* exceeding diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization; at posterior end of hysterosomal shield nearly uniformly parallel (Fig. 80*B*). Striae long. Distinct rudiments of *vi* present, situated at level of *se*. Setae *si* distinctly posterior *se*. Setae *si* exceeding slightly longer than *se*, as thick as *se*. Setae c_1 long, nearly as long as *se*, distinctly longer than d_1-h_1, situated on anterior edge of hysterosomal shield. Setae c_3 nearly spiniform, situated on weakly developed, small sclerite. Setae c_p not reaching *im* and setae e_2. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2. Setae e_2 not touching hysterosomal shield. Setae h_3 non-applicable. Setae h_3 non-applicable. Lateral gland openings situated on hysterosomal shield. Setae *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *kT* III filiform. Setae *1a*, *4b*, and *3a* conoidal; *g* and *4a* spiniform, with attenuated tips. Posterior apodemes II and anterior apodemes III partially fused. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV present, not connected to anterior apodeme III. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}). Conoids ps_2 anterior to ps_1, situated outside outer level of $ad_1 + ad_2$. Suckers ad_3 not enlarged, smaller than central suckers, without rough sclerotization. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present, very small. Posterio-medial longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, shorter than leg II, but longer than femur II. Tarsal setae *la* I–II microsetae. Tarsal setae *ra* I–II not bifid, spiniform. Tarsal setae *wa* I–II

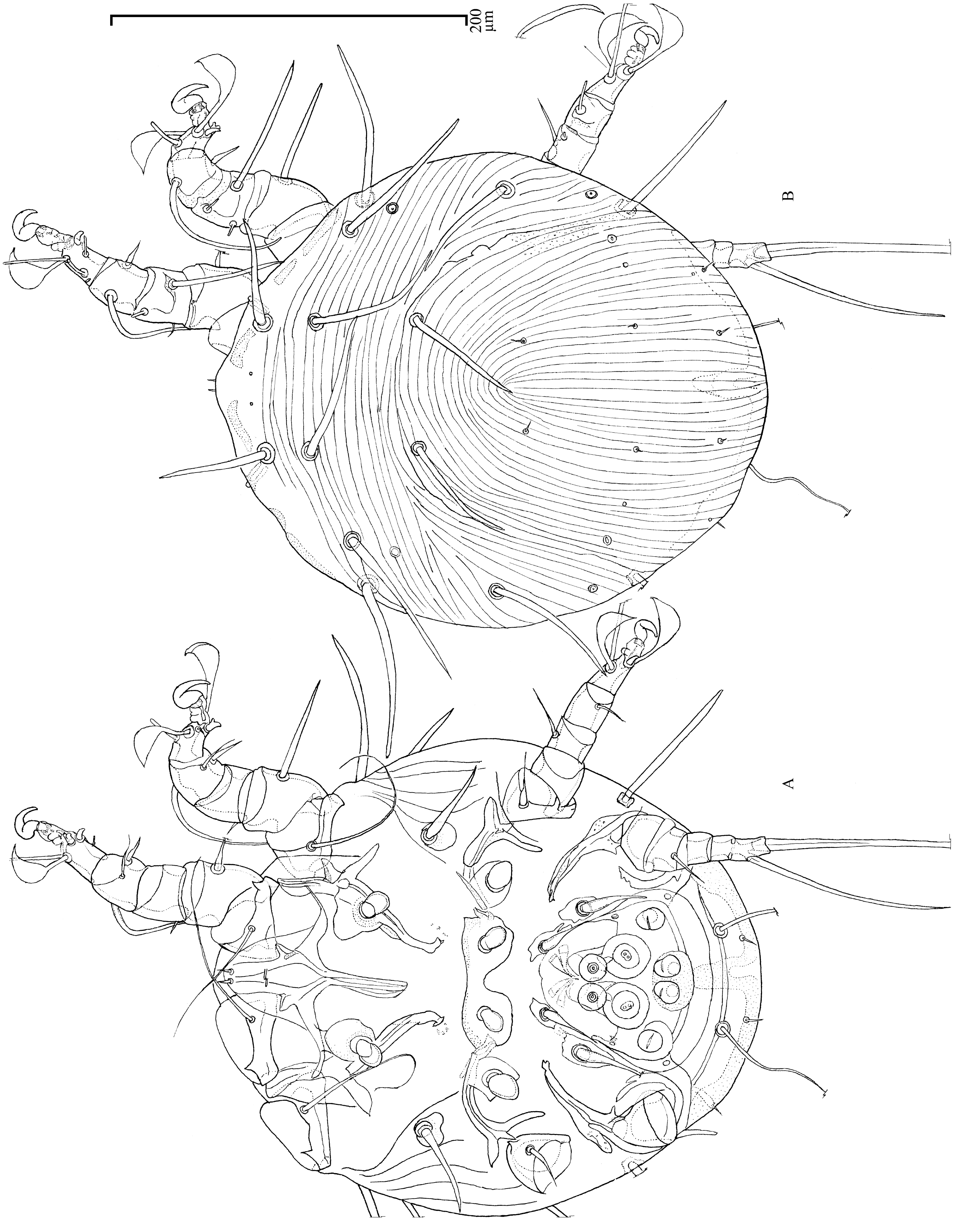

Fig. 80. *Sennertia sayutara*, heteromorphic deutonymph (BMOC 04-0508-284, holotype). A, B - ventral and dorsal view.

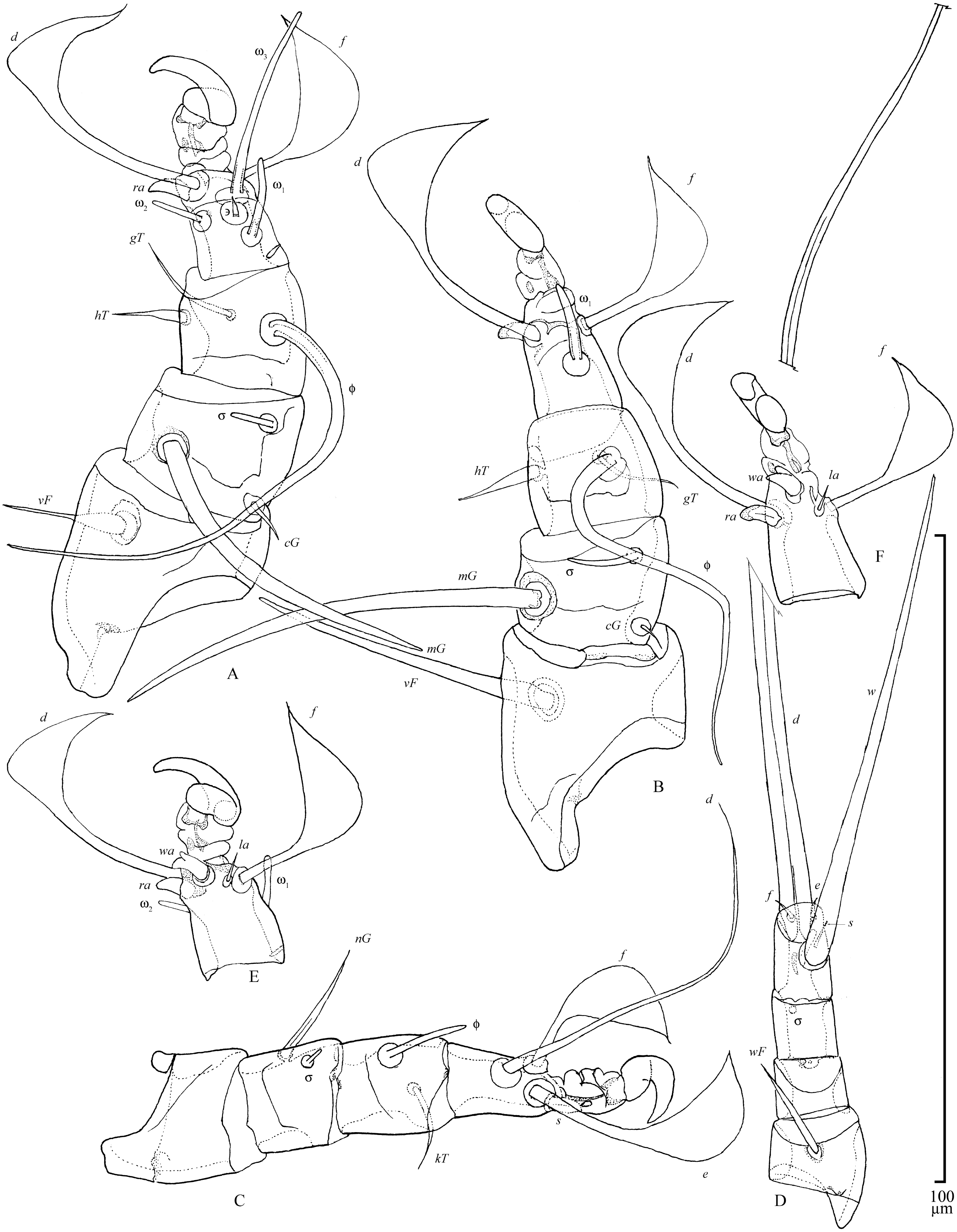

Fig. 81. *Sennertia sayutara*, heteromorphic deutonymph (BMOC 04-0508-283,-284). A–D - legs I–IV, respectively; E, F - tarsi I–II.

spiniform, bifid apically, *s* III spiniform, simple. Tarsal setae *d* I–II foliate, shorter than *f* I–II. Tarsal setae *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Setae *sR* III not protruding femur III. Seta *d* III situated shifted from tarsal base, distance distinctly exceeding diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter than width of trochanter IV. Setae *w* IV almost as 1/2 of *d* IV width, distinctly longer than leg IV. Setae *w* IV situated on middle of tarsus IV. Setae *s* IV present, very short. Setae *wF* IV not protruding tibia IV. *Other instars* unknown.

Variation. Sclerites surrounding alveoli of *4b* fused (BMOC 04-0508-284#1, 3, -283#1, 2) or separated (BMOC 04-0508-284#2). Sclerites surrounding alveoli of *1a* fused with proximal acetabular extension of apodeme I (BMOC 04-0508-284#1, 3, -283#1, 2) or free (BMOC 04-0508-284#2).

Hosts. *Ceratina laticeps*.

Distribution. Costa Rica: San Jose.

Etymology. The specific name is an arbitrary combination of letters, considered as a noun.

Biology. Found in the metasomal acarinarium of the host.

Sennertia hurdi sp. n.

Material. Holotype: HDN—**MEXICO**: **Oaxaca** Presa Benito Juárez, nr. Jalapa de Marquez, hwy 190, 6:10–6:16 am, 8 Sep 1968, D. H. Janzen *Passiflora*, ex *Xylocopa tabaniformis tabaniformis* (on propodeum), LACM 208290 BMOC 04-1122-021. Paratypes: 12 HDNs—same data as holotype; 18 HDNs—same data, LACM 208289 BMOC 04-1122-020; 37 HDNs—**Temascal**, 27 Sep 1963, D. H. Janzen, *Cucurbita pepo* (Violales: Cucurbitaceae), ex *X. t. azteca* (on 1st metasomal tergite), LACM 208285 BMOC 04-1122-023; 17 HDNs—2 mi N "La Tinaja", 6:30 am, 21 Oct 1963, No collector, ex *Xylocopa tabaniformis azteca* (on propodeum), LACM 208284 BMOC 04-1122-022. Holotype in LACM, paratypes in LACM, UMMZ, UNAM.

Description. *Phoretic deutonymph* (Fig. 82, Fig. 83; Table 26, p. 211). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 almost 2 times longer than d_1; distinctly longer than h_1; c_1 long, nearly as long as *se*; situated anterior to hysterosomal shield. Setae d_1 and e_1 distinctly longer than h_1; situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2; not touching hysterosomal shield. Setae h_3 shorter than 110. Lateral gland openings situated outside hysterosomal shield, with usual distinct transverse slit. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Setae *4a* not reaching transverse level of pores *ip*. Posterior apodemes II and anterior apodemes III free. Posterior processes of coxal apodemes IV not reaching level of anterior cuticular suckers rudiments. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, short. Ventral hysterosoma smooth. Genual setae *mG* I–II simple; *mG* II almost as long as leg II or longer. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, blade-like. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II slightly widened. Tarsal setae *d* and *f* I–II almost symmetrical; *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Seta *wF* IV almost reaching apex of tarsus or slightly protruding it.

Other instars unknown.

Hosts. *Xylocopa* (*Notoxylocopa*) *tabaniformis tabaniformis*; *Xylocopa tabaniformis azteca*.

Distribution. Mexico: Oaxaca.

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Notes. Closely related to *S. ignota*, *S. longipilis*, and an undescribed species from *X. funesta*. The differences between them are given in the key to species above.

Etymology. The new species in named after Paul D. Hurd, the renowned authority in systematics of *Xylocopa*.

Sennertia lucrosa sp. n.

?*Trichodactylus xylocopae* (non Donnadieu, 1868): Osborn, 1893: 1021 [California, ex *Xylocopa varipuncta* (as *Xylocopa aeneipennis*)].

?*Trichotarsus xylocopae* (non Donnadieu, 1868): Banks, 1902: 176.

?*Trichotarsus xylocopa* (non Donnadieu, 1868): Banks, 1902: 176 (lapsus; authorship attributed to Dufour; California, ex *Xylocopa*)

?*Trichotarsus* sp. Nininger, 1916: 164 (California, ex *Xylocopa varipuncta* and *Xylocopa tabaniformis orpifex*).

Material. Holotype: 1 HDN—**USA**: **California**, Los Angeles Co., Los Angeles, Crenshaw Dist, 14 Apr 1958, V. Reaves, ex male *Xylocopa varipuncta* (around wing bases), FMNH BMOC 03-0630-038. Paratypes: 11 HDNs—same data as holotype. 16 HDNs (one with pharate tritonymph)—same data, metanotum, 19 Mar 1917, H. Klotz, USNM, BMOC 05-0420-076; 19 HDNs—Ventura Co., Oxnard, San Dunes, *Brassica* sp (no 651), 16 Apr 1950, R. S.

Fig. 82. *Sennertia hurdi*, heteromorphic deutonymph (BMOC 04-1122-021, holotype). A, B - ventral and dorsal view.

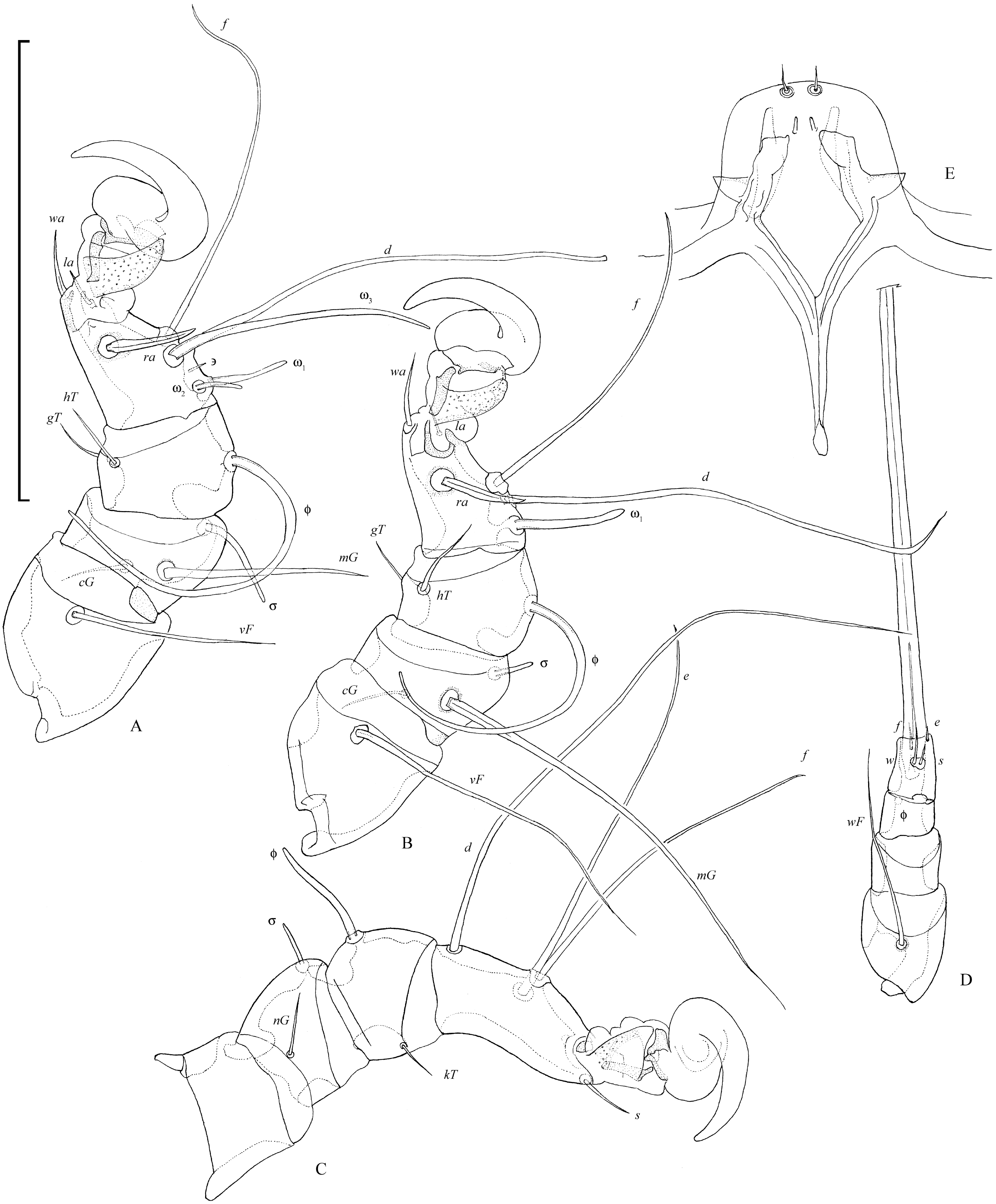

Fig. 83. *Sennertia hurdi*, heteromorphic deutonymph (BMOC 04-1122-020). A–D - legs I–IV, respectively; E - rostral projection and anterior apodemes I, ventral view.

Erdmann, ex *X. t. orpifex* (1st metasomal tergite), LACM 208288 BMOC 04-1122-019; 16 HDNs—San Diego Co., Escondido, 2 Jan 1934, M. A. Cazier, ex *X. t. orpifex* (posterior mesosoma), AMNH BMOC 04-0508-322; 21 HDNs—San Diego Co., San Diego, 30 Jun 1937, F.W. Furry, #10, *ex X. varipuncta* (mesosoma & propodeum), UMMZ BMOC 90-1212-021; 19 HDNs—Orange Co., Santa Ana, 21 Mar 1942, P.D. Hurd, ex *X. varipuncta* (propodeum), UMMZ BMOC 90-1212-022; 20 HDNs—Los Angeles Co., Los Angeles, Silver Lake Heights [label reads "Silver Lake Hill"], 24 Jul 1933, A.L. Olson, #5, ex *X. varipuncta* (mesosoma), UMMZ BMOC 90-1212-023; 18 HDNs—Los Angeles Co., Claremont, March 1916, Melville H. Hatch, ex *X. varipuncta* (1st metasomal tergite), UMMZ BMOC 04-0809-001; 47 HDNs—Los Angeles Co., Los Angeles, Crenshaw Dist, 1 May 1957, V. Reaves, ex *X. varipuncta* (1st metasomal tergite), FMNH BMOC 03-0630-036; 3 HDNs—San Bernardino Co., 1–7 Apr 1918, J. C. Bradley, ex female *X. varipuncta*, CUIC HK 84-1217-001; 13 HDNs—**Arizona**, Santa Cruz Co., Patagonia, 28 June 1953, A. & H. Dietrich, ex female *X. californica*, CUIC HK 85-0108-002; 1HDNs—Patagonia Mountains, ex *X. californica*, 1 Jun 1917, Oslar, INHS Insect Collection 62340, BMOC 04-1222-003; 10 HDNs—Santa Cruz Co., Santa Rita Mountains, Madera Canyon, elev. 1523 m, 31°43.37′N 110°52.80′W, 4 Sep 2003, P. Klimov, ex *X. californica arizonensis*, UMMZ BMOC 03-0904-004; 10 HDNs—**Texas**, Uvalde Co., Uvalde, 14 Jun 1932, J. O. Martin, ex *X. c. arizonensis* (posterior wing bases), CAS BMOC 03-0604-037; 13 HDNs—Jeff Davis Co., Davis Mountains, 6 Jul 1936, J. N. Knull, ex *X. c. californica* (orig: "*X. californica oregonensis*") (lateral propodeum), OSU OSUC 0121524 BMOC 03-1106-069; 17 HDNs—**MEXICO**: **Baja California**, 1 mi NE San Pedro, 8 Sep 1967, J. Chemsak, A. & M. Michelbacher, ex female *Xylocopa* (pronotum), AMNH BMOC 04-1112-006; 19 HDNs—**Baja California Sur**, Los Frailes, 18 Mar 1953, P. H. Arnaud, ex *X. californica diamesa* (propodeum), CAS BMOC 03-0604-040; 36 HDNs—**Chiapas**, Navenchauc, ex *Xylocopa guatemalensis*, on lateral propodeum, 2 Apr 1953, R. O. Bechtel & E. I. Sehlinger, USNM, BMOC 05-0420-219; 19 HDNs—**Colima**, Isla Clarión, ex *Xylocopa clarionensis*, on propodeum, 7–8 May 1955, McDonald & Blodget, LACM ENT 208588, BMOC 05-0102-024; 10 HDNs—same locality, 27 Apr 1925, H. H. Keifer, ex *X. clarionensis* (metanotum), CAS BMOC 03-0604-043; 9 HDNs—**Morelos**, Cuernavaca, 26 Mar 1959, H. E. Evans, ex *X. guatemalensis* CUIC HK 85-0107-001; 17 HDNs—**Puebla**, 5 mi SW Chapulco, 5800', ex *X. mexicanorum* on scutellum, 14 Jul 1970, E. Fisher & P. Sullivan, LACM ENT 208590, BMOC 05-0102-026; 13 HDNs—**Sonora**, San Francisco Hermosillo, ex *Hyptis emoryi* (Lamiaceae), ex *X. californica arizonensis*, over body, 14 Aug 1991, LaBerge, INHS Hymenoptera 8634, BMOC 04-1222-211; 2 HDNs—no locality ex *X. guatemalensis* on metanotum, no date, C. F. Baker, USNM, BMOC 05-0420-218; 9 HDNs—no locality, ex *X. guatemalensis*, on propodeum, no date, C. F. Baker, USNM, BMOC 05-0420-220; 2HDNs—no locality, ex *X. guatemalensis* on propodeum, no date, C. F. Baker, USNM, BMOC 05-0420-221; 2HDNs—no locality, ex *X. guatemalensis* on propodeum, no date, C. F. Baker, USNM, BMOC 05-0420-222; 27 HDNs—Volcán de Colima, ex *X. guatemalensis* posterio-lateral mesosoma, 2 Apr 1909, Joh. Laue, USNM, BMOC 05-0420-217. Holotype in FMNH, paratypes in AMNH, CAS, CUIC, FMNH, INHS, LACM, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 84, Fig. 85; Table 26, p. 211). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*; exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 subequal to or less than 1. 3 times longer than d_1; distinctly longer than h_1; long, nearly as long as *se*; situated anterior to hysterosomal shield. Setae d_1 and e_1 distinctly longer than h_1; d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2; not touching hysterosomal shield. Lateral gland openings situated outside hysterosomal shield. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers absent. Longitudinal hysterosomal sclerite present, short. Ventral hysterosoma smooth. Genual setae *mG* I–II simple. Genual setae *mG* II distinctly shorter than leg II, but longer than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II bifid, blade-like. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II slightly widened. Tarsal setae *d* and *f* I–II almost symmetrical, not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV distinctly not reaching base of tarsus IV. Ratio tarsus IV/anterior suckers 1.2–2.1 (1.6 ± 0.19, n = 72); ratio tarsus IV/*hT* II 0.7–1.3 (0.9 ± 0.11, n = 72).

Other instars unknown.

Hosts. *Xylocopa* (*Neoxylocopa*) *varipuncta* (type host), *Xylocopa* (*Neoxylocopa*) *clarionensis*, *Xylocopa* (*Neoxylocopa*) *mexicanorum*, *Xylocopa* (*Notoxylocopa*) *tabaniformis orpifex*, *Xylocopa* (*Notoxylocopa*) *guatemalensis*, *Xylocopa* (*Xylocopoides*) *californica arizonensis*, *Xylocopa* (*Xylocopoides*) *californica*, *Xylocopa* (*Xylocopoides*) *californica diamesa*.

Distribution. USA: Arizona, California (type locality), Texas; Mexico: Baja California, Baja California Sur, Colima, Chiapas, Morelos, Puebla, Sonora.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20lucrosa&-max=200&-find

Biology. This mite species may destroy a small percentage of *X. tabaniformis orpifex* and *X. varipuncta* larvae in their nests (Nininger, 1916). Such behavioral features of the bee hosts as use of common surface entrance for several intraspecific or interspecific nest tunnels (*X. t. orpifex* and *X. varipuncta*) and consuming provision from adjoining nests by newly emerg-

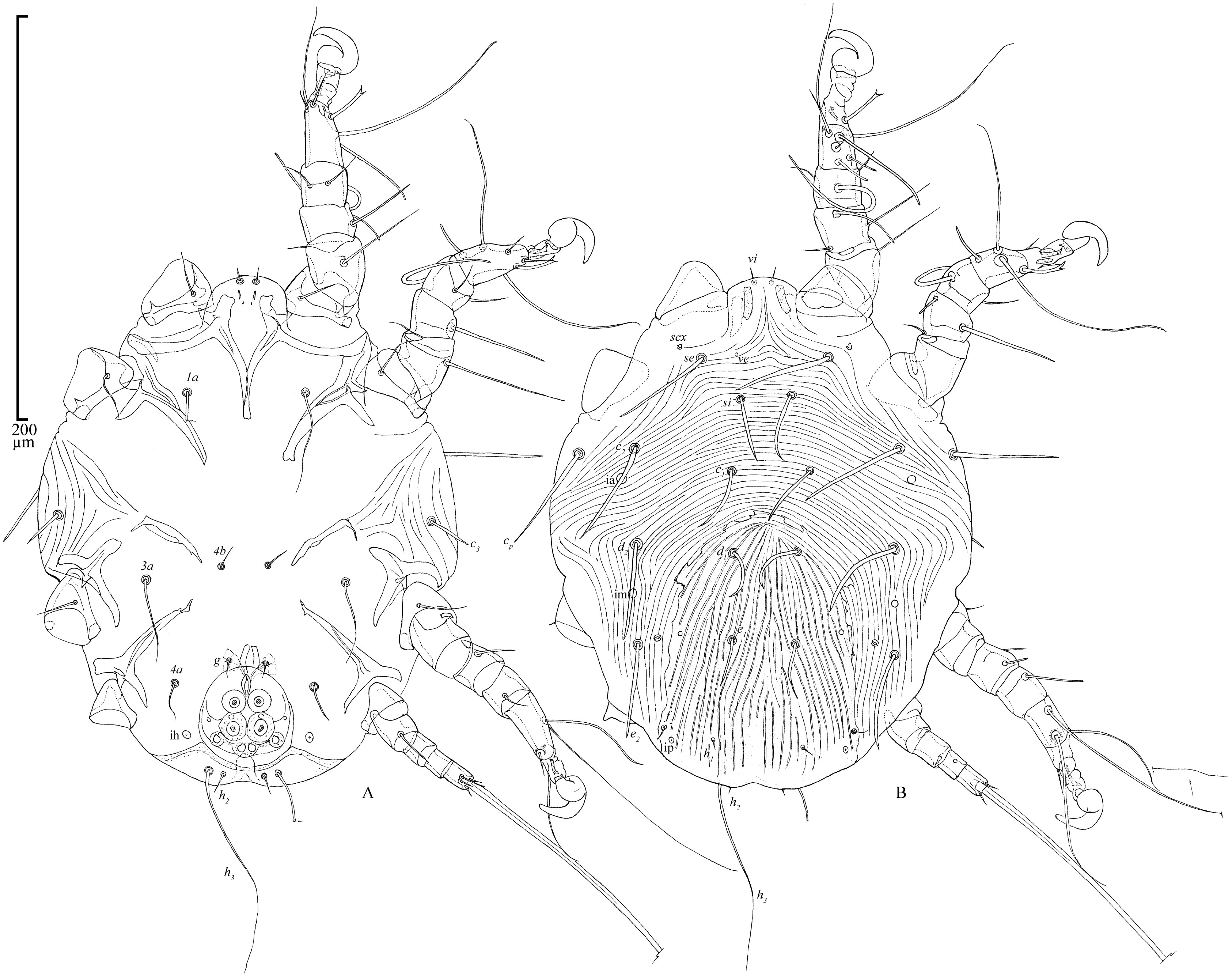

Fig. 84. *Sennertia lucrosa*, heteromorphic deutonymph (BMOC 03-0630-038). A, B - ventral and dorsal view.

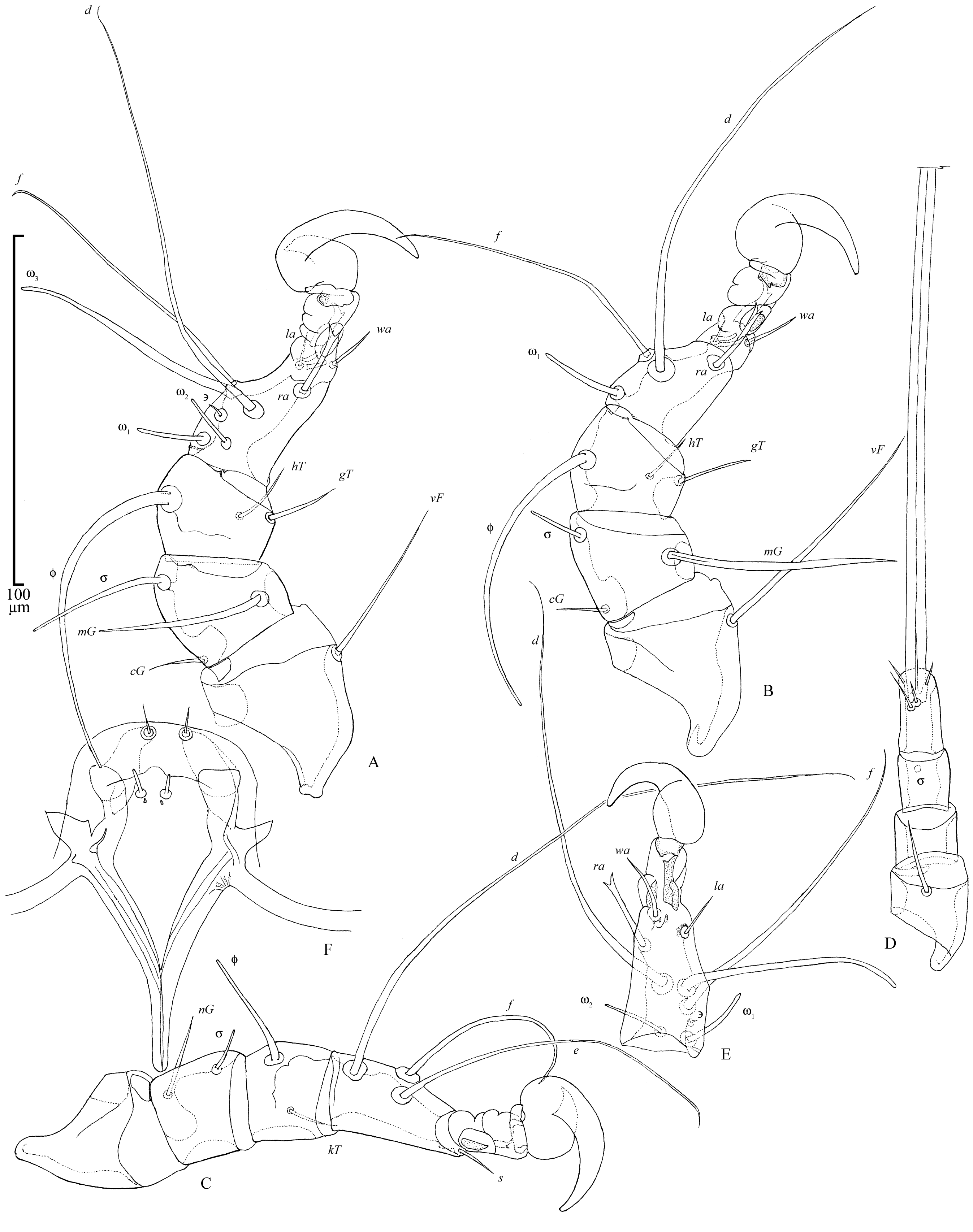

Fig. 85. *Sennertia lucrosa*, heteromorphic deutonymph (BMOC 03-0630-038). A–D - legs I–IV, respectively; E - tarsus II, ventral view; F - rostral projection and anterior apodemes I, ventral view.

ing bees (*X. t. orpifex*) (Cruden, 1966; Nininger, 1916) may facilitate mite dispersal.

Etymology. Lucrosus is a Latin adjective (=gainful, profitable).

Notes. Similar to *Sennertia faini* Baker & Delfinado-Baker, 1983 (see key to species above for differences). See also notes below.

We constructed CVA models for *S. lucrosa* (n = 72, all known localities and hosts) and *Sennertia faini* (n = 6, type series). The models including 2–10 log-transformed Darroch and Mosimann shape variables separate the two with 100% accuracy in both analysis and jackknife cross-validation. Ratios created by using raw variables with the highest and the lowest correlation with the canonical function allow for almost complete bivariate discrimination (see key to species above). *Sennertia faini* is only known from the type series collected from the honey bee from Guatemala. We do not have any mites similar to either *S. lucrosa* or *S. faini* s. str. from Central America, so the relationships between the two morphospecies and possible host effect in *S. faini* cannot be determined. However, the distribution of *Xylocopa guatemalensis* and the occurrence of *S. lucrosa* on this host in central Mexico might indicate that the differences of *S. faini* and *S. lucrosa* are influenced by host effect of the former, and therefore both belong to the same species.

Correlation of heteromorphic deutonymphs and feeding instars is based on the sharing of the same host species and relative abundance of *S. lucrosa* deutonymphs.

Sennertia faini

Baker & Delfinado-Baker, 1983

Sennertia faini Baker & Delfinado-Baker, 1983: 117: Fig. 7–13 (holotype and 5 paratype HDNs in USNM); Alzuet & Abrahamovich, 1987: 350
Sennertai faini [sic!] Baker & Delfinado-Baker, 1983: 119
Senertia faini: [sic!] Ramaraju & Mohanasundaram, 2001: 107

Material Holotype HDN (wash) and 5 paratypes (wash, body hairs)—**GUATEMALA: Sololá**, San Lucas Tolimán (Godínez-Patulul Highway), ex *Apis mellifera*, 1 Oct 1980, J. Cummings, USNM.

Host. *Apis mellifera* (alcoholic washings of dead honeybees and on bee hairs)

Distribution. Guatemala: Sololá

Note. Similar to *Sennertia lucrosa* (see notes on *Sennertia lucrosa* p. 164 and key to species above)

Sennertia segnis sp. n.

Material. Holotype: 1 HDN—**USA**: **California**, Tulare Co., 2 mi N Hartland [label reads Fresno Co., 2 mi N Hartland], *Asclepias* (Gentianales: Asclepiadaceae), ex *Xylocopa californica californica* wing bases, 24 Aug 1979, S. Muzzio, CAS, BMOC 03-0604-039. Paratypes: 7 HDNs—same data as holotype; 23 HDNs—Mendocino Co., Ryan Creek, N of Willits, ex *X. tabaniformis orpifex* (dorsal mesosoma), 10 May 1955, R. Craig, USNM, BMOC 05-0420-388; 1 HDN—Modoc Co., 4 mi S Lake City, ex *X. c. californica* on propodeum, 9 Jul 1946, P. D. Hurd, R. F. Smith, UMMZ BMOC 04-0810-003; 7 HDNs—Riverside Co., Banning, ex *X. c. arizonensis* wing bases, 28 May 1928, E. C. Van Dyke, CAS BMOC 03-0604-038; 15 HDNs—Riverside Co., Keen Camp, ex *X. c. diamesa* on lateral propodeum, 24 May 1946, D. J. & J. N. Knulle OSU 0121529, BMOC 03-1106-070; 13 HDNs—San Bernardino Co., Seven Oaks, ex *X. c. arizonensis* posterior wing bases, 25 May 1936, G. M. Kohls, FMNH, BMOC 03-0630-033; 2 HDNs—San Diego Co., Cuyamaca, ex *X. c. arizonensis* on propodeum, 1 May 1934, E. E. Seibert, UMMZ, BMOC 04-0810-002; 9HDNs—**Arizona**, Pima Co., Tucson, ex f *X. californica* propodeum & posterior wing bases, 1 Jun 1917, Oslar, INHS Insect Collection 62339, BMOC 04-1222-002; 21 HDNs—same locality, ex *X. californica* propodeum, 1 Jun 1917, Oslar, INHS Insect Collection 62495, BMOC 04-1222-155; 1 HDN—Patagonia Mountains, ex *X. californica* propodeum & posterior wing bases, 1 Jun 1917, Oslar, INHS Insect Collection 62340, BMOC 04-1222-003; 2 HDNs—**MEXICO**: **Michoacán de Ocampo**, Carapan, ex *X. cyanea*, on mesosoma, 1 Sep 1962 D. M. Janzen, USNM, BMOC 05-0420-130; 9HDNs—**Puebla**, Tehuacan, ex *X. cyanea* on axillar areas, no date, A. Heyne, USNM, BMOC 05-0420-129. Holotype in CAS, paratypes in CAS, FMNH, INHS, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 86, Fig. 87; Table 26, p. 211). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae *si* exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 subequal to or less than 1. 3 times longer than d_1; distinctly longer than h_1; long, nearly as long as *se*; situated anterior to hysterosomal shield. Setae d_1 and e_1 distinctly longer than h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated outside hysterosomal shield. Setae *4b*, *g*, and *4a* without distinct rhomb-like, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Posterior processes of coxal apodemes IV non-applicable. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers absent. Longitudinal hysterosomal sclerite present, short. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, *mG* II distinctly shorter than leg II, but longer than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II bifid, blade-like. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II slightly widened. Tarsal setae *d* and *f* I–II almost symmetrical, not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hys-

Fig. 86. *Sennertia segnis*, heteromorphic deutonymph. A–C - legs I–III (BMOC 03-0604-039, holotype). A, B - ventral and dorsal view.

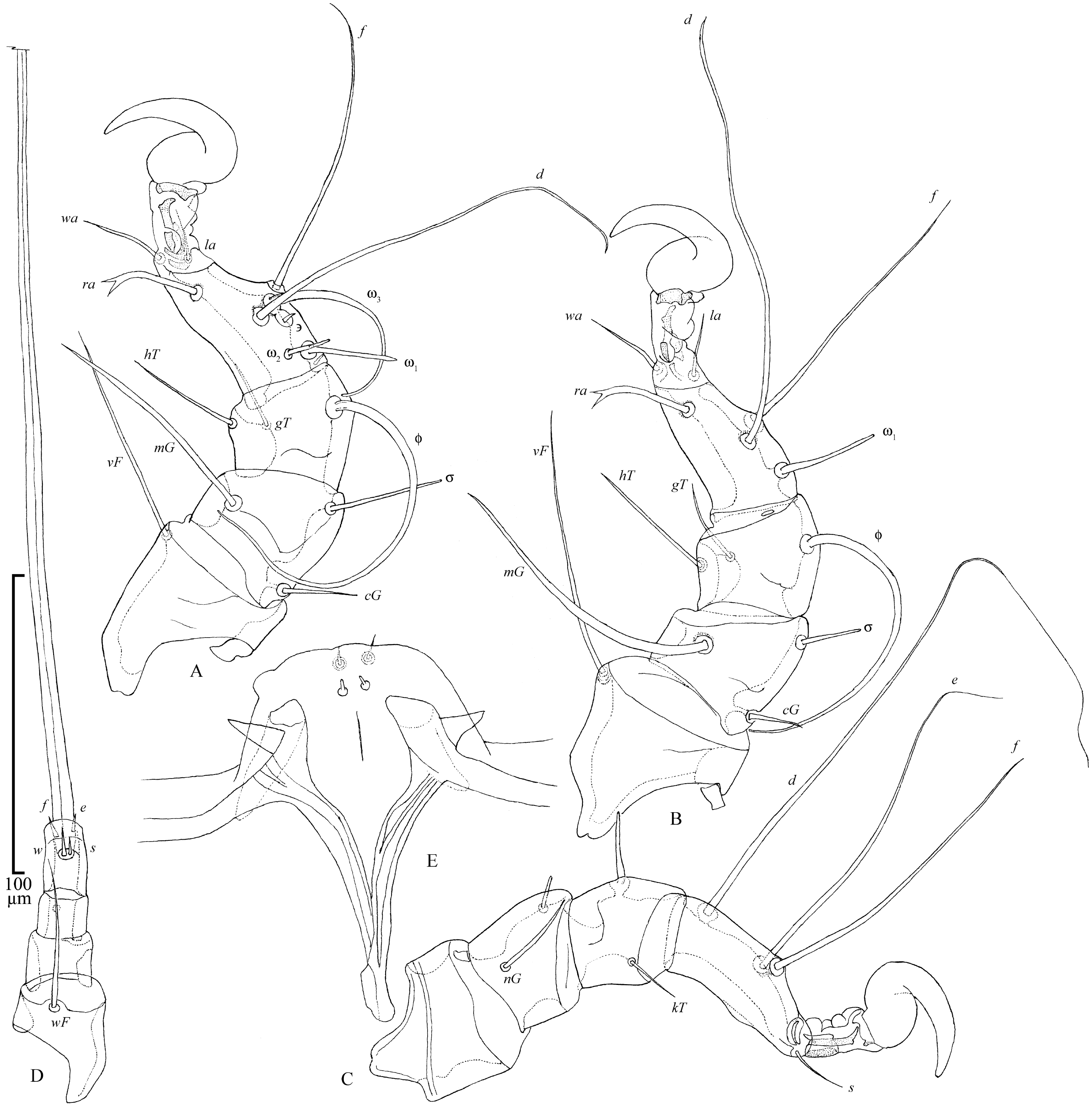

Fig. 87. *Sennertia segnis*, heteromorphic deutonymph. A–C - legs I–III (BMOC 03-0630-039, holotype), respectively; D, E - leg IV, rostral projection and anterior apodemes I, ventral view.

terosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV almost reaching or slightly protruding apex of tarsus IV.

Other instars unknown (tritonymph was observed inside pharate HDN but it cannot be fully described).

Distribution. USA: Arizona, California (type locality); Mexico: Michoacán de Ocampo, Puebla.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20lucrosa&-max=200&-find

Hosts. *Xylocopa* (*Xylocopoides*) *californica*, *Xylocopa* (*Xylocopoides*) *californica arizonensis*, *Xylocopa* (*Xylocopoides*) *cal-*

ifornica diamesa, *Xylocopa* (*Xylocopoides*) *cyanea*, *Xylocopa* (*Notoxylocopa*) *tabaniformis orpifex*.

Etymology. Segnis (=slow, tardy) is a Latin adjective.

Sennertia americana
Delfinado & Baker, 1976

Sennertia americana Delfinado & Baker, 1976: 84, Figs 31–32 (Holotype HDN in and 59 paratype HDNs in USNM; original type repository NYSM (holotype), NYSM and USNM (paratypes)); OConnor, 1988: 341; OConnor, 1993b: 164; Ramaraju & Mohanasundaram, 2001: 107.

Sennertia (Amsennertia) americana: Fain, 1981a: 147; Alzuet & Abrahamovich, 1987: 346; Lombert *et al*., 1987: 113, Figs 1–30 (description of ontogeny); OConnor, 1993a: 362 (acquisition of genus-level characters).

Material (all from *Xylocopa virginica*). 26 HDNs—**USA**: **Florida**, Alachua Co., Gainesville, (propodeum), 10 May 1924, L. E. Jeffries, UMMZ BMOC 04-0917-001; 13 HDNs—Chipola Lake, male (propodeum), 9 Apr 1927, no collector, CUIC HK 85-0108-003; 11 HDNs (paratypes)—Florida, Lee Co., female, 28 Feb. 28, 1937, KVK, USNM; 16HDNs—**Illinois**, Macoupin Co., Carlinville, *Crataegus mollis* (T. & G.) Scheele (Rosaceae), on propodeum & 1st metasomal tergite, 26 Apr 1971, J. C. Marlin, INHS Insect Collection 62498, BMOC 04-1222-158; 10HDNs—same locality, *Prunus serotinus* Erhart (Rosaceae), 1st metasomal tergite, 9 May 1971, J. C. Marlin, INHS Insect Collection 62499, BMOC 04-1222-159; 11 HDNs—**Maryland**, Baltimore Co., Baltimore, (propodeum), 28 Apr 1957, R.G. Beard, CUIC BMOC 79-1205-002; 5 HDNs—**Michigan**, Washtenaw Co., Ann Arbor, Green Brier Apts, 24 May 2000, A. Dowling, UMMZ BMOC 04-1008-001; **New York**, 6 HDNs (1 holotype and 10 paratypes)—Albany Co., Albany, 6 Jun 1901, no collector, USNM; 15 HDNs Dutchess Co., Amenia (propodeum), 9 May 1978, M. O'Brien, UMMZ BMOC 04-0917-002; 28 HDNs (paratypes)—Dutchess Co., Poughkeepsie, Apr 1901, no collector, USNM; 4 HDNs—Tompkins Co., Ithaca, Cornell Campus, (near wing base), 4 Sep 1975, R. J. Pollack, UMMZ BMOC 76-1017-002; 10 HDNs—**North Carolina**, Craven Co., Fairfield Harbour, 15 ft., marsh/woods (dorsolateral propodeum), 9–11 May1994, D.C. Marshall, UMMZ BMOC 94-1104-001; 1 female, 2 males, 1 TN—**Pennsylvania**, Huntingdon Co., Marklesburg, nest, 1 Aug 1981, R. Fisher, UMMZ BMOC 82-0521-019; 1 L, 2 PNs, 1 HDN, 1 TN, 3 females, 3 males—same data, USNM; 1 pharate HDN—**Texas**, Dallas Co., ex *X. v. texana* (mesosoma), 1 Jul 1931, J.K.G. Silvey, UMMZ BMOC 90-1212-020; 17 HDNs—**Virginia**, Amherst Co., Sweet Briar Station, (propodeum), 27 Apr 1938, E. Herbold, UMMZ BMOC 90-1212-025; 4 HDNs—**North America**, male (propodeum), no date, R. Latham, CUIC HK 85-0108-004. Voucher specimens in CNC, CUIC, INHS, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 88, Fig. 89; Table 27, p. 211). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae *si* exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 distinctly longer than d_1-h_1; long, nearly as long as *se*; situated anterior to hysterosomal shield. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 shorter than 1/4 of distance between them; situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2; not touching hysterosomal shield. Lateral gland openings situated outside hysterosomal shield. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening, filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Posterior processes of coxal apodemes IV nonapplicable. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, *mG* II almost as long as leg II or longer. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, filiform. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II slightly widened. Tarsal setae *d* and *f* I–II almost symmetrical, not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV distinctly protruding apex of tarsus IV.

Adults. Supracoxal seta *scx* situated on supracoxal sclerite, anterior to outer ridge of supracoxal sclerite. Alveoli of setae *ve* absent. Dorsal idiosomal cuticle tuberculate or mammillate (except for posterio-medial opisthosomal region in female). Dorsal cuticular pattern more or less uniform. Dorsal idiosomal setae c_1-h_1 spiniform, short (not reaching half of distance to next posterior pair of setae). Dorsal idiosomal setae c_p, c_3, h_3 widened distally, compressed dorso-ventrally at apex, barbs more numerous at apex. Dorsal setae e_2 and f_2 spiniform, distinctly shorter than h_3. Prodorsal shield distinctly elongated, length/width 1.7–1.8, without falsifoveate pattern. Coxal fields III opened. Proximal acetabular extensions of *ap′* I partially border antiaxial margins of coxal fields I. Proximal acetabular extensions of *ap′* II partially border antiaxial margins of coxal fields II. Distal acetabular extensions of *ap′* II and *ap″* II separate. Proximal acetabular extensions of *ap′* III completely border antiaxial margins of coxal fields III. Distal acetabular extensions of *ap′* III and *ap″* III fused. Proximal acetabular extensions of *ap′* IV completely border antiaxial margins of coxal fields IV. Distal acetabular extensions of *ap′* IV and *ap″* IV separate or not developed. Opisthosomal gland openings approximately at level of e_2. Tarsal setae *ra* and *la* II present. Solenidion ω_2 I subapical. Famulus ε spiniform. Setae *ba* I longer than famulus ε. Setae *ba* II absent.

Female. Setae ad_1 and ad_2 absent. Setae ps_3 short, distinctly shorter than ps_2; anterior to *4a* level. External copulatory tube

Fig. 88. *Sennertia americana*, heteromorphic deutonymph (BMOC 04-0917-002). A, B - ventral and dorsal view.

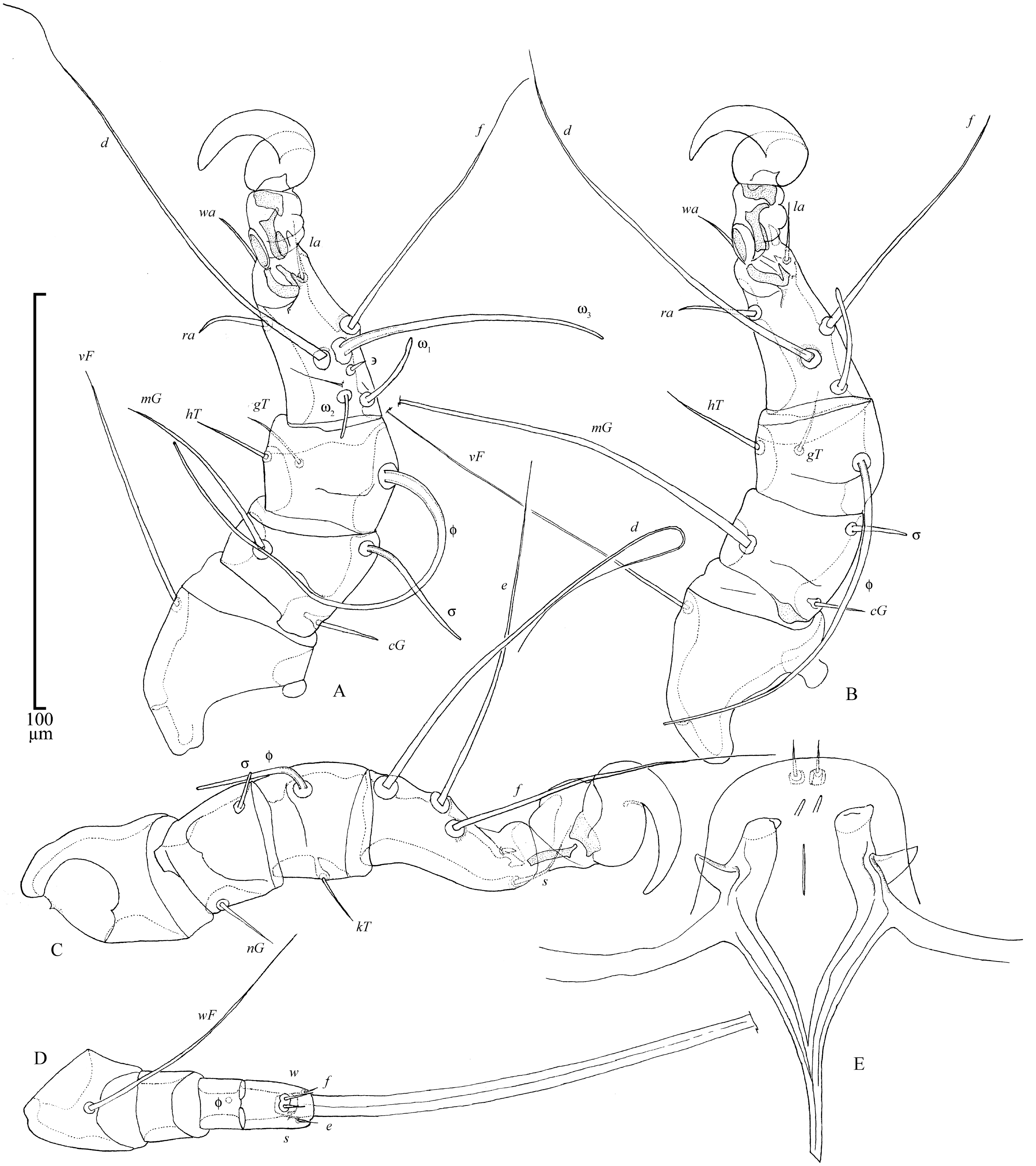

Fig. 89. *Sennertia americana*, heteromorphic deutonymph (BMOC 04-0917-002). A–D - legs I–IV, respectively; E - rostral projection and anterior apodemes I, ventral view.

absent. Setae h_3 nearly at level of h_2. Posterio-medial part of dorsal opisthosoma with distinct longitudinal linear pattern.

Male. Setae ad_1 absent. Genital setae short, transparent mammillae; situated on progenital folds. Pseudanal setae ps_3 outside progenital sclerites, spiniform. Dorsal supporting sclerites short, as long as 2 diameters of aedeagus at base or shorter. Setae *q* I present, *p* II absent. Pretarsal suckers IV same as pretarsal suckers I–III.

Protonymph. Tarsal setae *e* IV absent, *f* IV absent.

Larva. Dorsal idiosomal setae relatively longer than in other instars, protruding bases of subsequent setae.

Hosts. *Xylocopa* (*Xylocopoides*) *virginica* (type host), *Xylocopa* (*Xylocopoides*) *virginica texana*.

Distribution. USA: Florida, Illinois, Maryland, Michigan, New York (Albany Co., Albany—type locality), North Carolina, Pennsylvania, Texas, Virginia.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20americana&-max=200&-find

Biology. Feeding instars of this species were found only once (Lombert *et al*., 1987). At the time these collections were made in early August, adult *Xylocopa virginica* were emerging from the nests, and most cells were already empty. A few cells contained pharate or teneral adult bees. Some cells contained large provision masses consisting of nectar and pollen, but no developing bee larvae. All instars of *Sennertia americana* were located on the walls of these cells. The cells were also inhabited by *Horstia virginica* Baker, 1962 (Acaridae) and *Tortonia quadridens* Baker, 1962 (Suidasiidae). Since the two latter mite species are cleptoparasitic the ultimate cause of cell failure is uncertain.

Note. The slide marked "holotype" contains six specimens none of which is identified as the holotype.

Sennertia pirata sp. n.

Material. Holotype: 1 HDN—**BAHAMAS**: Bimini, South Bimini Island, ex *Xylocopa* sp. (a new species identified by P. Hurd) on 1st metasomal tergite, 11 Jul 1951, C. & P. Vaurie, AMNH BMOC 04-0508-310; Paratypes: 17 HDNs—same data; 29 HDNs—**BRITISH VIRGIN ISLANDS**: Guana Island, hotel area, 18°29'N 64°34'W, ex *X. mordax* propodeum, 5 Jul 1993, R. R. Snelling, LACM 208276, BMOC 04-1122-011; 11 HDNs—same locality, plantation area, *Centrosema virginianum* (Fabales: Fabaceae), ex *X. mordax* hind femur area, 29 Oct 1992, R. R. Snelling LACM 208277, BMOC 04-1122-012; 2HDNs-**CUBA**: **Ciudad de La Habana**, Havana, no date, ex m *Xylocopa cubaecola*, Baker, CUIC, HK 84-0907-003; 7 HDNs—**La Habana**, Vedado, ex *X. cubaecola* on propodeum, 1 Sep 1993, J. A. Genaro, USNM, BMOC 05-0420-125; 29 HDNs—**USA**: **Puerto Rico**, Ponce Co., Playa de Ponce (label reads Ponce), ex *X. mordax* mesosoma, 25 Mar 1939, T. H. Hubbell #5 UMMZ, HK 90-1212-009; 5 HDNs—**Virgin Islands of the United States**, St. Croix Co., Frederiksted, *X. mordax*, 25 Mar 1927, no collector, CUIC, HK 84-1210-002. Holotype in AMNH, paratypes in AMNH, CUIC, LACM, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 90, Fig. 91; Table 27, p. 213). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 distinctly longer than d_1-h_1, long, nearly as long as *se*, situated on anterior edge of hysterosomal shield. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 present. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated on hysterosomal shield. Setae *4b*, *g*, and *4a* with rhomb-like widening (sometime weakly-developed). Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, and *ra* I–II filiform or nearly filiform (*wa* I–II spiniform). Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}), anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma distinctly striated. Genual setae *mG* I–II simple, *mG* II almost as long as leg II or longer. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, blade-like. Tarsal setae *wa* I–II and *s* III spiniform (at least *s* III with rounded apices). Tarsal setae *d* I–II distinctly widened, lanceolate. Tarsal setae *d* and *f* I–II almost symmetrical, not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV not reaching apex of tarsus IV.

Hosts. *Xylocopa* (*Neoxylocopa*) *cubaecola*, *Xylocopa* (*Neoxylocopa*) *mordax*, *Xylocopa* sp.

Distribution. Bahamas, British Virgin Islands, Cuba, USA: Puerto Rico, Virgin Islands of the United States.

Etymology. Pirata (=sea-robber, corsair) is a Latin noun in apposition.

Sennertia shimanukii
Baker & Delfinado-Baker, 1983

Sennertia shimanukii: Baker & Delfinado-Baker, 1983: 117, Figs 1–6 (holotype and 37 (36 indicated originally) paratype HDNs in USNM); Ramaraju & Mohanasundaram, 2001: 107; Alzuet & Abrahamovich, 1987: 350.
Sennertia shimanuki Alzuet & Abrahamovich, 1990: 630 (*lapsus*)

Material (number of specimens measured for analysis p. 94 in parenthesis). Holotype HDN (wash) and 37 paratypes (wash, body hairs)—**GUATEMALA: Sololá**, San Lucas Tolimán, ex *Apis mellifera*, 1 Oct 1980, J. Cummings, USNM, BMOC 04-0822-004 (16 analysis); 12 HDNs—**MEXICO**: **Baja California Sur**, 2 mi S La Paz, ex *Xylocopa californica arizonensis* on propodeum, 6 Aug 1966, P. D. Hurd, USNM, BMOC 05-0420-096 (5 validation); 28 HDNs—**Nayarit**, Islas Tres Marías, Islas Maria Cleofas, ex *X. varipuncta* on 1st metasomal tergite, 27 Mar 1964, R. R. Snelling, 364 LACM ENT 208598, BMOC 05-0102-034 (5 validation); 16 HDNs—same data LACM

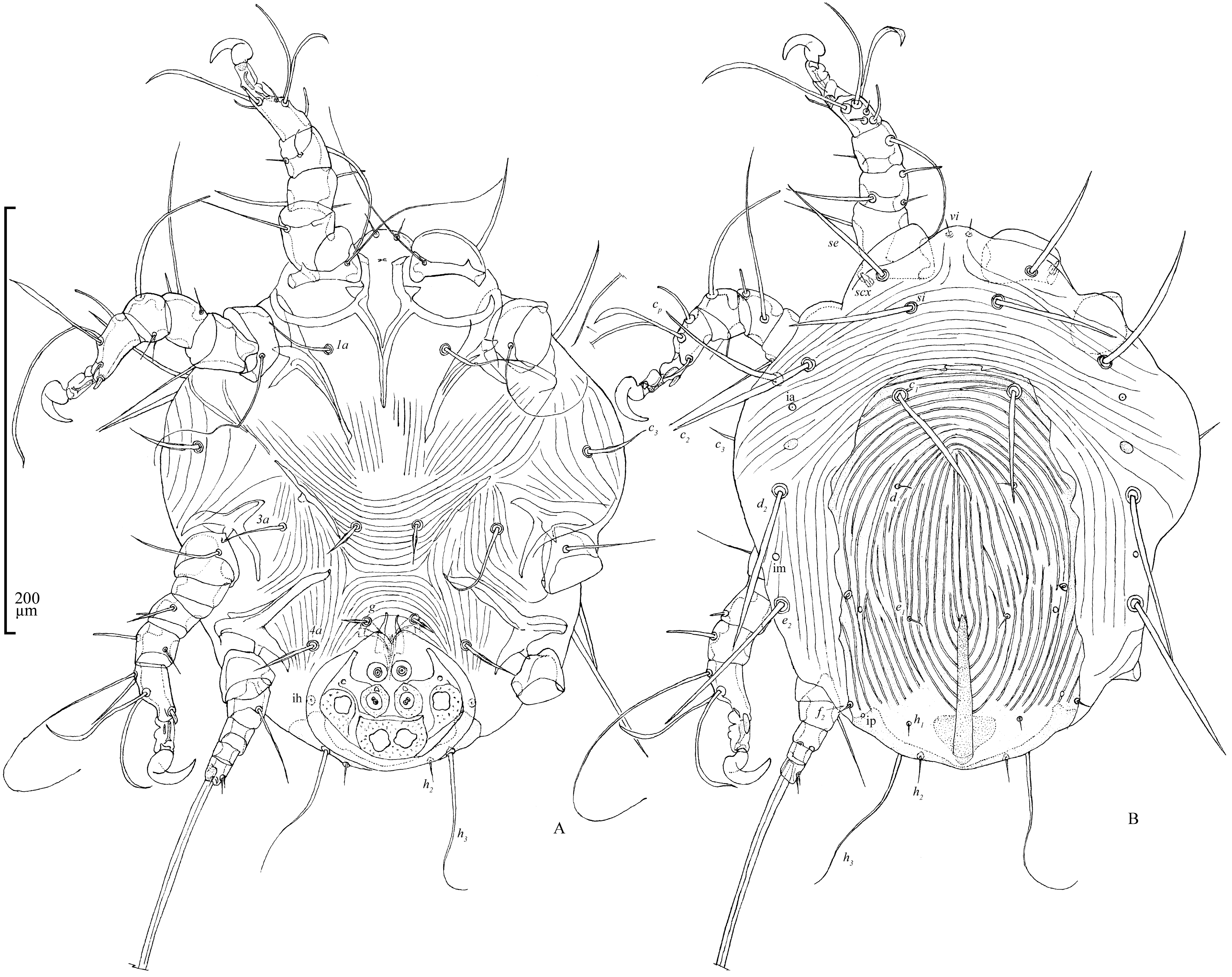

Fig. 90. *Sennertia pirata*, heteromorphic deutonymph (BMOC 04-0508-310, holotype). A, B - ventral and dorsal view.

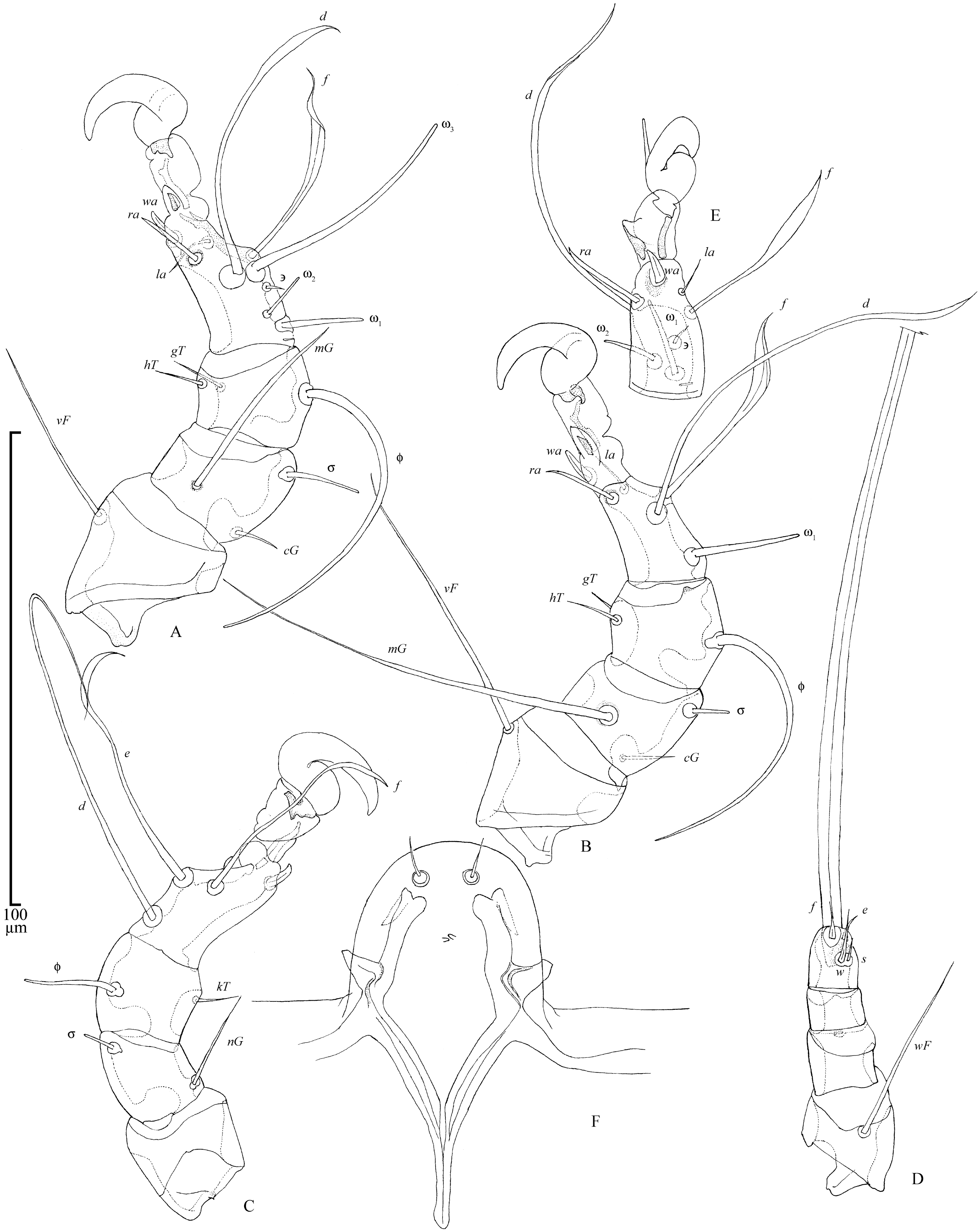

Fig. 91. *Sennertia pirata*, heteromorphic deutonymph (BMOC 04-0508-310). A–D - legs IV, E - tarsus I, ventral view; F - rostral projection and anterior apodemes I, ventral view.

ENT 208599, BMOC 05-0102-035 (5 validation); 30HDNs—**Veracruz**, Cotaxtla, ex *X. fimbriata* on 1st metasomal tergite, 5 Jul 1962, D. H. Janzen, USNM, BMOC 05-0420-154 (5 validation); 15+22 HDNs—**USA**: **Texas**, Hidalgo Co., ex *X. mexicanorum* on scutellum & metanotum + propodeum & wing bases, 8 Jun 1958, D. J. & J. N. Knull, OSU OSUC 0121357, BMOC 03-1106-088 (10 analysis, 5 revalidation); 18HDNs—Hidalgo Co., Hidalgo, ex *X. mexicanorum* on wing bases and propodeum, Apr 1939 (year illegible), Stanley Mulall (last letters illegible), USNM, BMOC 05-0420-075 (9 analysis); 28HDNs—Cameron Co., Brownsville, ex *X. mexicanorum* on metanotum, no date, no collector, USNM, BMOC 05-0420-269 (10 analysis); 19HDNs—ex *X. mexicanorum* on metanotum, no date, C. F. Baker, USNM, BMOC 05-0420-270 (4 analysis); 16HDNs—Cameron Co., Brownsville, ex *X. mexicanorum* on scutellum, 28 May 1904, H. S. Barber USNM, BMOC 05-0420-271 (9 analysis); 17 HDNs—same locality, ex *X. varipuncta* under tegulae, no date, G. Dorner, INHS Insect Collection 62490, BMOC 04-1222-150 (5 validation); 19 HDNs—ex *X. varipuncta* on 1st metasomal tergite, no date, INHS Insect Collection 62492, BMOC 04-1222-152 (5 validation); 21HDNs—**California**, Alameda Co., Oakland, Balsawood, ex *X. sonorina* on scutellum, 11 Aug 1940, R. M. Hayes, USNM, BMOC 05-0420-365 (5 validation); 3HDNs—San Bernardino Co., ex f *X. varipuncta*, 1–7 Apr 1918, J. C. Bradley, CUIC HK 84-1217-001. Voucher specimens in CUIC, INHS, LACM, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 92, Fig. 93; Table 14, p. 197). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield without sclerotization, formed by long striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*, exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 distinctly longer than d_1-h_1; long, nearly as long as *se*; situated on anterior edge of hysterosomal shield. Setae d_1 and e_1 nearly uniform in length with h_1; situated on hysterosomal shield. Sclerite between *ia* and d_2 present. Setae e_2 subequal with d_2; not touching hysterosomal shield. Lateral gland openings situated on hysterosomal shield. Setae *4b*, *g*, and *4a* with rhomb-like widening (sometime weakly-developed). Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II filiform. *wa* I–II spiniform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted; almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}); anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers present. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, *mG* II distinctly shorter than leg II, but longer than femur II. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, filiform. Tarsal setae *wa* I–II and *s* III spiniform (at least *s* III with rounded apices). Tarsal setae *d* I–II distinctly widened, lanceolate. Tarsal setae *d* and *f* I–II almost symmetrical, *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore present. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV slightly protruding apex of tarsus IV.

Other instars unknown.

Hosts. *Apis mellifera* (type host, accidental); *Xylocopa* (*Neoxylocopa*) *varipuncta*, *Xylocopa* (*Neoxylocopa*) *mexicanorum*, *Xylocopa* (*Neoxylocopa*) *sonorina*, *Xylocopa* (*Xylocopoides*) *californica arizonensis*, *Xylocopa* (*Neoxylocopa*) *fimbriata* (Apidae).

Distribution. Guatemala: Sololá (type locality); Mexico: Baja California Sur, Nayarit, Veracruz; USA: California, Texas.

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20shimanukii&-max=200&-find

Note. Similar to *Sennertia augustii* and *S. frontalis* (see p. 94).

Sennertia frontalis

Vitzthum, 1941

Sennertia frontalis Vitzthum, 1941: 308, Figs 1 (lectotype and 2 paralectotype HDN (designated by Fain, 1981a) in ZSMC A20031427 (Jürgen *et al*., 2005); Baker & Delfinado-Baker, 1983: 119 (comparison with *Sennertia shimanukii*); Ramaraju & Mohanasundaram, 2001: 109 (comparison with *Sennertia leucothorae*, *Sennertia bakeri*, and *Sennertia carpenteri*; year of species description indicated as 1930)

Sennertia (*Amsennertia*) *frontalis*: Fain, 1981a: 176, Figs 50–52 (redescription of HDN, included in key, lectotype designation); Alzuet & Abrahamovich, 1987: 346; Alzuet & Abrahamovich, 1990: 630 (comparison with HDN of *Sennertia augustii*; recollection); OConnor, 1993a: 362 (genus-level character acquisition)

Material (number of specimens measured for analysis p. 94 in parenthesis). 29 HDNs—**ARGENTINA**, **Entre Ríos**, Pronunciamiento, ex *X. frontalis* on propodeum, 1 Feb 1965, F. H. Walz, USNM, BMOC 05-0420-200 (10 analysis); 12HDNs—same data, on basal propodeum, 1 Jan 1965, F. H. Walz, USNM, BMOC 05-0420-201 (7 analysis); 5HDNs—same data, on propodeum, 1 Feb 1965, F. H. Walz, USNM, BMOC 05-0420-202 (2 analysis); 7HDNs—**BRAZIL: Amazonas**, Tapuruquára (Santa Isabel do Rio Negro), ex *X. frontalis* on 1st metasomal tergite, 1 Jun 1963, L. Guindani, USNM, BMOC 05-0420-196 (4 validation); 22HDNs—same data, on propodeum,1 Jun 1963, L. Guindani, USNM, BMOC 05-0420-197 (5 validation); 4HDNs—**São Paulo**, m *X. frontalis*, no date, Hammar, CUIC, HK 84-0818-001 (2 analysis); 1HDN—same data, *X. frontalis*, no date, Hammar, CUIC, HK 84-0820-005 (1 analysis); 4 HDNs—**SURINAME: Marowijne**, Cottica R., Moengo, f *X. frontalis*, 13 May 1927, no collector, CUIC HK 84-0827-003 (2 analysis); 6HDNs—**PERU: Loreto**, Pucallpa, 200 m., ex m *X. frontalis* on 1st metasomal tergite, 1 Jan 1965, J. Schunke, LACM 208298, BMOC 04-1122-027 (5 validation); 21 HDNs—**VENEZUELA: Monagas**, 42 km SE Maturín, ex m *X. frontalis* on propodeum, 12 Jul 1958, A. Menke, LACM, BMOC 04-1122-026 (5 validation); 28 HDNs—**PANAMA: "Canal Zone"**, Aldrook Field, *X. frontalis* on propodeum, 20 Mar 1938, L. J. Stannard, INHS, Insect Collection 62342, BMOC 04-1222-005 (5 revalidation); 26 HDNs—**HONDURAS: Progresso**,

Fig. 92. *Sennertia shimanukii*, heteromorphic deutonymph (BMOC 03-1106-088). A, B - ventral and dorsal view.

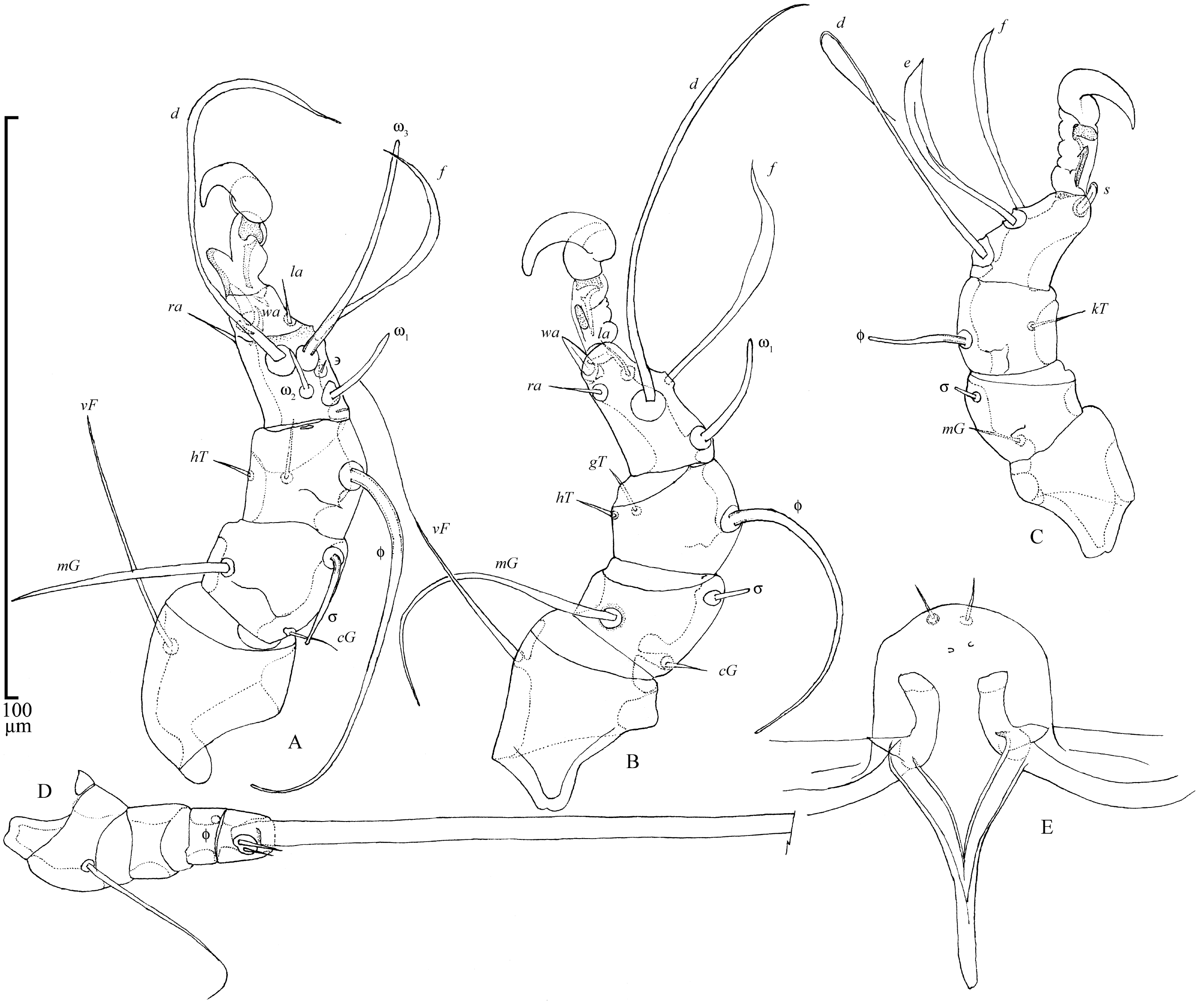

Fig. 93. *Sennertia shimanukii*, heteromorphic deutonymph (BMOC 03-1106-088). A–D - legs I–IV, respectively; E - rostral projection and anterior apodemes I, ventral view.

ex *X. nautlana* on mesosoma, 19 Mar 1923, T.H. Hubbell #121, UMMZ BMOC 90-1212-010 (11 analysis); 7HDNs—**MEXICO: Chiapas**, S. Jeronimo Tacaua, *X. frontalis* on 1st metasomal tergite, 20 Sep 1970, T. W. Taylor, LACM ENT 208602, BMOC 05-0102-038 (5 validation; 2 misclassified as *augustii*); 9 HDNs—Simojovel de Allende, ex m *X. nautlana* on propodeum, 12 Aug 1958, J. A. Chemsak, FMNH, BMOC 03-1008-056 (9 analysis).

Description. *Phoretic deutonymph* (Table 14, p. 197). Similar to *Sennertia augustii* and *S. shimanukii* (see p. 94).

Other instars unknown.

Hosts. *Xylocopa* (*Neoxylocopa*) *frontalis* (type host), *Xylocopa* (*Neoxylocopa*) *nautlana*.

Distribution. Argentina (type locality): Entre Ríos; Brazil: Amazonas, São Paulo; Suriname: Marowijne; Peru: Loreto; Venezuela: Monagas; Panama: “Canal Zone”; Honduras: Progresso; Mexico: Chiapas

http://141.211.243.61/bee_mites/?-db=ummz.fm&-format=mapq.js&IDENTITY=Sennertia%20frontalis&-max=200&-find

Sennertia loricata sp. n.

Material. Holotype: HDN—**USA**: **Florida**, Alachua Co., Gainesville, ex *Xylocopa micans* on propodeum, 17 May 1923, no collector, UMMZ, BMOC 04-0804-001. Paratypes: 27 HDNs—same data; 11 HDNs—same data (host sex m), on mesosoma, 6 Apr 1919, P. W. Fatting, CUIC, HK 85-0107-004; 1HDN- same data (over body), 4 May 1924, Alexander & Walker, UMMZ, BMOC 90-1212-007; 21 HDNs—same data (host sex male, on mesosoma), 25 Apr 1922, UMMZ, BMOC 90-1212-008; 13HDNs—Manatee Co., Manatee, ex *X. micans* (as *X. lucida*) on anterior scutum (host species probably misidentified), 8 Jul 1977, C. J. Bickner, USNM, BMOC 05-0420-258; 14 HDNs—Monroe Co., L. Matecumbe Key, ex *X. micans* lateral propodeum, 30 Jan 1935,

Fig. 94. *Sennertia loricata*, heteromorphic deutonymph (BMOC 85-0107-001, holotype). A, B - ventral and dorsal view.

Fig. 95. *Sennertia loricata*, heteromorphic deutonymph (BMOC 85-0107-004). A–D - legs I–IV, respectively; E - rostral projection and anterior apodemes I, ventral view. Scale bar: left: A, B, C; right: D, E.

no collector, OSU OSUC 0121544, BMOC 03-1106-083; 4 HDNs—Orange Co., Orlando, ex *X. micans* on dorsum, 20 Mar 1935 R. C. Osburn OSU OSUC 0121541, BMOC 03-1106-079; 15 HDNs—Volusia Co., Enterprise, ex *X. micans* over body, including 7th metasomal tergite, 1 Mar 1923, no collector, OSU OSUC 0121539 BMOC 03-1106-081; 32 HDNs—same data (on propodeum), OSU OSUC 0121542, BMOC 03-1106-082; 13 HDNs—**Louisiana**, Cameron Pr., Cameron, ex *X. micans*, 1st metasomal tergite, 1–14 June 1905, Jas. S. Hine, OSU OSUC 0121537, BMOC 03-1106-080; 1HDN—**Puerto Rico**, Ponce Co., Playa de Ponce (label reads Ponce), ex *X. mordax* on mesosoma, 25 Mar 1939, T. H. Hubbell #5, UMMZ, HK 90-1212-009; 12 HDNs—**Texas**, Bexar Co., San Antonio, ex *X. micans* on mesosoma, 16 Jun 1946, S. Camras, V. Dropkin, FMNH, BMOC 03-0630-034; 7 HDNs—Braggs Co., ex *X. micans* over body, 17 Aug 1937, R. W. Strandtmann, OSU OSUC 0121546, BMOC 03-1106-077; 21 HDNs—**Virginia** Suffolk (city), ex *X. micans* on 7th metasomal tergite, 20 May 1944, G. M. Boush, OSU OSUC 0121545, BMOC 03-1106-078; 20 HDNs—**MEXICO: Chiapas**, Tuxtla Gutiérrez, ex *X. barbatella barbatella* on lateral propodeum, 9 Jun 1964, J. C. & D. Pallister, AMNH, BMOC 04-0508-311; 17 HDNs—**Jalisco**, Playa Teopa, 8 km S Careyes, ex *X. muscaria* on lateral propodeum, 4 Oct 1985, J. G. Rozen, AMNH, BMOC 04-0508-319. Holotype in UMMZ, paratypes in AMNH, CUIC, FMNH, OSAL, UMMZ, UNAM, USNM.

Description. *Phoretic deutonymph* (Fig. 94, Fig. 95; Table 27, p. 213). Gnathosomal solenidia shorter than 1/3 of femur I width. Supracoxal setae *scx* situated on separate small sclerite. Hysterosomal shield lateral gland openings and bases of f_2 nearly on edge of hysterosomal shield, or the former outside the shield. Lateral edges of hysterosomal shield in anterior part not narrowing. Dorsal hysterosomal pouch absent. Distance between anterior margin of hysterosomal shield and setae si exceeds diameter of *si* bases. Striate pattern of idiosomal cuticle outside hysterosomal shield formed by long striae, with sclerotization, sclerotization situated between striae. Distinct rudiments of *vi* present. Setae *si* distinctly posterior *se*. Setae *si* exceed 1/2 of *se*, almost as thick as *se*. Diameter of *si* exceeds 1/2 of diameter of *se*. Setae c_1 distinctly longer than d_1-h_1, nearly as long as *se*, situated on anterior edge of hysterosomal shield. Setae d_1 and e_1 nearly uniform in length with h_1. Setae d_1 situated on hysterosomal shield. Sclerite between *ia* and d_2 absent. Setae e_2 subequal with d_2, not touching hysterosomal shield. Lateral gland openings situated outside hysterosomal shield. Setae *4b*, *g*, and *4a* without distinct rhomb-like widening filiform. Setae *4b*, *pR* I–II, *sR* III, *wF* IV, *gT* I–II, *hT* I–II, *kT* III, *ra* I–II, and *wa* I–II filiform. Posterior apodemes II and anterior apodemes III free. Anterior apodemes IV not interrupted, almost straight. Posterior apodeme IV absent. Conoids ps_2 posterior to anterior transverse level of central suckers (ad_{1+2}), anterior to ps_1, situated outside outer level of ad_{1+2}. Transparent margin of anterior suckers (ad_3) without rough sclerotization. Suckers ad_3 not enlarged, smaller than central suckers. Posterior and lateral borders of attachment organ not forming distinct frame. Sclerotized rudiment of anterior cuticular suckers absent. Longitudinal hysterosomal sclerite present, long. Ventral hysterosoma smooth. Genual setae *mG* I–II simple, *mG* II almost as long as leg II or longer. Tarsal setae *la* I–II longer than famulus ε. Tarsal setae *ra* I–II not bifid, blade-like. Tarsal setae *wa* I–II and *s* III filiform, needle-like, or widened basally but with attenuated end. Tarsal setae *d* I–II slightly widened. Tarsal setae *d* and *f* I–II almost symmetrical, *d* and *f* I not touching. Solenidion ω_3 closer to *f* I than to ω_1. Posterior condylophore absent. Anterior condylophore I–II with distal bending. Seta *d* III situated close to tarsal base, distance usually subequal or shorter than diameter of *d* III alveolus. Leg IV protruding posterior edge of hysterosoma. Tarsus IV not enlarged, shorter or less than 2 times longer than width of trochanter IV. Setae *w* IV thinner than *d* IV and distinctly shorter than leg IV, situated on middle of tarsus IV. Setae *s* IV present. Setae *wF* IV distinctly protruding apex of tarsus IV.

Other instars unknown.

Hosts. *Xylocopa* (*Schonnherria*) *micans*, *Xylocopa* (*Schonnherria*) *barbatella barbatella*, *Xylocopa* (*Schonnherria*) *muscaria*. One specimen found on *Xylocopa* (*Neoxylocopa*) *mordax*.

Distribution. USA: Florida, Louisiana, Puerto Rico, Texas, Virginia; Mexico: Chiapas, Jalisco.

Etymology. Loricatus (=clothed in mail, harnessed) is a Latin objective.

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APPENDIX 1. SPECIES OUTSIDE NORTH AMERICA INCLUDED IN THE MONOGRAPH

Chaetodactylus sp. 1

Material CHILE: Coquimbo, ex *Diadasia chilensis*. 10 HDNs - Tongoy, 30°15′11″S, 71°29′34″W, dorsal mesosoma & propodeum, 6 Jan 1956, W. Knecht, KU BMOC 96-0916-026; 13 HDNs - Condoriaco, 1350m, 29°42′08″S, 70°49′53″W, on dorsal & lateral propodeum, 22 Nov 1955, W. Knecht, KU BMOC 96-0916-027; 3 HDNs - El Calabaco, Nov 1959, wingbases, L. E. Peña, LACM, BMOC 97-0331-020. Voucher specimens in KU, LACM, UMMZ.

Chaetodactylus sp. 2

Material. 1HDN - **CHILE: Tarapacá**, Parinacota, 4400 m, ex *Anthidium espinosai* (propodeum), 17 Feb 1994, L. E. Peña, AMNH BMOC 04-0508-069.

Sennertia af. alfkeni (Oudemans, 1900)

Material. 4f (short setae), 1 f (long setae), 9 m (short setae), 2 m (long setae), 2 TNs, 12 PNs, 10 Ls - AUSTRALIA: Queensland, 15 mi N Cairns, ex *Xylocopa (Koptortosoma) aruana* nest, brood cell pollen provision, 17 Aug 1967, WAM #86-251 BMOC 86-0406-010. Voucher specimens in WAM, UMMZ.

Sennertia augustii Alzuet & Abrahamovich, 1990

Material. 11 HDNs - **ARGENTINA: Entre Ríos**, Pronunciamiento, ex *Xylocopa augusti* on scutellum, 1 Feb 1964, F. H. Walz, USNM, BMOC 05-0420-037 (10 analysis); 14 HDNs - same data, posterior mesosoma, 1 Mar 1965, F. H. Walz, USNM, BMOC 05-0420-041, (5 revalidation); 22 HDNs - **Lavalle Ajó**, Buenos Aires, ex *X. augusti* on lateral propodeum, 10 Nov 1920, A. Wetmore, USNM, BMOC 05-0420-046 (5 validation); 37 HDNs - **San Martin**, Corrientes, ex *X. augusti* on scutellum, 1 Jan 1947, Rick Huidobro, USNM, BMOC 05-0420-048 (5 validation); 22 HDNs - **Villa Encarnación**, on flowers of *Fuchsia*, ex *X. augusti* on propodeum, 17 Feb 1904, no collector, USNM, BMOC 05-0420-047 (5 validation); 20 HDNs - ARGENTINA?, No location, *X. augusti* on base of propodeum, no date, F. H. Walz, USNM, BMOC 05-0420-035 (10 analysis); 11 HDNs—**URUGUAY: Montevideo**, Montevideo, *X. augusti* on metanotum in two compact clusters, no date, Sivori CAS, BMOC 03-0604-034 (11 analysis); 3HDNs - **MEXICO: Michoacán**, Apatzingan, 366m, ex f *X. fimbriata* on 1st metasomal tergite, 7 Aug 1940, Hoogstraal, Knight, INHS Insect Collection 62338, BMOC 04-1222-001 (2 analysis; originally *shimanukii*, classified as *augustii*). Voucher specimens in CAS, INHS, UMMZ, USNM.

Sennertia af. basilewskyi Fain, 1974

Material. 22 HDNs—**CAMEROON**: Province du Sud, Sangmélima, Fulasi, ex *Xylocopa* (*Mesotrichia*) *torrida*, 1 Apr 1920, B.C.Z. Evans, UMMZ BMOC 90-1212-014. Voucher specimens in UMMZ.

Sennertia koptorthosomae (Oudemans, 1905)

Material. 3 m, 4 f - MALAYSIA: Negeri Sembilan, Kuala Pilah, ex *Xylocopa latipes* nest, 9 May 1979, Lukoschus (3104) (UMMZ, USNM); ?1 PN - same data, 30 Jun 1980, Ismail (UMMZ). Voucher specimens in UMMZ, USNM.

Notes. OConnor (1993b) found deutonymphs of two species of *Sennertia* associated with *Xylocopa latipes*: *S. koptorthosomae* and *S. hipposideros*. We have uncorrelated adults of *Sennertia* collected by F. Lukoschus in Malaysia in 1979 from the nest of this host. In these adults, the proximal acetabular extensions of anterior apodeme II are complete. Because the similar character state occurs in deutonymphs of *S. koptorthosomae* but not in *S. hipposideros*, we consider these adults as tentatively belonging to *S. koptorthosomae*. Correlation of the adults and the single protonymph is also tentative.

Sennertia leei Fain, 1982

Material. 82HDNs - **AUSTRALIA: New South Wales**, Woy Woy near Gosford, nest in *Banksia* branch, ex male *Xylocopa bombylans* on mesosoma and anterior metasoma, 27 Jan 1971, T. F. Houston, WAMP 86-481, BMOC 86-1022-017; 3HDNs - Sydney, ex *X. bombylans*, 7 Feb 1909, no collector, CUIC, BMOC 79-1205-004; 22 HDNs - **Queensland**, near Tamborine Village, nest in *Tristania*, ex m *X. bombylans* on mesosoma, 20 Sep 1968, T.F. Houston, WAM 86-480, BMOC 86-1022-016; 2f, 2m, 6TNs - Tamborine, nest of *X. bombylans*, 20 Sep 1968, T. F. Houston, WAMP 86-253, BMOC 86-0406-005 (tentative association); 10 HDNs - **South Australia**, Kangaroo Island, Cape Borda, nest, ex f *Xylocopa aerata* on mesosoma, 22 Oct 1970 G. Cameron WAM 86-482 BMOC 86-1022-018; 20 HDNs - same data, WAM 86-483 BMOC 86-1022-019; 23 HDNs - same data, male, WAM 86-484 BMOC 86-1022-020; 21 HDNs - same data, WAM 86-485 BMOC 86-1022-021. Voucher specimens in CUIC, UMMZ, WAMP.

Sennertia scutata Fain, 1974

Material. 3m, 3f, 1PN - **SOUTH AFRICA**: Western Cape Prov., Worcester, Karoo Gardens, ex *Ceratina truncata* nest, H. V. Daly (A135), UMMZ BMOC 79-1125-003; 1f, 3 m, 1TN, 2 PN, 1L - 23.3 mi N Barrydale, ex *Ceratina truncata* nest in stem *Cotyledon paniculatum* (Rosales: Crassulaceae), H. V. Daly, UMMZ BMOC 79-1125-005; 6f, 4m, L - Worcester, Karoo Gardens, *Ceratina* sp., lab nests, 4 Nov 1970, H. Daly, UMMZ BMOC 79-1125-002; 4f, 1m - 1.5. 1 mi N Barrydale, *Ceratina* sp. nest., 10 Nov 1970, H. Daly, #148 UMMZ BMOC 79-1125-004.

Voucher specimens in EMEC, UMMZ. (tentative correlation, no HDNs known from these series)

Sennertia sp. 1.

Material. 5f, 4m - **SOUTH AFRICA:** "Cape Prov.", Worcester, Heatlie Farm, *Xylocopa* sp., nest, 20 Oct 1970, H. V. Daly, A37, UMMZ BMOC 79-1125-001. Voucher specimens in UMMZ.

Sennertia sp. 2. (*Senneria vaga*-group)

Material. 7 f (including 3 with developing larvae and prelarvae), 2m, TN, PN, L - **ARGENTINA**: "Córdova", ex *Centris* (*Paracentris*) *mourei* (as "*Centris nigrilabris* m. n."), no date, Davis, AMNH BMOC 04-0508-223. Voucher specimens in AMNH, UMMZ.

Specimens of the *Sennertia frontalis*-group misclassified by analysis (p. 111)

Material. 20HDNs - **BRAZIL: Santa Catarina**, Corupá, ex *Xylocopa brasilianorum*, 1 Dec 1953, A. Maller, USNM, BMOC 05-0420-077 (5 validation, originally classified as *shimanukii*, model showed that this is *augustii*); 12 HDNs - **MEXICO: Chiapas**, 4 mi SE Soyaló, ex *X. frontalis* under tegulae, 4 Jul 1956, J. W. McSwain, USNM, BMOC 05-0420-194 (4 validation, originally as *shimanukii* classified as *augustii*); 21HDNs - **EL SALVADOR**: Mt. San Salvador, ex *X. frontalis* 1st metasomal tergite, 8 Jul 1968, M. E. Erwin & D. Q. Cavagnaro, USNM, BMOC 05-0420-195 (validation, originally *shimanukii* classified as *augustii*); 23HDNs—**GUATEMALA**: Suchitepéquez, Finca Variedades, 500 ft., ex *X. fimbriata* on 1st metasomal tergite, 1 Jul 1947, F. Johnson, AMNH, BMOC 04-0508-315 (5 validation, classified as *augustii* (3), *frontalis* (2), and *shimanukii*)

APPENDIX 2. CHARACTERS USED IN PHYLOGENETIC RECONSTRUCTION OF CHAETODACTYLIDAE

Character Matrix

	1 10 20 30 40 50
Centriacarus turbator	000000101100000100000100000000000000001010000100001
Centriacarus guahibo	000100101100000100000100000000000000001010000100001
Roubikia panamensis	001-00001100001000000000000001101100002010100100101
Roubikia latebrosa	001-00001000001000000000000001101100002010100100101
Achaetodactylus ceratinae	111-01000110111110111000010112101211112101111111111
Achaetodactylus leleupi	111-01000110111110111000010112101211112110111111111
Ochaetodactylus decellei	111-?1000110111110111000010112111211112110111111111
Chaetodactylus melitomae	010010001111111111011111110012101211112110111111110
Chaetodactylus ludwigi	010010001111111011011111111012101211112110111111110
Chaetodactylus osmiae	010010001111111011011111111112101211112110111111110
Sennertia zhelochovtsevi	011-1--11111111110111110111112101211112101111011111

? = unknown and - = non-applicable characters; characters 4, 10, and 32 are parsimony uninformative.

Character List

1. Gnathosomal solenidion: 0) present; 1) absent
2. Setae on free palpi: 0) present; 1) absent
3. Free palpi: 0) present; 1) absent
4. Free palpi: 0) longer than width at base; 1) shorter than width at base
5. Alveoli *ve*: 0) dorsal, distinctly anterior to *se*; 1) dorsal, approximately at level of *se*; 2) ventral
6. Prodorsal shield striation: 0) longitudinal anteriorly and transverse posteriorly; 1) longitudinal; 2) absent
7. Posterior edge of prodorsal shield: 0) longer than lateral edges; 1) shorter than or nearly equal to lateral edges
8. Prodorsal shield: 0) present; 1) absent
9. Setae *se* situated: 0) on prodorsal shield; 1) on soft cuticle
10. Setae *si*: 0) at least twice as long as *se*; 1) less than twice as long as *se*
11. Setae c_2 situated: 0) on same transverse level as c_1; 1) distinctly anterior to level of c_1
12. Setae e_2 situated: 0) on hysterosomal shield; 1) outside hysterosomal shield or touching it
13. Setae *1a* and *3a*: 0) touching posterior borders of respective coxal fields and filiform (conoids in outgroup); 1) Setae *1a* and *3a* not touching posterior borders of respective coxal fields, if touching then inflated and elongated
14. Cupules *ia* situated: 0) on hysterosomal shield; 1) outside hysterosomal shield
15. Cupules *im* situated: 0) at level of bases of legs III, approximately at middle of line connecting d_2 and e_2; 1) distinctly posterior to bases of legs III, laterad of line connecting d_2 and e_2
16. Cupules *im*: 0) ventral, ventro-lateral; 1) dorsal
17. Cupules *ip*: 0) anterior to setae f_2; 1) posterior to setae f_2
18. Cupules *ih* situated: 0) on sides of attachment organ; 1) incorporated into lateral sclerotized borders of attachment organ
19. Posterior part of posterior apodemes of coxal fields II: 0) not displaced posteriorly to anterior apodemes III; 1) displaced posteriorly to anterior apodemes III
20. Coxal fields III: 0) closed; 1) open
21. Coxal fields IV: 0) closed; 1) open
22. Transverse medial extension of posterior apodemes IV: 0) well-developed; 1) absent
23. Anterior extension of posterior apodemes IV: 0) present, connecting with anterior apodeme III; 1) absent or not connecting
24. Ventral longitudinal sclerites of progenital chamber at posterior part: 0) conspicuous; 1) inconspicuous
25. Ventral longitudinal sclerites of progenital chamber at anterior part: 0) conspicuous; 1) inconspicuous
26. Posterior and lateral cuticular suckers (Fig. 8 *A*): 0) present; 1) absent
27. Suckers ad_3 (excluding transparent margin): 0) larger than inner unsclerotized area of suckers ad_{1+2}; 1) smaller or nearly equal to inner unsclerotized area of suckers ad_{1+2}
28. Anterior cuticular suckers (Fig. 8 *A*): 0) present; 1) vestigial or absent
29. Bases of anterior cuticular suckers: 0) inserted on separate apodemes (may touch or overlap posterio-lateral sclerotized border of the attachment organ) (Fig. 8 *A*, *C*); 1) incorporated into the border (Fig. 8 *D*)
30. Apodemes of ps_1: 0) separated; 1) partially fused anteriorly; 2) completely fused
31. Setae *wa* and *f* I–II: 0) *wa* I–II submedial, *f* I–II apical, near tarsal apices; 1) *wa* I–II apical or subapical, *f* I–II at level or proximal to *wa* I–II and far from tarsal apices
32. Solenidion ω_2: 0) present; 1) absent
33. Empodial claws I–III: 0) not twisted; 1) twisted
34. Dorsal cuticular folds of ambulacra I–III: 0) absent (Fig. 17 *J*); 1) weakly developed, with distal part smaller than proximal (Fig. 17 *H*); 2) well-developed, with distal part distinctly larger than any of proximal folds (Fig. 17 *C*)
35. Condylophores of tarsi I–III: 0) weakly developed, almost symmetrical; 1) well-developed, distinctly asymmetrical - anterior longer, posterior shorter, incorporated into posterio-lateral lobe
36. Supporting sclerites of condylophores (latero-apical sclerites of tarsus): 0) indistinct from the tarsus, not connected

by dorsal bridge (Fig. 17 *G*, *J*); 1) distinct from the tarsus, connected by dorsal bridge (Fig. 17 *C*)

37. Disto-dorsal lobe of distal part of caruncle (Fig. 17 *B*): 0) absent; 1) present, well developed
38. Dorsal condylar plate of femur-tibia joint (Fig. 17 *A*): 0) broad; 1) absent or indistinct
39. Tarsi I–II with: 0) 8 setae (*e* present); 1) 7 setae (*e* absent, *p* and *q* present); 2) 5 setae (*e*, *p*, and *q* absent)
40. Tarsal setae *ra* and *la* I–II: 0) foliate; 1) simple or spiniform
41. Genual seta *cG* I : 0) distinctly shorter than genu I and unmodified; 1) longer or slightly shorter than genu I and modified
42. Genual setae: 0) *cG* I longer than *cG* II; 1) *cG* I–II subequal
43. Tarsal setae *q* III: 0) present; 1) absent
44. Tarsal setae *w*, *r*, and *p* III: 0) present; 1) absent
45. Tarsal seta *s* III: 0) foliate; 1) simple
46. Sigma III: 0) present; 1) absent, represented by alveolus
47. Tarsus IV with: 0) 8 setae (*s*, *p*, *q* present); 1) maximum 5 setae (*s*, *p*, *q* always absent)
48. Tarsal setae *e*, *f* IV: 0) foliate or slightly lanceolate; 1) simple or absent
49. Tarsal setae w IV: 0) longer than leg IV; 1) distinctly shorter than leg IV or absent
50. Tibial setae *kT* IV: 0) present; 1) absent
51. Solenidion ϕ IV: 0) present; 1) absent, represented by alveolus

APPENDIX 3. CHARACTERS USED IN PHYLOGENETIC RECONSTRUCTION OF *CHAETODACTYLUS*

Character Matrix

	1 10 20 30 40 50 60
Centr. turbator	0000400-31210100000000011000101001000000100010000000200100210000000
A. ceratinae	0020210-10210000101000022020001001100110010011000100211-14020000000
melitomae	0000000-10110100A00000000021100000100110010011000A00000000011111111
anthidii	0100100-10010101A00000011011100110000111111101001100101000201111111
zachvatkini	0100000-10010101100000011001100011000011111101001100101000201111111
reaumuri	0100100-20010101101000011001101111001111111101001100100001201111111
osmiae	0100300-20010101000000011001101111001111111101001100101000201111111
nipponicus	0100100-20010101000000011001101111001111111101001100101000201111111
claudus	0100100-10010101001000011001100110001111111101001100101000201111111
birulai	0100100-20010101000000011021101111001111111101001100100013A1111111
hirashimai	0100000-20010001000010011001100010001111111101A011001000003011111111
hopliti	0100100-2001000100011111001100110021111111101A011001000003011111111
krombeini & *claviger*	0100100-20010001000111211A011011100211111111011011001000003011111111
chrysidis	0100010-10010001100000011000001111000111111101001100111-0030111111
micheneri	0100000-00010101111000001000000A11001011111101001100101010011111111
rozeni	0100000-00010101101000001000001111010111111101001100101010011111111
azteca	0100000-10010111001000001011100010000000110001000000101010001111111
sp. 1	0000000-00010101100000000100110001010001001000100010010101001111111
sp. 2	0000000-00010101A0100000100110001012001001100101010010101000111111
lassulus	0011011-00011111A010000010011100101100000010110101001010 2-01111111
ludwigi & *dalyi*	1000100-20010111000000000102110101110000000000000000001000102401111111
dementjevi	0000100-31010100101000001021100010120010000001000100100010001111111
furunculus	1020100-31201110100000000102000001010000000000110001101010100011111111
antillarum	1000100-31201110000000000102110001012000000000011000A000010100011111111
kouboy	0000100-41010101101000001021100010100010010001000100101023011111111
gibbosi	0000100131000100001000000102110001010000000000010001001010100111111111
lithurgi & *abditus*	00001000310001000010000001021100010100000000000100010010 10BC011111111

A = 0,1; B = 1,2; C = 0,3; - = non-applicable. Unreliable characters 8, 16, 17, 19, 31, 34, 39, and 42 were excluded fom the analysis. Characters 3, 4, 7, 18, 23, 25, 26, 30, 51, and 52 are parsimony-uninformative. Characters 61–67 are invariable within the genus *Chaetodactylus*. Undescribed species: *Ch*. sp. 1- ex *Diadasia chilensis* (Chile); *Ch*. sp. 2 - ex *Anthidium espinosai* (Chile) (see also Appendix 1).

Character List

1. Longitudinal sclerites on rostral projection (extensions of coxal apodemes I): 0) well sclerotized, distinct; 1) weakly sclerotized, indistinct
2. Longitudinal sclerites on rostral projection (extensions of coxal apodemes I): 0) separated by distinct space and diverging posteriorly (Fig. 56 *B*); 1) touching or almost touching each other medially, not diverging (Fig. 66 *B*)
3. Alveoli *ve* situated: 0) on prodorsal shield or touching it; 1) outside prodorsal shield; 2) absent
4. Prodorsal shield: 0) extends anterior *se*; 1) not extending anteriorly *se*
5. Prodorsal shield: 0) transversely striated; 1) with pattern of short transverse lines; 2) longitudinally striated; 3) with lens-like transverse pattern; 4) with reticulate pattern longitudinal anteriorly and transverse posteriorly
6. Lateral angles of prodorsal shield: 0) not attenuated; 1) attenuated

7. Setae *si* situated: 0) on prodorsal shield; 1) outside prodorsal shield
8. Ratio of length of prodorsal shield/length of seta d_1: 0) 2.4–4.4 (3.2 ± 0.43); 1) 4.7–7.3 (5.8 ± 0.70)
9. Hysterosomal shield, except for anterio-lateral part: 0) longitudinally striated, most lines longer than half of length of hysterosomal shield; 1) longitudinally striated, most lines long but shorter than half of hysterosomal shield; 2) with pattern of short longitudinal lines; 3) linear pattern indistinct because of reticulate pattern; 4) linear and reticular patterns present
10. Reticulate pattern of hysterosomal shield: 0) absent; 1) present
11. Lateral hysterosomal sclerites: 0) ventro-lateral, with anterior end situated at anterior level of coxal apodemes III and posterior end near attachment organ; 1) dorsal, split onto three small separate sclerites, one of them posterior to cupule *im*, and two anterior; 2) absent
12. Longest dorsal setae: 0) slightly pectinate at tips; 1) smooth
13. Setae c_1 situated: 0) on hysterosomal shield; 1) outside hysterosomal shield
14. Setae c_2 situated: 0) on prodorsal shield; 1) outside prodorsal shield
15. Setae d_2 situated: 0) on hysterosomal shield; 1) outside hysterosomal shield
16. Setae c_p: 0) distinctly anterior to level of c_2; 1) almost on same transverse level of c_2 (distance between them usually not exceeding 2 diameters of bases of c_2)
17. Setae *si*: 0) longer than 1/2 of distance between their bases; 1) shorter than 1/2 of distance between their bases
18. Setae h_3: 0) shorter than combined length of femur, genu, and tibia I; 1) longer than combined length of femur, genu, and tibia I
19. Setae h_1: 0) slightly or distinctly shorter than e_1; 1) nearly of same length with e_1
20. Coxal setae *1a*: 0) filiform; 1) distinctly inflated at bases
21. Coxal setae *1a* situated: 0) on soft cuticle; 1) on sclerite fused with anterior apodemes II
22. Coxal setae *3a* and *4b* situated: 0) on soft cuticle; 1) on sclerites
23. Sclerites surrounding alveoli of coxal setae *3a* and *4b*: 0) absent; 1) small, ring-like, sclerite of *3a* not fused to anterior apodeme IV; 2) large, irregular in shape, sclerite of *3a* fused to anterior apodeme IV
24. Ventral setae *4b*: 0) short, at least 2 times shorter than *3a*; 1) as long as *3a* or less than 2 times shorter; 2) longer than *3a*
25. Coxal setae *4a*: 0) more than 2 times shorter than *3a*; 1) almost as long as *3a*; 2) longer than *3a*
26. Sternal apodeme: 0) not bifurcated posteriorly; 1) bifurcated posteriorly
27. Posterior apodeme II: 0) present, exceeding 1/2 of lateral edge of sternal shield; 1) present, equal or less than 1/2 of lateral edge of sternal shield; 2) absent, or if present, interrupted anteriorly
28. Proximal acetabular extensions IV: 0) connected; 1) disjunct
29. Distal acetabular extensions of apodemes IV: 0) connected; 1) disjunct
30. Longitudinal striation between coxae III–IV: 0) absent; 1) present
31. Attachment organ width (including transparent margin): 0) distinctly shorter than distance between *4a*; 1) equal or exceeding distance between *4a*
32. Lateral “horns” of attachment organ lateral sclerites: 0) not reaching level of *4a*; 1) reaching level of *4a*
33. Suckers ad_3 (excluding transparent margin): 0) larger than inner unsclerotized area of suckers ad_1+2; 1) smaller or nearly equal to inner unsclerotized area of suckers ad_{1+2}
34. Anterior edge of ps_2 bases: 0) posterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}; 1) anterior to posterior edge of inner unsclerotized area of suckers ad_{1+2}
35. Semicircular sclerite distal to base of *wa* I–II: 0) absent; 1) present
36. Solenidion σ I: 0) from 0.3 to 0.6 of genu I; 1) shorter than 0.3 of genu I; 2) exceeding 0.6 of genu I
37. Setae *mG* and usually *cG* I: 0) shorter or equal to combined length of genu and tibia I; 1) longer than combined length of genu and tibia I
38. Genual setae *cG* I: 0) pectinate; 1) smooth
39. Genual setae *mG* I: 0) pectinate; 1) smooth
40. Genual setae *mG* II : 0) shorter than combined length of femur, tibia, and genu II; 1) nearly equal or exceeding combined length of femur, tibia, and genu II
41. Femoral setae *vF* II: 0) distinctly shorter than combined length of femur, tibia, and genu II; 1) nearly equal or longer than combined length of femur, tibia, and genu II
42. Genual setae *mG* II: 0) pectinate; 1) smooth
43. Genual setae *mG* II: 0) slightly longer or shorter than *mG* I; 1) distinctly longer than *mG* I
44. Genual setae *mG* II: 0) shorter or nearly equal to *vF* II; 1) longer than *vF* II
45. Solenidia ω_1 and ω_3: 0) close to each other, distance less than 3 diameters of alveolus of famulus ε; 1) distinctly separated, distance exceeds 3 diameters of alveolus of famulus ε
46. Tarsal setae *la* I–II: 0) lanceolate; 1) filiform
47. Tarsal setae *wa* I–II: 0) filiform, slightly widened at base; 1) spiniform
48. Ventral side of claws I–III (visible only at high magnification): 0) smooth; 1) finely striated
49. Genual setae *nG* III: 0) at most reaching base of tarsus III; 1) clearly extending beyond base of tarsus III
50. Seta *nG* III: 0) pectinate; 1) smooth
51. Solenidion σ III: 0) absent; 1) present but vestigial
52. Seta *s* III: 0) subapical; 1) submedial
53. Solenidion ϕ IV: 0) longer than genu IV; 1) shorter than genu IV; 2) absent
54. Tarsal seta *s* IV: 0) present; 1) absent
55. At least one setae of *w* or *s* IV: 0) longer than 1.5 of maximum width of tarsus IV; 1) shorter than 1.5 of maximum width of tarsus IV

56. Tarsal setae *w* and *s* IV: 0) uniform in length and width; 1) not-uniform, w at least 1.5 times shorter than *s*
57. Tarsal setae *f* (and often *e* IV): 0) longer than tarsus IV; 1) shorter than tarsus IV; 2) absent
58. Tarsal setae *f* and *e* IV: 0) symmetric, nearly equal; 1) asymmetric, *f* distinctly shorter than *e* IV; 2) asymmetric, *e* distinctly shorter than *f* IV; 3) both absent; 4) *e* absent
59. Tarsal setae *e* IV: 0) uniform in length and width with *w* and *s* IV, or absent; 1) distinctly longer than *w* and *s* IV, shorter than tarsus IV; 2) longer than tarsus IV; 3) longer than legs IV; 4) microsetae, at least 2 times shorter than *f* IV
60. Tarsus IV: 0) more than 2 times longer than its basal width; 1) 1.5–2.0 times longer than its basal width; 2) as long as its width
61. Setae e_2 situated: 0) on hysterosomal shield; 1) outside hysterosomal shield or touching it
62. Transverse medial extension of posterior apodemes IV: 0) well-developed; 1) absent
63. Alveoli *ve*: 0) dorsal, distinctly anterior to *se*; 1) dorsal, approximately at level of *se*; 2) ventral
64. Ventral longitudinal sclerites of progenital chamber at anterior part: 0) conspicuous; 1) inconspicuous
65. Ventral longitudinal sclerites of progenital chamber at posterior part: 0) conspicuous; 1) inconspicuous
66. Cupules *ih* situated: 0) on sides of attachment organ; 1) incorporated into lateral sclerotized borders of attachment organ
67. Solenidion ϕ IV: 0) present; 1) absent, represented by alveolus

APPENDIX 4. CHARACTERS USED IN PHYLOGENETIC RECONSTRUCTION OF *SENNERTIA*

Character Matrix

	1 5 10 15
Roubikia	000011100200110
Achaetodactylus decellei	000011100000010
zhelochovtsevi	011011100000001
surinamensis	100011101100011
devincta	100011100100101
ignota	001011100000001
loricata	001011100100001
argentina	011011101100001
Asiosennertis delfinadoae	011000001100001
Afrosennertia queenslandica	011100001111001
Afrosennertia jeanalexi	011100001111001
cerambycina	100000001100001
bifida	100000001100011
alfkeni	100000001100101
horrida	100010111100101
potanini	000010111100001

Character 15 is invariable within *Sennertia*.

Character List

1. Anterior border of hysterosomal shield: 0) posterior to halfway between *si* and c_1; 1) at least halfway between *si* and c_1, or more anterior
2. Lateral edges of hysterosomal shield in anterior part: 0) not narrowing; 1) distinctly narrowing
3. Setae c_1 situated : 0) on hysterosomal shield; 1) outside hysterosomal shield (or touching it)
4. Setae d_1 situated: 0) on hysterosomal shield; 1) outside hysterosomal shield
5. Setae *si*: 0) microsetae, distinctly shorter *se*; 1) long, minimum 1/3 of *se*
6. Setae *si*: 0) microsetae, distinctly shorter and thinner than *se*; 1) exceeding 1/2 of *se*
7. Setae *si*: 0) distinctly thinner than *se*; 1) as thick or almost as thick as *se*
8. Setae *si*: 0) distinctly posterior *se*; 1) on the same level or slightly anterior or posterior to *se*
9. Setae c_1: 0) long, nearly as long as *se*; 1) microsetae
10. Setae d_1 and e_1: 0) distinctly longer than h_1; 1) nearly as long as h_1; 2) d_1 distinctly longer than e_1 and h_1
11. Solenidion ω_3: 0) closer to *f* I than to ω_1; 1) closer to ω_1 than to *f* I
12. Tarsus IV: 0) not enlarged, shorter or less than 2 times longer than width of trochanter IV; 1) enlarged, more than 2 times longer than width of trochanter IV
13. Setae *w* IV: 0) thinner than *d* IV and distinctly shorter than leg IV; 1) almost 1/2 of *d* IV width, distinctly longer than leg IV
14. Legs IV: 0) extending beyond posterior edge of hysterosoma; 1) not extending beyond posterior edge of hysterosoma
15. Setae c_2 situated: 0) on same transverse level as c_1; 1) distinctly anterior to level of c_1

APPENDIX 5. MORPHOMETRIC ANALYSIS OF THE *SENNERTIA FRONTALIS* COMPLEX

Table 14. Measurements (range, mean ± standard deviation) of 5 putative groups of heteromorphic deutonymphs belonging to the *Sennertia frontalis* complex. Three groups found by PCA are in parenthesis.

	Structure	*shimanukii* (1)	USA (1)	ex *nautlana* (2)	*frontalis* (2)	*augustii* (3)
abc	idiosoma, length	212–306, 248 ± 26[p]	207–312, 254 ± 27[aq]	195–254, 229 ± 14[t]	208–287, 238 ± 17[y]	195–314, 258 ± 28[ag]
abc	idiosoma, width	160–233, 190 ± 21[p]	175–251, 209 ± 21[aq]	152–198, 178 ± 12[t]	176–232, 200 ± 14[y]	152–269, 213 ± 29[ag]
abc	hyst shield, length	148–218, 174 ± 18[p]	156–229, 185 ± 21[aq]	139–181, 158 ± 9[t]	150–187, 170 ± 10[y]	160–231, 191 ± 21[ag]
ab	hyst shield, width anterior	71–115, 90 ± 13[p]	72–132, 95 ± 15[aq]	71–95, 83 ± 6[t]	69–103, 89 ± 8[y]	63–135, 100 ± 20[ag]
ab	hyst shield, width at f_2 level[1]	75–115, 92 ± 12[p]	75–127, 99 ± 14[aq]	68–95, 83 ± 6[t]	73–106, 90 ± 7[y]	74–143, 105 ± 16[ag]
abc	gnathosomal solenidion	1–2, 2 ± 0[o]	1–3, 2 ± 0[aq]	1–1, 1 ± 0[t]	1–2, 1 ± 0[y]	1–3, 2 ± 1[ag]
a	sternum	22–32, 25 ± 4[e]	22–26, 24 ± 1[j]	23–30, 27 ± 3[e]	23–30, 28 ± 3[e]	23–33, 29 ± 4[f]
a	apodeme II	43–62, 52 ± 7[e]	42–54, 46 ± 3[j]	40–54, 48 ± 5[e]	48–55, 51 ± 3[e]	50–63, 57 ± 5[f]
a	posterior apodeme II	33–44, 38 ± 4[d]	33–42, 36 ± 3[j]	30–41, 36 ± 4[e]	39–48, 44 ± 4[e]	39–50, 45 ± 4[f]
a	apodeme III	24–28, 27 ± 2[e]	23–29, 25 ± 2[j]	23–27, 25 ± 2[e]	23–29, 26 ± 2[e]	25–32, 29 ± 2[f]
a	apodeme IV	41–53, 47 ± 4[e]	42–53, 48 ± 3[j]	41–49, 44 ± 3[e]	43–50, 47 ± 3[e]	48–59, 55 ± 4[f]
a	*vi*	5–11, 7 ± 2[e]	6–8, 7 ± 1[j]	4–6, 6 ± 1[e]	5–7, 6 ± 1[e]	6–7, 7 ± 1[f]
a	*si*	49–55, 52 ± 3[e]	40–56, 51 ± 5[j]	47–63, 54 ± 6[e]	49–61, 55 ± 5[e]	59–73, 69 ± 5[f]
a	*se*	41–52, 48 ± 4[e]	41–51, 47 ± 4[j]	36–54, 45 ± 7[e]	41–53, 48 ± 4[e]	46–75, 61 ± 8[l]
a	c_1	44–47, 46 ± 1[e]	42–53, 46 ± 3[j]	45–58, 53 ± 5[e]	44–55, 51 ± 4[e]	54–66, 61 ± 4[f]
a	c_2	48–56, 52 ± 4[e]	49–61, 55 ± 4[j]	43–58, 53 ± 6[e]	50–60, 54 ± 4[e]	50–82, 67 ± 9[l]
abc	c_3	20–29, 24 ± 3[p]	21–38, 29 ± 4[aq]	23–35, 29 ± 3[t]	26–38, 31 ± 4[y]	24–40, 32 ± 5[ag]
a	c_p	46–55, 51 ± 3[e]	46–59, 52 ± 4[j]	33–54, 46 ± 8[e]	46–60, 52 ± 6[e]	51–71, 64 ± 8[f]
a	d_1	4–8, 6 ± 2[e]	4–5, 5 ± 0[j]	4–6, 5 ± 1[e]	4–5, 4 ± 1[e]	3–8, 6 ± 2[f]
abc	d_2	59–86, 68 ± 7[p]	57–95, 78 ± 10[aq]	52–85, 64 ± 8[t]	53–86, 67 ± 9[y]	59–104, 84 ± 10[ag]
a	e_1	6–8, 7 ± 1[e]	4–7, 5 ± 1[j]	3–6, 5 ± 1[e]	3–5, 4 ± 1[e]	4–7, 5 ± 1[f]
abc	e_2	59–84, 68 ± 7[p]	61–94, 78 ± 9[ap]	48–81, 61 ± 8[t]	50–89, 65 ± 10[y]	59–99, 82 ± 10[ag]
a	f_2	4–7, 6 ± 1[e]	4–7, 5 ± 1[j]	5–6, 5 ± 1[e]	4–5, 4 ± 0[e]	6–8, 7 ± 1[f]
a	h_1	4–6, 5 ± 1[e]	3–5, 4 ± 1[j]	3–5, 4 ± 1[e]	3–5, 4 ± 1[e]	3–7, 5 ± 1[f]
a	h_2	5–8, 7 ± 1[e]	4–7, 6 ± 1[j]	5–7, 6 ± 1[e]	4–7, 5 ± 1[e]	7–9, 8 ± 1[f]
a	h_3	47–61, 53 ± 6[e]	41–50, 44 ± 3[i]	39–44, 42 ± 3[c]	46–52, 49 ± 3[e]	52–66, 61 ± 6[e]
	1a	75–78, 77 ± 2[b]	52–71, 60 ± 9[d]	65–72, 68 ± 5[b]	69–72, 70 ± 2[b]	64–75, 69 ± 8[b]
a	*4b*	13–17, 15 ± 1[e]	14–17, 16 ± 1[j]	16–20, 18 ± 1[e]	16–21, 19 ± 2[e]	17–19, 18 ± 1[f]
	3a	57[a]	53–77, 64 ± 9[i]	54–80, 67 ± 11[d]	62–86, 72 ± 9[e]	78–88, 83 ± 7[b]
a	*4a*	16–20, 18 ± 1[e]	16–19, 17 ± 1[j]	17–23, 19 ± 2[e]	17–20, 18 ± 2[e]	18–23, 20 ± 2[f]
a	*g*	10–14, 12 ± 1[e]	11–15, 13 ± 1[j]	11–15, 13 ± 1[e]	13–15, 13 ± 1[e]	13–14, 14 ± 0[f]
a	length of attachment organ[2]	34–43, 39 ± 3[e]	32–39, 35 ± 2[j]	28–36, 33 ± 3[e]	34–39, 36 ± 2[e]	38–47, 43 ± 3[f]
a	width of attachment organ[3]	48–57, 54 ± 4[e]	45–53, 49 ± 3[j]	39–51, 46 ± 4[e]	44–54, 50 ± 4[e]	51–63, 57 ± 4[f]
a	anterior sucker (ad_3)[3]	6–9, 8 ± 1[e]	6–8, 7 ± 1[j]	6–7, 6 ± 1[e]	6–8, 7 ± 0[e]	7–9, 9 ± 1[f]
a	median shield (ad_1+ad_2, ad_3)	13–16, 14 ± 1[e]	12–14, 13 ± 1[j]	11–13, 12 ± 1[e]	11–13, 12 ± 1[e]	13–18, 15 ± 1[f]
abc	anterior lateral conoid (ps_2)	6–9, 7 ± 1[p]	6–9, 7 ± 1[aq]	5–6, 6 ± 0[s]	5–7, 6 ± 1[y]	5–8, 7 ± 1[ag]
a	posterior lateral conoid (ps_1)	7–9, 8 ± 1[e]	6–8, 7 ± 1[j]	7–8, 7 ± 1[e]	7–8, 8 ± 0[e]	8–9, 8 ± 1[f]
a	leg I	90–115, 101 ± 9[e]	82–111, 97 ± 9[j]	85–100, 91 ± 6[e]	93–107, 100 ± 6[e]	98–134, 118 ± 13[f]
a	tarsus I	27–34, 30 ± 3[e]	24–33, 27 ± 3[j]	23–27, 25 ± 2[e]	26–28, 27 ± 1[e]	26–41, 34 ± 5[f]
a	empodium I	15–26, 20 ± 4[e]	14–18, 16 ± 1[i]	14–21, 17 ± 2[e]	15–28, 21 ± 5[e]	13–25, 20 ± 5[f]
a	ω_1 I	13–17, 15 ± 1[e]	14–16, 15 ± 1[i]	13–14, 13 ± 0[c]	12–16, 15 ± 2[e]	14–20, 17 ± 2[f]
	ω_2 I	7–12, 9 ± 2[e]	6–9, 8 ± 1[f]	6–6, 6 ± 0[b]	5–7, 6 ± 1[e]	9–12, 10 ± 1[d]
a	ω_3 I	32–48, 40 ± 6[e]	32–41, 37 ± 3[j]	29–43, 36 ± 5[e]	32–45, 39 ± 5[e]	38–54, 49 ± 6[f]
a	*ε* I	3–5, 4 ± 1[e]	3–5, 3 ± 1[j]	2–3, 3 ± 0[d]	3–4, 4 ± 0[d]	3–4, 4 ± 1[f]
a	*f* I	35–51, 43 ± 6[e]	33–48, 39 ± 5[j]	33–54, 42 ± 11[c]	36–55, 45 ± 7[e]	33–54, 44 ± 8[f]
ab	*d* I	68–105, 80 ± 11[p]	56–109, 83 ± 14[aq]	56–91, 70 ± 9[t]	56–100, 80 ± 11[y]	58–114, 85 ± 14[ac]
a	*ra* I	11–13, 11 ± 1[e]	9–13, 11 ± 1[j]	11–13, 12 ± 1[d]	11–15, 13 ± 1[e]	9–16, 13 ± 3[f]
a	*la* I	9–10, 10 ± 0[e]	7–10, 9 ± 1[j]	7–9, 8 ± 1[d]	9–11, 10 ± 0[e]	10–12, 11 ± 1[f]
a	*wa* I	7–8, 7 ± 1[e]	6–9, 8 ± 1[j]	6–10, 7 ± 1[e]	7–9, 8 ± 1[e]	7–10, 9 ± 1[f]
	gT I	10–12, 11 ± 1[d]	9–11, 10 ± 1[g]	8–10, 9 ± 1[c]	10–13, 12 ± 2[c]	10–13, 12 ± 1[f]
a	*hT* I	7–10, 9 ± 1[e]	6–8, 7 ± 1[i]	4–10, 7 ± 3[d]	6–10, 9 ± 2[e]	8–11, 9 ± 1[f]
	ϕ I	63 ± 0[b]	71–74, 72 ± 2[b]	66–74, 69 ± 4[c]	61–72, 67 ± 6[d]	
a	*mG* I	34–46, 42 ± 5[e]	33–41, 37 ± 3[j]	35–48, 39 ± 5[e]	33–48, 41 ± 5[e]	40–58, 51 ± 7[f]
a	*cG* I	8–11, 10 ± 1[e]	7–9, 8 ± 1[j]	7–13, 9 ± 3[e]	6–11, 8 ± 2[e]	7–11, 9 ± 1[e]
abc	*σ* I	11–19, 15 ± 2[p]	11–22, 17 ± 3[aq]	9–17, 12 ± 2[s]	9–17, 13 ± 2[y]	10–20, 16 ± 2[ad]
a	*vF* I	43–53, 48 ± 4[e]	40–49, 44 ± 3[j]	38–49, 43 ± 4[e]	43–48, 46 ± 2[e]	44–55, 51 ± 4[f]
	pR I	73–83, 78 ± 7[b]	67–83, 74 ± 6[g]	67–74, 71 ± 4[c]	66–80, 73 ± 10[b]	91–100, 95 ± 7[b]
a	leg II	85–109, 97 ± 9[e]	87–107, 96 ± 7[j]	83–107, 93 ± 9[e]	88–105, 96 ± 6[e]	94–127, 114 ± 13[f]

(continued)

Table 14. (Continued)

	Structure	***shimanukii* (1)**	**USA (1)**	**ex *nautlana* (2)**	***frontalis* (2)**	***augustii* (3)**
a	tarsus II	23–32, 28 ± 4^{e}	24–31, 27 ± 2^{j}	23–28, 26 ± 3^{e}	26–30, 28 ± 2^{e}	26–35, 33 ± 4^{f}
a	empodium II	16–25, 20 ± 4^{e}	13–18, 16 ± 2^{h}	14–23, 17 ± 4^{e}	15–21, 18 ± 3^{e}	15–30, 24 ± 5^{f}
a	ω_1 II	19–23, 21 ± 2^{e}	17–23, 20 ± 2^{j}	17–20, 18 ± 2^{b}	16–21, 19 ± 2^{e}	20–24, 23 ± 2^{f}
a	*f* II	40–53, 47 ± 5^{e}	39–52, 45 ± 4^{j}	36–55, 45 ± 8^{d}	37–57, 48 ± 7^{e}	36–61, 53 ± 9^{f}
a	*d* II	72–103, 89 ± 12^{e}	70–94, 82 ± 8^{i}	57–97, 75 ± 15^{e}	73–94, 86 ± 8^{e}	61–104, 88 ± 15^{f}
abc	*ra* II	9–14, 12 ± 1^{p}	9–15, 12 ± 1^{ap}	11–15, 12 ± 1^{t}	10–18, 13 ± 2^{x}	9–17, 14 ± 2^{af}
a	*la* II	7–10, 9 ± 1^{e}	8–11, 9 ± 1^{j}	8–9, 8 ± 0^{e}	9–11, 10 ± 1^{e}	9–11, 10 ± 1^{f}
a	*wa* II	7–9, 8 ± 1^{e}	7–9, 8 ± 1^{j}	7–9, 8 ± 1^{e}	7–9, 8 ± 1^{e}	8–10, 9 ± 1^{f}
	gT II	9–11, 10 ± 1^{d}	8–11, 9 ± 1^{i}	8^{a}	7–11, 9 ± 2^{d}	8–13, 11 ± 2^{f}
a	*hT* II	7–10, 9 ± 1^{e}	6–9, 7 ± 1^{i}	4–7, 6 ± 1^{e}	8–10, 9 ± 1^{e}	6–13, 9 ± 2^{f}
	ϕ II	49–61, 56 ± 5^{e}	48–63, 56 ± 6^{f}	55^{a}	54–74, 61 ± 9^{d}	
abc	*mG* II	64–90, 75 ± 8^{p}	51–97, 76 ± 12^{ao}	65–104, 78 ± 10^{s}	71–111, 85 ± 9^{y}	61–116, 89 ± 15^{ab}
a	*cG* II	7–8, 8 ± 1^{e}	7–11, 9 ± 1^{i}	5–10, 7 ± 2^{d}	7–13, 9 ± 2^{e}	6–11, 9 ± 2^{f}
a	σ II	6–8, 7 ± 1^{e}	5–7, 6 ± 1^{i}	6–8, 7 ± 1^{d}	6–8, 7 ± 1^{e}	6–10, 8 ± 1^{f}
a	*vF* II	56–80, 70 ± 9^{e}	54–73, 63 ± 6^{j}	64–84, 72 ± 9^{d}	48–74, 65 ± 11^{e}	52–88, 74 ± 14^{e}
	pR II	66–89, 80 ± 9^{e}	63–81, 70 ± 8^{e}	78^{a}	77–97, 86 ± 10^{c}	77–105, 91 ± 14^{d}
a	leg III	70–86, 79 ± 7^{e}	73–91, 81 ± 6^{j}	70–82, 77 ± 5^{e}	78–90, 85 ± 5^{e}	85–122, 99 ± 15^{e}
a	tarsus III	22–29, 25 ± 3^{e}	22–29, 25 ± 3^{j}	21–26, 24 ± 2^{e}	24–28, 26 ± 2^{e}	27–38, 32 ± 5^{e}
a	empodium III	16–23, 19 ± 3^{e}	13–19, 16 ± 2^{i}	15–20, 17 ± 2^{e}	16–23, 20 ± 3^{e}	16–29, 23 ± 6^{d}
	d III	89–111, 97 ± 9^{e}	74–90, 84 ± 6^{e}	78–99, 91 ± 11^{c}	87–114, 102 ± 12^{e}	84–109, 100 ± 13^{c}
	e III	47–56, 51 ± 4^{e}	49–53, 51 ± 2^{f}	41–66, 50 ± 11^{d}	49–59, 54 ± 4^{e}	41–63, 50 ± 9^{d}
a	*f* III	36–44, 41 ± 3^{e}	34–49, 40 ± 5^{i}	34–64, 43 ± 12^{e}	37–59, 46 ± 8^{e}	37–69, 54 ± 12^{e}
a	*s* III	6–8, 7 ± 1^{e}	6–7, 7 ± 0^{j}	6–8, 7 ± 1^{e}	7–8, 7 ± 1^{e}	7–9, 8 ± 1^{e}
	kT III	8–11, 9 ± 1^{e}	6–10, 8 ± 1^{h}	7–9, 8 ± 1^{b}	8–11, 9 ± 1^{e}	7–13, 10 ± 2^{e}
a	ϕ III	15–23, 18 ± 3^{e}	14–23, 19 ± 3^{j}	15–20, 16 ± 2^{e}	15–18, 17 ± 1^{e}	17–26, 22 ± 4^{e}
a	*nG* III	9–20, 15 ± 4^{e}	9–15, 12 ± 2^{i}	10–16, 14 ± 2^{e}	12–18, 14 ± 2^{e}	10–18, 14 ± 3^{f}
a	σ III	4–6, 5 ± 1^{e}	3–6, 5 ± 1^{h}	3–5, 4 ± 1^{c}	4–6, 5 ± 1^{e}	5–7, 6 ± 1^{f}
	sR III	40–44, 42 ± 2^{e}	32–50, 37 ± 7^{h}	29–40, 34 ± 6^{c}	29–38, 35 ± 3^{e}	37–52, 45 ± 8^{c}
a	leg IV	42–49, 45 ± 3^{e}	44–51, 48 ± 3^{j}	39–48, 45 ± 3^{e}	46–49, 47 ± 1^{e}	49–62, 55 ± 4^{f}
a	tarsus IV	8–10, 9 ± 1^{e}	9–11, 10 ± 1^{j}	9–12, 10 ± 1^{e}	8–15, 11 ± 2^{e}	11–13, 12 ± 1^{f}
	d IV	269–358, 311 ± 31^{e}	261–339, 290 ± 26^{j}	294–330, 313 ± 18^{c}	284–384, 342 ± 43^{e}	327–376, 352 ± 35^{b}
	e IV	3–6, 5 ± 1^{d}	*3a*	5^{a}	2–4, 3 ± 1^{e}	3–6, 5 ± 1^{f}
	f IV	4–7, 5 ± 2^{c}	4–6, 5 ± 1^{d}	5–6, 5 ± 1^{c}		
abc	*w* IV	7–12, 9 ± 1^{p}	5–11, 8 ± 1^{aq}	10–20, 14 ± 3^{t}	9–14, 11 ± 2^{y}	7–16, 12 ± 2^{ag}
a	*s* IV	4–4, 4 ± 0^{d}	3–4, 4 ± 0^{j}	3–4, 4 ± 1^{c}	3–5, 4 ± 1^{d}	2–4, 4 ± 1^{m}
abc	*vF* IV	31–58, 42 ± 7^{o}	24–61, 41 ± 9^{aq}	42–54, 47 ± 4^{r}	35–54, 43 ± 5^{y}	34–71, 51 ± 9^{ag}

In first column: a = 74-variable dataset, b = 16-variable dataset, c = 13-variable subset; superscript: 1 = excluding bases of f_2; 2 = medial horn-posterior sclerotized end; 3 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . aa = 27 . . . aq = 43. hyst=hysterosomal.

Table 15. Best subset Canonical variates analyses on 16-variable/3 group data matrices.

Size	**Shape number**	**Classification accuracy**		**Log-shape number**	**Classification accuracy**	
		internal	**jackknife**		**internal**	**jackknife**
1	1	61.3	61.3	1	62.00	62.00
2	1	77.4	77.4	1	78.10	77.40
3	1	84.7	83.2	1	86.10	85.40
4	2	87.6	86.9	2	88.3–90.5	88.30
5	8	88.3–89.8	88.3	1	91.20	91.20
6	1	91.2	90.5	1	92.70	**92**^{c}
7	2	92–92.7	91.2	2	92.70	92.00
8	2	92.7	92	8	92–94.2	92.00
9	1	93.4	**92.7**^{a}	59	91.2–93.4	91.2
10	21	92–94.2	92	4	92.7–94.9	92.70
11	4	92.7–94.2	92.7	1	94.90	**93.4**^{b}
12	6	92.7–94.2	92.7	1	95.60	93.40
13	2	93.4	92.7	3	94.2–95.6	92.70
14	1	94.2	92.7	5	94.2–94.9	92.00
15	2	92.7–94.2	91.2	1	94.20	91.20
16	1	94.2	89.10	1	94.20	89.80

Optimal (a–b) and suboptimal (c) subsets: a = 1 3 6 7 10 12 13 14 16; b = 1 2 3 6 8 10 12 13 14 15 16; c = 1 7 8 9 15 16 (numbers identify variables as arranged on Table 14).

Table 16. Best subset analyses of 13-variable/2 group data matrices.

		Classification accuracy					
				External (n = 90)			
Optimal subsets[a]	**Analysis**[b]	**Internal**	**Jackknife**	**LR DM**	**LR DM_LN**	**CVA DM**	**CVA DM_LN**
4 5 6 7	LR DM	98.1	-	94.7	90.7	93.3	93.3
3 4 5 6	LR DM	97.1	-	94.7	94.7	93.3	94.7
3 4 5 6 7	LR DM	97.1	-	94.7	93.3	92	93.3
4 5 6	LR DM	97.1	-	94.7	93.3	96	93.3
3 4 5 6	LR DM_LN	97.1	-	94.7	94.7	93.3	94.7
4 5 6	CVA DM	96.2	94.2	94.7	93.3	96	93.3
4 5 6 9 11 12	CVA DM_LN	99	99	86.7	86.7	93.3	94.7
2 3 4 5 6 9 12	CVA DM_LN	99	99	88	84	93.3	94.7
2 4 5 6 9 11 12	CVA DM_LN	99	99	89.3	90.7	94.7	94.7
4 5 6 9 10 11 12	CVA DM_LN	99	99	89.3	86.7	94.7	94.7
4 5 6 9 11 12 13	CVA DM_LN	99	99	78.7	80	94.7	94.7
2 3 4 5 6 7 9 12	CVA DM_LN	99	99	90.7	86.7	92	94.7
2 4 5 6 9 10 11 12	CVA DM_LN	99	99	84	82.7	93.3	94.7
2 4 5 6 9 11 12 13	CVA DM_LN	99	99	86.7	89.3	94.7	94.7
4 5 6 7 9 11 12 13	CVA DM_LN	99	99	92	90.7	92	94.7
4 5 6 9 10 11 12 13	CVA DM_LN	99	99	90.7	86.7	93.3	94.7
2 4 5 6 7 9 10 11 12	CVA DM_LN	99	99	89.3	84	93.3	94.7
2 4 5 6 7 9 11 12 13	CVA DM_LN	99	99	89.3	90.7	90.7	94.7
2 4 5 6 9 10 11 12 13	CVA DM_LN	99	99	88	89.3	93.3	94.7
4 5 6 7 9 10 11 12 13	CVA DM_LN	99	99	90.7	90.7	93.3	94.7
3 4 5 6	CVA DM_LN	97.1	97.1	94.7	94.7	93.3	94.7
1 3 4 5 6	CVA DM_LN	97.1	97.1	92	92	93.3	94.7
4 5 6 7 10 11	CVA DM_LN	96.2	96.2	88	92	93.3	94.7

a - numbers identify variables as arranged on Table 14; subsets with maximal hit rate for all analyses are underlined. b - LR = Logistic regression; CVA = Canonical variates analysis, DM = Darroch and Mosimann shape variables, DM_LN = log-transformed (base e) DM variables.

Table 17. Three-group Canonical variates analyses: Loadings, unstandardized function coefficients, and constants.

	Loadings		Coefficients	
Variable[a]	**CV1**	**CV2**	**CV1**	**CV2**
σ I	−0.511	0.183	−10.313	12.43
w IV	0.465	0.067	12.815	12.143
c_3	0.373	0.218	7.422	7.99
mG II	0.33	0.099	1.744	2.684
gnathosomal solenidion	−0.306	−0.3	−15.471	69.206
vF IV	0.277	−0.138	1.702	0.815
ra II	0.251	0.036	7.904	−1.2
idiosoma, length	−0.078	0.567	−0.997	2.663
idiosoma, width	−0.06	0.386	1.051	0.829
e_2	−0.287	−0.352	0.018	−0.42
d_2	−0.208	−0.348	0.66	−1.291
anterior lateral conoid (ps_2)	−0.312	0.318	−8.163	56.011
hysterosomal shield, length	−0.168	0.28	0.38	−2.162
Constant			−15.301	−46.2

[a] ordered by absolute size of correlation within function.

Table 18. Three-group Canonical variates analyses: Classification accuracy.

		Predicted Group Membership			
Sample (accuracy)	**Group**	**1**	**2**	**3**	**Total**
Analysis	1	58(98.3%)	0	1(1.7%)	59
(94.2%)	2	0	39(86.7%)	6 (13.3%)	45
	3	1(3%)	0	32(97%)	33
Analysis cross-validated	1	56(94.9%)	0	3(5.1%)	59
(91.2%)	2	0	38(84.4%)	7(15.6%)	45
	3	2(6.1%)	0	31(93.9%)	33
Holdout (n = 90)	1	21(42%)	1(2%)	28(56%)	50
(63.3%)	2	0	22(88%)	3(12%)	25
	3	0	1(6.7%)	14(93.3%)	15

Groups: 1 = *Sennertia shimanukii* & USA, 2 = *S. frontalis* and *X. nautlana*&, 3 = *S. augustii*.

Table 19. Classification accuracy of the three-variable logistic regression model.

	Analysis			External validation		
	Group 0	**Group 1**	**Accuracy(%)**	**Group 0**	**Group 1**	**Accuracy(%)**
Group 0	58	1	98.3	46	4	92
Group 1	2	43	95.6	0	25	100
Overall			97.1			94.7

Group 0 = *shimanukii*, Group 1 = *frontalis*.

Table 20. Three-variable logistic regression model.

Variable	**B**	**SE**	**Wald**	**P**	**Exp(B)**	**95.0% CI for Exp(B) Lower-Upper**
gnathosomal solenidion	317.819	224.008	2.013	0.156	1.06E+138	0-
c_3	31.373	12.099	6.723	0.01	4.22E+13	2119.67–8.402E+23
d_2	4.646	4.208	1.219	0.269	104.204	0.027–397571.338
Constant	−119.993	66.381	3.268	0.071	0	

B = Logit coefficients (logits); SE = standard error; Wald = Wald statistic, P = p-value for Wald statistic; Exp(B) = odds ratio; CI = confidence interval.

APPENDIX 6. MEASUREMENTS OF HETEROMORPHIC DEUTONYMPHS OF *CHAETODACTYLUS* AND *SENNERTIA*

Table 21. Measurements of four species of *Chaetodactylus* (range, mean ± SD).

Structure	**melitomae**	**antillarum**	**furunculus**	**kouboy**
idiosoma, length	245–329, 290.8 ± 29.1[j]	236–271, 252 ± 9[j]	252–296, 280.1 ± 13.5[j]	264–362, 321.7 ± 33.2[j]
idiosoma, width	211–265,244.2 ± 19.6[j]	195–242, 215 ± 13[j]	206–263, 230.5 ± 16.9[j]	254–348, 302 ± 31.6[j]
prodorsal shield, length	72–97, 84 ± 7.8[j]	61–78,71.6 ± 5.6[j]	80–91, 86.3 ± 3.3[j]	96–114, 106.4 ± 6[j]
prodorsal shield, width	138–183, 167.4 ± 16.3[j]	109–145, 124.4 ± 9[j]	132–151, 139.9 ± 5.7[j]	159–183, 174.1 ± 8.4[j]
hyst shield, length	126–178, 152.6 ± 15.7[j]	123–151, 137.1 ± 7.5[j]	136–173, 156.4 ± 10.3[j]	137–185, 167.9 ± 16.5[j]
hyst shield, width anterior	159–218, 194.5 ± 18.7[j]	164–211, 186 ± 14.7[j]	179–216, 194.3 ± 13.1[j]	228–286, 256 ± 19.3[j]
hyst shield, width at f_2 level[1]	72–95, 83.7 ± 7.3[j]	90–111, 97.3 ± 5.7[j]	92–110, 101.8 ± 5.5[j]	101–129,112.5 ± 8.7[j]
length of free palpi	10–13, 11.7 ± 1.3[j]	9–11,9.9 ± 0.5[j]	10–12, 11.2 ± 0.5[j]	9–13, 11.3 ± 1.4[j]
width of free palpi, base	6–8,7.3 ± 0.7[j]	6–7,6.8 ± 0.3[j]	6–8,6.8 ± 0.6[j]	6–10,8.1 ± 1.4[j]
gnathosomal solenidion	17–24, 21.4 ± 2.2[j]	11–17,14.9 ± 1.8[j]	12–15, 13 ± 0.9[j]	9–11,9.9 ± 1.1[j]
sternum	35–51, 42.2 ± 5.4[j]	41–51,45.9 ± 3.2[j]	39–47, 43.7 ± 2.7[j]	43–57, 51.1 ± 4.3[j]
apodeme II	62–81, 75.2 ± 6.7[j]	59–70, 64.2 ± 4[j]	56–71, 63.6 ± 4.5[j]	66–86, 77.6 ± 6.3[j]
apodeme III	50–62, 56.8 ± 3.9[j]	44–53, 48.2 ± 2.7[j]	49–57, 53 ± 2.4[j]	55–70, 64.2 ± 5.8[j]
apodeme IV	55–70, 65.3 ± 5.7[j]	55–58, 55.8 ± 1.2[j]	55–68, 62.8 ± 4.1[j]	64–81, 73.1 ± 5.7[j]
posterior apodeme IV[2]	36–52, 41.7 ± 5.3[i]	16–26, 19.4 ± 3.7[j]		29–44, 34.2 ± 5.4[j]
vi	5–10,8.2 ± 1.4[j]	5–10,7.5 ± 1.7[j]	11–16,12.9 ± 1.6[j]	8–13, 11 ± 1.5[j]
si	14–18, 16.2 ± 1.1[j]	23–36, 28.6 ± 4.3[j]	13–21, 16.5 ± 2.1[j]	13–20, 16.5 ± 2.4[j]
se	31–44,38.1 ± 4.1[j]	48–61, 51.3 ± 3.8[j]	31–37,34.5 ± 1.7[j]	41–53,46.1 ± 3.9[j]
c_1	13–17, 15.4 ± 1.7[g]	23–30, 26.4 ± 2.5[h]	14–16, 14.7 ± 0.9[j]	8–13, 11.5 ± 1.3[i]
c_2	28–37, 32.1 ± 3.1[j]	42–56, 48 ± 5.3[j]	35–47, 41.8 ± 4[j]	44–55, 50.2 ± 3.7[j]
c_3	25–34, 30.3 ± 2.8[j]	30–41, 35.2 ± 3.6[j]	25–30, 27.7 ± 2.1[j]	29–41, 34.8 ± 4.3[j]
c_p	32–44, 38.1 ± 4.1[j]	48–59, 52.4 ± 4[j]	41–56,48.8 ± 4.6[j]	43–56, 51.5 ± 4.6[i]
d_1	10–13, 11.3 ± 1.1[j]	18–30, 23.6 ± 3.3[j]	15–20, 16.7 ± 1.7[j]	8–13,9.8 ± 1.7[j]
d_2	11–20,12.4 ± 2.7[j]	43–61, 50.4 ± 5.1[j]	26–35, 30.2 ± 3.3[i]	16–25, 21 ± 2.8[i]
e_1	6–12, 9 ± 1.9[i]	18–30, 21.9 ± 3.6[j]	12–16, 14.4 ± 1.6[j]	5–8,7.3 ± 0.9[j]
e_2	5–11, 9.4 ± 1.8[i]	36–52, 44.5 ± 5.6[j]	24–30, 26.4 ± 2.3[i]	10–21, 15.4 ± 3.5[j]
f_2	7–9, 8.1 ± 0.7[j]	23–35, 29.4 ± 3.8[j]	13–22, 16.6 ± 3.3[j]	7–11, 9.2 ± 1.4[j]
h_1	5–9, 7.3 ± 0.9[j]	13–18, 15.6 ± 1.7[j]	10–12, 10.7 ± 0.7[j]	6–9, 7 ± 0.9[j]
h_2	8–13, 9.9 ± 1.8[j]	16–23, 19 ± 2.5[j]	19–27, 22.6 ± 2.6[j]	8–13, 10.9 ± 1.6[j]
h_3	8–13, 10 ± 1.8[j]	16–22, 17.9 ± 1.9[j]	17–21, 19.1 ± 1.6[j]	11–14,12.9 ± 1.1[j]
1a	42–79, 62.2 ± 12.4[i]	42–48, 45.2 ± 2.5[j]	43–49, 46 ± 1.8[j]	40–51, 45.5 ± 3.6[j]
4b	11–16,13.1 ± 1.3[j]	16–23, 19.4 ± 1.8[i]	22–33, 27.7 ± 3.1[j]	12–23, 18.3 ± 3.6[i]
3a	34–51, 44.9 ± 5.7[j]	40–50, 44.4 ± 3.8[j]	40–44, 42 ± 1.3[j]	27–37, 32.6 ± 3.2[j]
4a	12–17, 14.3 ± 2[j]	28–40, 34.2 ± 3.3[j]	26–38, 31.7 ± 3.5[i]	23–32, 26.3 ± 2.7[j]
g	8–9, 8.6 ± 0.4[i]	9–12, 10 ± 1.1[j]	8–15, 11.4 ± 1.7[j]	6–12, 9.6 ± 2.4[g]
length of attachment organ[3]	26–36, 32.6 ± 3.5[j]	42–50, 46.8 ± 2.4[j]	40–45, 43.2 ± 1.7[j]	45–53, 49.1 ± 2.4[j]
width of attachment organ[4]	37–44, 41.9 ± 2.4[j]	42–49, 45.7 ± 2.2[j]	44–50, 46.6 ± 2[j]	45–55, 51.4 ± 3.4[j]
anterior sucker (ad_3)[4]	10–12, 11.2 ± 0.6[h]	8–9, 9.2 ± 0.3[j]	10–11, 10.4 ± 0.5[j]	10–12, 11 ± 0.7[j]
median shield (ad_1+ad_2, ad_3)	11–16,14.1 ± 1.4[j]	16–18, 17.1 ± 0.5[j]	13–18, 15.9 ± 1.7[j]	20–23, 21.7 ± 1.3[j]
anterior lateral conoid (ps_2)	3–5, 4.2 ± 0.7[j]	3–4, 3.6 ± 0.3[j]	3–4, 3.6 ± 0.3[j]	4–6, 5.6 ± 0.9[j]
posterior lateral conoid (ps_1)	3–5, 4 ± 0.7[j]	3–4, 3.6 ± 0.5[j]	3–5, 3.7 ± 0.5[j]	4–7, 5.8 ± 0.9[j]
anterior cuticular conoid	2–4, 3.1 ± 0.5[j]	2–3, 2.8 ± 0.5[j]	1–3,1.9 ± 0.4[j]	3–5, 3.6 ± 0.6[j]
ih	4–5, 5 ± 0.4[j]	4–5, 4.7 ± 0.3[j]	4–5, 4.4 ± 0.5[j]	4–5, 4.9 ± 0.3[j]
leg I	128–163, 150.4 ± 13[j]	109–122, 115.9 ± 3.9[j]	136–153, 146.1 ± 5.2[i]	128–166, 149.9 ± 12.5[j]
tarsus I	40–47, 44.4 ± 2.6[j]	30–34, 31.6 ± 1.1[j]	41–46,43.3 ± 1.7[i]	38–52, 45.9 ± 4.5[j]
empodium I	18–22, 20.5 ± 1.5[j]	17–25, 19.8 ± 2.6[j]	18–32, 24.2 ± 3.9[j]	23–39, 32.1 ± 5.2[j]
ω_1 I	18–24, 20.8 ± 1.6[j]	17–20, 17.6 ± 0.8[h]	21–23,21.8 ± 0.9[i]	21–24,23.4 ± 1.1[g]
ω_2 I	13–16, 14.7 ± 1.1[j]	12–16, 13.7 ± 1.1[j]	13–16, 14.4 ± 1.2[h]	10–14, 11.8 ± 1.4[g]
ω_3 I	31–41,36.9 ± 3.2[j]	29–32, 30.6 ± 1[j]	34–44, 38.5 ± 2.9[j]	33–38, 35.6 ± 1.8[h]
ε I	3–6, 4.2 ± 1[j]	3–5, 3.2 ± 0.6[j]	6–7, 6.5 ± 0.5[g]	4–6, 4.8 ± 0.9[g]
f I	50–59, 55.6 ± 3.4[i]	42–56, 47.2 ± 4.9[i]	48–58, 52 ± 3.2[j]	51–67,59.2 ± 4.8[j]
d I	56–80, 69.7 ± 7.2[j]	61–70,65.6 ± 2.5[i]	73–80, 77.1 ± 2[i]	80–100, 88.5 ± 6.2[j]
ra I	12–16, 13.9 ± 1.7[j]	16–21, 17.9 ± 1.5[j]	22–27, 24.4 ± 1.7[j]	19–25, 21.4 ± 2.1[i]
la I	20–25, 22 ± 1.8[j]	17–21, 18.9 ± 1.1[i]	22–27, 25 ± 1.4[i]	20–25, 22.6 ± 1.5[j]
wa I	30–41, 35.2 ± 2.7[j]	23–33, 28.1 ± 3.1[j]	31–35,32.6 ± 1.4[j]	31–41,36.3 ± 3.6[j]
gT I	20–32, 28 ± 3.6[j]	19–32, 26.5 ± 3.7[j]	22–31, 26.3 ± 2.9[j]	13–22, 17.1 ± 3[i]
hT I	20–27, 24.2 ± 2.8[j]	20–27, 22.6 ± 2.1[j]	24–29, 25.9 ± 1.7[i]	11–17,13.1 ± 1.9[i]
ϕ I	44–44, 43.9 ± 0.4[d]	53–64, 58.5 ± 3.9[e]	69[a]	36–44, 40.1 ± 2.9[e]

(continued)

Table 21. (Continued)

Structure	**melitomae**	**antillarum**	**furunculus**	**kouboy**
mG I	26–36, 32.2 ± 3.4^{j}	27–34, 31 ± 2.5^{j}	33–42, 38.1 ± 3.3^{j}	25–34, 29.7 ± 3.7^{j}
cG I	42–58, 51.1 ± 4.8^{j}	37–44, 40.5 ± 2.5^{j}	36–47, 40.2 ± 3.3^{j}	34–44, 38.3 ± 3.4^{i}
σ I	16–20, 17.3 ± 1.6^{j}	26–30, 28 ± 1.1^{j}	16–20, 18.4 ± 1.4^{j}	8–13, 11 ± 1.8^{i}
vF I	32–42, 37.8 ± 3.5^{j}	44–55, 47.9 ± 2.9^{j}	48–62, 55.1 ± 3.8^{j}	32–47, 37.9 ± 5^{j}
pR I	73–106, 95.3 ± 11.1^{j}	47–55, 50.9 ± 2.6^{j}	48–58, 52.7 ± 3.1^{j}	19–49, 33.8 ± 9.3^{j}
leg II	125–161, 148.4 ± 13^{j}	108–117, 113.1 ± 3.4^{i}	130–148, 139.8 ± 5^{j}	125–179, 152.3 ± 15.7^{j}
tarsus II	37–49, 44.1 ± 3.6^{j}	30–38, 32.7 ± 2.4^{j}	40–45, 42 ± 1.4^{j}	39–51, 46.1 ± 3.7^{j}
empodium II	18–22, 20 ± 1.2^{j}	18–25, 23 ± 2.5^{j}	18–27, 22 ± 2.7^{j}	24–39, 33.6 ± 3.8^{j}
ω_1 II	21–25,22.9 ± 1.2^{j}	22–25, 23.5 ± 0.9^{j}	25–27, 25.9 ± 0.9^{j}	22–27, 24.5 ± 1.7^{j}
f II	44–59, 51 ± 4.3^{j}	38–60, 47.3 ± 7.1^{j}	47–52, 49.8 ± 1.8^{j}	55–61, 59 ± 2^{j}
d II	56–75, 67.5 ± 6.1^{j}	58–69, 64.3 ± 4.2^{j}	68–83, 73 ± 4.7^{i}	78–95, 86.9 ± 6.8^{h}
ra II	12–16, 14.3 ± 1^{i}	17–22, 18.6 ± 1.4^{j}	23–27, 24.9 ± 1.3^{i}	16–25, 21.1 ± 3.1^{i}
la II	18–23, 21.3 ± 2.2^{j}	17–21, 18.7 ± 1.5^{i}	22–26, 23.2 ± 1.5^{j}	20–27, 22.7 ± 2^{j}
wa II	33–37, 35.3 ± 1.6^{j}	27–31, 28.8 ± 1.3^{i}	28–36, 32.2 ± 2.1^{j}	31–41,36.5 ± 3.4^{j}
gT II	17–24, 21 ± 2.6^{j}	18–29, 21.3 ± 3.8^{i}	21–25,22.3 ± 1.7^{j}	12–19, 14.8 ± 2.5^{i}
hT II	20–30, 26.4 ± 3^{j}	18–23, 20.3 ± 1.7^{j}	19–23, 20.6 ± 1.2^{j}	12–18, 14.9 ± 2^{j}
ϕ II	42–50, 46.5 ± 3.4^{e}	56–64, 60.1 ± 5.5^{b}	68–70, 69 ± 1.4^{b}	39–42, 40.6 ± 1.6^{c}
mG II	30–42, 37.4 ± 3.6^{i}	34–39, 36.9 ± 2.3^{j}	30–35, 32.4 ± 2.1^{h}	23–39, 32.8 ± 5.4^{i}
cG II	11–16,13.5 ± 1.3^{j}	8–15, 11.1 ± 2^{j}	10–13, 11.2 ± 1^{j}	9–12, 10.6 ± 1.3^{j}
σ II	12–17, 14.4 ± 1.5^{j}	10–12, 10.8 ± 0.5^{j}	13–17, 15 ± 1.1^{j}	8–10, 9 ± 0.8^{h}
vF II	36–49, 43 ± 4.3^{j}	41–47,43.4 ± 2^{j}	49–59, 53.1 ± 3.2^{j}	34–43, 37.6 ± 2.5^{j}
pR II	75–117, 96.8 ± 13.4^{h}	47–50, 48.5 ± 1.4^{j}	48–56, 50.2 ± 2.6^{h}	34–48, 39.8 ± 5.1^{i}
leg III	103–137, 124.1 ± 11.9^{j}	94–105, 99.9 ± 3.4^{j}	109–122, 115.2 ± 4^{j}	110–128, 120.5 ± 5.5^{j}
tarsus III	37–50, 45 ± 4.2^{j}	29–34, 31.7 ± 1.7^{j}	36–41, 38.7 ± 1.9^{j}	38–44, 41.5 ± 1.9^{j}
empodium III	16–19, 17.2 ± 1.3^{j}	19–22, 20.8 ± 1^{i}	17–24, 22.3 ± 2.1^{j}	24–31, 27.2 ± 2^{j}
d III	73–109, 91.9 ± 11.9^{j}	105–129, 116.8 ± 9^{i}	112–157, 138 ± 13.9^{j}	101–145, 119 ± 18.6^{f}
e III	48–65, 54.8 ± 5.2^{i}	34–47, 42.6 ± 4.1^{i}	50–58, 54.5 ± 3.4^{h}	57–75, 67.2 ± 7.2^{e}
f III	41–55,47.3 ± 4.3^{j}	29–41, 37.8 ± 3.6^{i}	43–49, 45.5 ± 1.9^{j}	48–56, 51.8 ± 3.1^{h}
s III	29–35, 32.2 ± 2^{j}	20–25, 22.7 ± 1.9^{i}	21–26,22.7 ± 1.7^{j}	23–30, 25.9 ± 2.1^{j}
kT III	20–29, 24.6 ± 2.7^{j}	20–24, 22.6 ± 1.6^{j}	19–23, 21 ± 1.1^{i}	9–13, 11.4 ± 1.3^{j}
ϕ III	27–37, 33.3 ± 3.3^{j}	30–34, 31.8 ± 1.6^{j}	26–30, 28.2 ± 1.5^{j}	14–21, 16.9 ± 2^{j}
nG III	37–50, 44.8 ± 4.3^{j}	29–34, 31 ± 1.5^{j}	33–40, 35.6 ± 2.3^{j}	16–23, 20 ± 2.5^{j}
sR III	54–97, 81.6 ± 14.9^{j}	26–33, 28.3 ± 2.4^{i}	28–38, 33.6 ± 3.4^{j}	23–31, 26.7 ± 2.7^{j}
leg IV	66–89, 77.4 ± 7.8^{i}	72–83, 75.8 ± 3.8^{j}	97–107, 102.1 ± 3^{j}	68–80, 74.1 ± 3.8^{j}
tarsus IV	23–31, 27.6 ± 2.9^{i}	22–28, 26.2 ± 1.9^{j}	34–36, 35 ± 0.8^{j}	19–22, 20.4 ± 1.1^{j}
d IV	250–351, 309.1 ± 42.8^{f}	231–265,250.5 ± 11.3^{j}	230–285, 267.3 ± 18.7^{h}	318–365, 336 ± 22.5^{e}
e IV	30–55, 44.1 ± 8.9^{h}	12–21, 16.8 ± 3.2^{j}	19–34, 23.6 ± 5^{j}	
f IV	39–57, 49.8 ± 7^{i}	12–25, 17.3 ± 4.5^{j}	19–26, 22.2 ± 2.8^{j}	
w IV	34–55, 47.8 ± 7.7^{i}	11–21,16.7 ± 3.4^{j}	15–18, 16.2 ± 0.9^{j}	4–6, 5 ± 0.7^{j}
s IV	32–55, 45 ± 7.5^{i}	9–13, 11.3 ± 1.4^{f}	10–13, 11.4 ± 0.8^{j}	6–8, 7.1 ± 0.7^{j}
ϕ IV	28–36, 31.8 ± 2.5^{i}	14–16, 15.1 ± 0.9^{d}	17–22, 19.3 ± 2^{h}	7–8, 7.3 ± 0.1^{d}
vF IV	32–47, 40.5 ± 5^{j}	23–36, 29.4 ± 3.7^{j}	42–48, 43.4 ± 2.5^{j}	13–18, 15.2 ± 1.9^{j}

Superscript: 1 = excluding bases of f_2; 2 = from free end to outer posterior edge of coxa IV; 3 = medial horn-posterior sclerotized end; 4 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10. hyst=hysterosomal.

Table 22. Measurements of four species of *Chaetodactylus* (range, mean ± SD).

Structure	**lithurgi**	**abditus**	**gibbosi**	**azteca**
idiosoma, length	218–362, 304.7 ± 31.19[cm]	243–324, 282.3 ± 15.42[bn]	246–331, 293.7 ± 20.02[bg]	306–348, 318.1 ± 14[h]
idiosoma, width	245–305, 269.0 ± 25.76[e]	217–243, 230.4 ± 11.32[e]	218–306, 252.6 ± 24.68[j]	250–298, 274.6 ± 16.6[h]
prodorsal shield, length	59–92, 78.2 ± 6.85[cm]	64–90, 74.9 ± 4.94[bn]	64–101, 81.0 ± 8.23[bg]	81–105,93.2 ± 7.2[h]
prodorsal shield, width	111–183,148.6 ± 13.46[cm]	120–175, 142.7 ± 13.12[bn]	121–187,152.0 ± 15.29[bg]	144–184, 161.2 ± 13.3[h]
hyst shield, length	115–191, 161.4 ± 17.45[bc]	117–162, 137.1 ± 11.62[ad]	125–176, 150.1 ± 15.57[y]	158–183, 168.7 ± 9.5[h]
hyst shield, width anterior	159–257, 209.7 ± 19.77[bc]	157–215, 189.9 ± 15.21[ad]	172–248, 207.1 ± 18.22[z]	203–234, 215.8 ± 10.7[h]
hyst shield, width at f_2 level[1]	76–148, 117.9 ± 14.69[cm]	87–112, 100.2 ± 5.64[bn]	89–136, 113.5 ± 10.91[bg]	109–123, 113.2 ± 4.4[h]
length of free palpi	8–12, 10.4 ± 1.50[e]	8–11, 9.6 ± 1.16[e]	9–12, 10.9 ± 0.95[j]	9–12, 11 ± 1.3[h]
width of free palpi, base	5–8, 6.8 ± 1.13[e]	5–8, 6.7 ± 1.18[e]	6–8, 7.4 ± 0.67[j]	6–8, 7.4 ± 0.7[h]
gnathosomal solenidion	14–18, 16.2 ± 1.62[e]	16–21, 17.7 ± 2.05[e]	16–19, 17.2 ± 1.01[j]	8–9, 8.6 ± 0.7[h]
sternum	47–55, 50.5 ± 2.78[e]	41–55,47.6 ± 4.99[e]	41–58,50.2 ± 6[j]	55–62, 57.6 ± 2.7[h]
apodeme II	55–84, 70.4 ± 6.07[bc]	59–72, 64.9 ± 4.43[j]	62–82, 72.0 ± 5.87[z]	70–75, 72.5 ± 1.9[h]
apodeme III	41–67,58.4 ± 6.18[bc]	45–59, 52.8 ± 3.34[ad]	46–65, 55.9 ± 4.55[z]	53–64, 58.5 ± 4.1[h]
apodeme IV	57–64, 61.0 ± 3.04[e]	52–59, 55.1 ± 2.50[e]	52–66, 59.4 ± 4.09[j]	62–78, 67.3 ± 5.4[h]
posterior apodeme IV[2]	25–28, 26.7 ± 1.60[e]	19–21, 20.1 ± 0.85[e]	12–31, 21.6 ± 5.25[j]	25–34, 29.6 ± 2.9[h]
vi	11–14,13.0 ± 1.13[e]	11–14,12.2 ± 1.26[e]	9–14, 11.5 ± 1.78[j]	8–12, 9.5 ± 1.5[h]
si	24–51, 37.1 ± 6.21[cl]	29–55, 39.6 ± 4.67[bm]	18–47, 28.1 ± 5.18[bf]	25–37, 31.4 ± 3.7[h]
se	50–62, 55.4 ± 5.68[e]	48–55, 50.3 ± 3.28[e]	41–59,51.9 ± 5.24[i]	47–62, 52.3 ± 4.8[h]
c_1	15–30, 21.1 ± 3.75[cj]	13–22, 17.3 ± 1.79[bk]	9–15, 11.7 ± 1.31[bc]	24–36, 28.3 ± 3.8[h]
c_2	49–57, 53.8 ± 3.30[e]	45–51, 48.2 ± 2.41[e]	43–55, 49.5 ± 3.33[i]	45–62, 55.4 ± 6.4[h]
c_3	36–44, 39.9 ± 2.98[e]	34–38, 35.7 ± 1.38[e]	33–44, 39.3 ± 4.19[j]	36–44, 40.1 ± 2.5[h]
c_p	53–62, 58.7 ± 3.68[e]	47–59, 52.6 ± 4.75[e]	45–62, 53.4 ± 4.94[j]	47–65, 57.9 ± 7.2[h]
d_1	16–32, 23.4 ± 3.45[cj]	20–33, 26.2 ± 2.84[bm]	10–18, 14.2 ± 1.81[bf]	23–32, 27.6 ± 2.8[h]
d_2	40–47, 44.2 ± 2.76[e]	33–43, 37.8 ± 3.92[e]	37–46, 40.5 ± 2.77[j]	39–51, 46.3 ± 5[h]
e_1	13–29, 21.3 ± 3.28[cj]	18–32, 23.7 ± 2.93[bn]	9–18, 13.4 ± 1.98[bg]	19–26, 22.7 ± 2.1[h]
e_2	33–45, 38.7 ± 4.55[e]	32–38, 35.3 ± 2.43[e]	30–48, 37.1 ± 5.09[j]	30–39, 33.9 ± 3.6[h]
f_2	29–37, 33.8 ± 3.65[e]	27–34, 30.5 ± 3[e]	28–38, 32.0 ± 3.47[i]	16–27, 20.8 ± 3.8[h]
h_1	11–29,21.3 ± 3.29[ck]	16–28, 21.3 ± 2.69[bn]	11–19,14.9 ± 1.83[bg]	16–20, 18.2 ± 1.6[h]
h_2	17–39, 27.5 ± 4.44[cl]	10–28, 18.0 ± 3.69[bn]	17–31, 24.2 ± 3.28[bg]	16–22, 18.3 ± 2.2[h]
h_3	17–21, 18.9 ± 1.40[e]	16–20, 18.4 ± 1.97[e]	16–23, 18.1 ± 2.27[j]	21–29,24.1 ± 3[h]
1a	60–72, 64.2 ± 5.19[d]	54–58, 56.6 ± 1.86[d]	52–64, 59.7 ± 4.41[f]	106–137, 123.9 ± 14.3[e]
4b	13–22, 16.5 ± 1.66[az]	13–19, 15.8 ± 1.53[ac]	16–21, 17.2 ± 1.30[z]	15–17, 15.7 ± 0.6[h]
3a	34–38, 35.3 ± 1.48[e]	33–44, 38.7 ± 4.76[e]	32–47, 39.2 ± 3.97[j]	87–101, 95.2 ± 5.6[g]
4a	23–37, 28.9 ± 3.01[cj]	27–42, 33.4 ± 3.34[bf]	21–34,27.0 ± 2.85[bf]	101–134,120.6 ± 11[g]
g	8–13, 9.8 ± 1.34[aw]	6–12, 9.0 ± 1.26[ab]	8–15, 11.0 ± 1.78[z]	9–12, 10 ± 1.3[h]
length of attachment organ[3]	47–61, 54.5 ± 3.21[cm]	42–56, 49.8 ± 2.96[bn]	47–62, 53.9 ± 3.23[bg]	36–42, 38.7 ± 1.9[h]
width of attachment organ[4]	56–62, 58.7 ± 2.83[e]	53–62, 56.1 ± 3.69[e]	55–59, 56.4 ± 1.80[j]	51–56,53.1 ± 1.7[h]
anterior sucker (ad_3)[4]	9–10, 9.6 ± 0.61[e]	9–11, 9.8 ± 0.61[e]	9–11, 9.7 ± 0.71[j]	9–11, 9.8 ± 0.5[h]
median shield (ad_1+ad_2, ad_3)	18–23, 20.7 ± 1.26[bc]	16–22, 18.7 ± 1.34[ad]	18–23, 20.1 ± 1.28[z]	18–20, 18.8 ± 0.9[h]
anterior lateral conoid (ps_2)	4–6, 5.6 ± 1.13[e]	4–6, 5.1 ± 0.78[e]	5–6, 5.5 ± 0.68[j]	4–6, 4.8 ± 0.7[h]
posterior lateral conoid (ps_1)	4–7, 5.9 ± 0.98[e]	5–6, 5.5 ± 0.78[e]	4–7, 5.9 ± 0.76[j]	5–6, 5.2 ± 0.5[h]
anterior cuticular conoid	2–4, 3.2 ± 0.52[e]	3–5, 3.8 ± 0.77[e]	3–5, 3.8 ± 0.75[j]	3–5, 3.6 ± 0.8[h]
ih	5–6, 5.5 ± 0.62[e]	3–5, 4.6 ± 0.78[e]	3–6, 4.8 ± 1.05[j]	3–7, 4.9 ± 1.1[h]
leg I	131–139,134.8 ± 3.46[e]	122–134, 125.9 ± 4.86[e]	117–140, 126.7 ± 8.16[j]	137–149, 144.6 ± 4.7[h]
tarsus I	36–41, 38.7 ± 2.11[e]	34–41, 37.6 ± 2.37[e]	31–41,35.8 ± 3.81[i]	40–45, 43.1 ± 1.7[h]
empodium I	22–32, 26.2 ± 4.74[e]	27–30, 28.5 ± 1.31[e]	23–37, 29.1 ± 5.12[j]	34–39, 35.3 ± 1.8[h]
ω_1 I	19–36, 22.6 ± 2.73[bb]	21–27,23.2 ± 1.24[ac]	16–21, 18.8 ± 1.57[s]	24–27, 25.8 ± 1.1[h]
ω_2 I	9–17, 12.2 ± 1.98[au]	11–14,12.6 ± 0.91[k]	8–12, 9.5 ± 1.07[o]	14–16, 14.5 ± 0.8[g]
ω_3 I	32–47, 38.4 ± 3.24[bc]	34–47, 38.1 ± 3.32[ac]	31–39,34.7 ± 2.37[y]	44–49, 46.7 ± 1.9[h]
ε I	3–7, 5.0 ± 0.73[ap]	3–6, 4.4 ± 0.80[j]	3–7, 4.7 ± 1[u]	5–7, 5.5 ± 0.9[g]
f I	44–70, 58.0 ± 5.70[cf]	45–67, 54.8 ± 5.19[bl]	48–69, 59.0 ± 5.15[az]	65–75, 69.1 ± 3.4[h]
d I	62–95, 77.7 ± 8.03[bb]	62–89, 73.7 ± 6.30[aa]	69–92, 80.0 ± 6.47[w]	90–105, 95.3 ± 5.2[h]
ra I	20–28, 24.1 ± 2.18[at]	20–27, 22.4 ± 1.90[i]	21–27,24.3 ± 1.87[t]	14–18, 15.3 ± 1.4[g]
la I	23–29, 26.4 ± 2.23[e]	24–27, 25.4 ± 0.89[e]	22–28, 25.1 ± 2.40[i]	23–28, 25.1 ± 1.8[h]
wa I	30–44, 36.1 ± 3.42[az]	29–41, 34.9 ± 2.78[ad]	31–37,34.1 ± 2.27[w]	34–41, 38 ± 2.7[h]
gT I	31–34,32.0 ± 1.10[e]	23–33, 26.7 ± 3.59[e]	26–33, 29.0 ± 2.70[i]	17–32, 25.9 ± 6.6[f]
hT I	23–29, 26.3 ± 2.68[e]	20–28, 23.7 ± 2.84[e]	20–28, 22.7 ± 2.93[i]	23–29, 25.2 ± 1.9[h]
ϕ I	45[a]		50[a]	53–73, 63.2 ± 11.7[d]
mG I	37–44, 39.0 ± 3.31[d]	28–36, 32.4 ± 3.48[e]	29–39, 34.5 ± 3.38[j]	37–46, 41 ± 3.3[h]
cG I	55–66, 59.7 ± 4.32[e]	47–55, 50.5 ± 3.09[e]	47–62, 55.5 ± 5.39[j]	36–50, 44.2 ± 5.4[h]
σ I	11–21,15.9 ± 1.76[ax]	16–21, 17.8 ± 1.38[aa]	13–19, 15.7 ± 1.48[u]	16–20, 17.7 ± 1.5[h]

(continued)

Table 22. (Continued)

Structure	**lithurgi**	**abditus**	**gibbosi**	**azteca**
vF I	41–60,51.1 ± 5.28^{bc}	45–63, 53.6 ± 4.13^{ac}	41–53,47.3 ± 2.81^{x}	62–76, 69.1 ± 4.3^{h}
pR I	62–70, 65.9 ± 4.10^{d}	50–64, 58.1 ± 6.42^{d}	51–69,58.9 ± 6.33^{g}	117–140, 125.8 ± 12.7^{c}
leg II	127–136, 131.7 ± 3.09^{e}	118–134, 127.0 ± 8.24^{e}	114–144, 126.6 ± 10.22^{j}	142–161, 148.4 ± 7.6^{h}
tarsus II	37–41, 38.7 ± 1.62^{e}	35–39, 37.5 ± 1.87^{e}	31–41,36.6 ± 3.04^{i}	41–48,43.7 ± 2.6^{h}
empodium II	23–31, 29.0 ± 3.37^{e}	26–31, 28.2 ± 1.95^{e}	22–34, 28.2 ± 4.19^{j}	33–37, 35.2 ± 1.4^{h}
ω_1 II	20–28, 24.7 ± 2.03^{ax}	23–28, 25.4 ± 1.44^{z}	19–25, 22.0 ± 2.01^{x}	27–34, 30.2 ± 2.5^{h}
f II	45–66, 57.2 ± 5.53^{cj}	45–66, 54.4 ± 4.54^{bk}	45–69, 58.5 ± 4.94^{be}	62–74, 66.5 ± 3.7^{h}
d II	65–94, 78.4 ± 8.31^{ba}	61–81,72.6 ± 5.31^{ab}	69–87, 78.6 ± 4.65^{y}	90–108, 97 ± 6.3^{h}
ra II	22–27, 25.4 ± 2.07^{e}	22–26, 24.0 ± 1.73^{d}	20–28, 25.5 ± 2.85^{h}	15–18, 16.4 ± 1.2^{g}
la II	24–28, 25.7 ± 1.68^{d}	20–27, 23.4 ± 2.47^{e}	20–34, 25.8 ± 4.08^{i}	19–24, 21.5 ± 1.9^{h}
wa II	28–38, 32.3 ± 4.43^{e}	32–34, 33.1 ± 0.89^{e}	29–37, 33.2 ± 3.01^{j}	33–42, 38.5 ± 2.9^{h}
gT II	23–28, 25.3 ± 2.25^{e}	20–25, 22.1 ± 2.51^{c}	16–27, 21.9 ± 3.74^{g}	26–28, 26.8 ± 0.9^{e}
hT II	16–29, 21.5 ± 2.55^{ck}	19–29, 24.2 ± 1.85^{bl}	16–24, 20.0 ± 1.99^{bg}	25–29, 26.7 ± 1.4^{h}
ϕ II	41–51,46.4 ± 7.17^{b}	59^{a}	51–52,51.9 ± 0.55^{b}	66–75, 71.2 ± 5^{c}
mG II	41–47,42.8 ± 2.83^{e}	32–38, 36.0 ± 2.64^{e}	32–46, 40.2 ± 4.81^{j}	46–66, 55 ± 6^{h}
cG II	11–12,11.4 ± 0.70^{e}	10–12, 11.2 ± 1.02^{e}	10–15, 12.2 ± 1.70^{j}	15–18, 15.9 ± 1.1^{h}
σ II	10–12, 10.8 ± 0.92^{d}	9–13, 11.4 ± 1.30^{e}	9–11, 10.4 ± 1.02^{h}	10–11, 10.9 ± 0.4^{g}
vF II	34–52, 43.4 ± 4.57^{cm}	39–59, 48.5 ± 3.74^{bn}	30–48, 39.9 ± 3.71^{bf}	98–120, 106.9 ± 7^{h}
pR II	62–78, 67.5 ± 6.38^{e}	51–78,61.4 ± 11.59^{d}	52–70, 61.1 ± 7.25^{g}	105–159, 131.6 ± 19.4^{f}
leg III	95–110, 103.5 ± 5.65^{e}	95–111, 103.0 ± 7.66^{e}	92–108, 100.9 ± 5.49^{j}	121–140,127.9 ± 6.7^{h}
tarsus III	25–42, 33.9 ± 4^{ba}	28–37, 32.0 ± 2.57^{j}	23–37, 30.8 ± 3.40^{z}	36–47, 40.8 ± 3.1^{h}
empodium III	17–31, 23.3 ± 3.37^{bc}	16–27, 20.9 ± 3.48^{ad}	17–33, 25.9 ± 3.26^{z}	25–30, 27.6 ± 1.8^{h}
d III	112–165, 140.0 ± 11.45^{ao}	129–144, 135.7 ± 6.18^{h}	112–150, 129.4 ± 9.92^{q}	151–192,168.3 ± 14.4^{h}
e III	50–59, 54.3 ± 4.60^{e}	48–56, 52.9 ± 3.72^{e}	51–62,56.5 ± 4.45^{h}	64–76, 70.2 ± 5.3^{e}
f III	36–59, 48.8 ± 5.09^{az}	41–48,43.5 ± 2.49^{j}	44–59, 49.7 ± 3.87^{x}	58–69, 64.2 ± 4.4^{h}
s III	25–28, 26.3 ± 1.61^{d}	25–31, 26.8 ± 2.79^{e}	25–31, 27.7 ± 1.89^{h}	24–28, 26 ± 1.2^{g}
kT III	20–26, 22.9 ± 2.03^{e}	18–23, 21.2 ± 2.02^{e}	12–24, 19.9 ± 4.61^{j}	18–24, 19.9 ± 2.2^{g}
ϕ III	16–27, 20.9 ± 2.57^{ax}	17–28, 23.1 ± 2.44^{aa}	16–22, 18.6 ± 1.65^{t}	23–30, 26.4 ± 2.4^{h}
nG III	23–35, 28.8 ± 2.95^{bc}	27–31, 28.1 ± 1.61^{j}	22–33, 27.0 ± 2.98^{z}	19–35, 28.2 ± 5.3^{h}
sR III	27–43, 34.0 ± 3.05^{ba}	31–47,35.8 ± 3.85^{aa}	27–34, 31.4 ± 2.47^{x}	33–64, 46.2 ± 11.3^{g}
leg IV	62–69, 64.6 ± 2.37^{e}	58–67, 63.0 ± 3.57^{e}	59–69, 64.4 ± 2.92^{j}	87–105, 94.8 ± 6.2^{h}
tarsus IV	14–25, 20.6 ± 2.46^{bc}	18–23, 21.0 ± 1.41^{ad}	16–21, 18.9 ± 1.09^{z}	28–34, 31.2 ± 2.5^{h}
d IV	315–343, 327.3 ± 11.27^{e}	265–329, 287.4 ± 26.78^{e}	264–388, 306.0 ± 44.01^{f}	371–423,393.1 ± 23^{d}
e IV	4–11, 7.0 ± 1.60^{az}	3–8, 6.1 ± 1.29^{aa}	4–9, 7.6 ± 1.53^{z}	11–12,11.8 ± 0.5^{h}
f IV	5–9, 7.3 ± 1.42^{e}	6–8, 6.7 ± 0.70^{e}	5–11, 8.2 ± 1.74^{h}	12–14, 12.6 ± 0.8^{h}
w IV	6–16, 10.5 ± 3.83^{e}	9–12, 10.2 ± 1.36^{e}	8–19, 11.3 ± 4.05^{h}	10–12, 10.7 ± 1^{h}
s IV	5–11, 7.8 ± 2.14^{e}	9–13, 10.7 ± 1.37^{e}	5–9, 7.6 ± 1.90^{g}	10–12, 10.6 ± 0.6^{h}
ϕ IV	8–14, 10.9 ± 1.27^{w}	9–15, 12.3 ± 2.26^{f}	8–12, 9.8 ± 0.99^{l}	7–11, 9.2 ± 1.5^{h}
vF IV	28–33, 31.0 ± 1.78^{e}	22–31, 26.0 ± 2.31^{ab}	22–33, 27.3 ± 2.92^{y}	34–51, 40.1 ± 5.9^{h}

Superscript: 1 = excluding bases of f_2; 2 = from free end to outer posterior edge of coxa IV; 3 = medial horn-posterior sclerotized end; 4 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10 . . . cm = 91. hyst = hysterosomal.

Table 23. Measurements of three groups of *Chaetodactylus micheneri* (range, mean ± SD).

Structure	micheneri (group 1)	micheneri (group 2)	micheneri (group 3)
idiosoma, length	251–380, 333 ± 29^{ai}	268–356, 310 ± 20^{t}	307–378, 352 ± 18^{p}
idiosoma, width	214–346, 295 ± 30^{ai}	243–333, 270 ± 27^{t}	287–347, 316 ± 15^{p}
prodorsal shield, length	69–109, 90 ± 9^{ai}	69–91, 80 ± 7^{t}	74–97, 88 ± 6^{p}
prodorsal shield, width	137–232, 187 ± 23^{ai}	150–205, 173 ± 12^{t}	170–220, 190 ± 13^{p}
hyst shield, length	150–223, 194 ± 19^{ai}	168–207, 186 ± 10^{t}	172–195, 181 ± 6^{p}
hyst shield, width anterior	162–296, 249 ± 30^{ai}	198–264, 227 ± 19^{t}	226–273, 247 ± 13^{p}
hyst shield, width at f_2 level[1]	98–154, 129 ± 12^{ai}	109–156, 126 ± 12^{t}	115–139, 129 ± 7^{p}
length of free palpi	7–13, 10 ± 1^{ai}	8–11, 9 ± 1^{t}	8–12, 10 ± 1^{p}
width of free palpi, base	5–9, 7 ± 1^{ai}	5–9, 7 ± 1^{t}	6–7, 6 ± 0^{p}
gnathosomal solenidion	5–19, 14 ± 3^{ai}	11–16, 13 ± 1^{t}	9–16, 12 ± 2^{p}
sternum	42–69, 56 ± 7^{ai}	47–62, 54 ± 4^{t}	52–62, 59 ± 3^{p}
apodeme II	56–88, 77 ± 7^{ai}	66–90, 75 ± 5^{t}	70–89, 82 ± 5^{p}
apodeme III	53–80, 67 ± 6^{ai}	50–75, 59 ± 6^{t}	64–73, 68 ± 3^{p}
apodeme IV	20–86, 70 ± 11^{ai}	58–78, 66 ± 5^{t}	66–79, 73 ± 3^{p}
posterior apodeme IV[2]	20–42, 31 ± 5^{ai}	18–36, 26 ± 5^{s}	24–37, 32 ± 4^{p}
vi	6–14, 11 ± 2^{ah}	9–14, 12 ± 1^{s}	8–12, 10 ± 1^{o}
si	16–27, 20 ± 3^{ai}	9–22, 16 ± 4^{s}	22–29, 26 ± 2^{p}
se	37–76, 61 ± 10^{ai}	57–77, 63 ± 5^{t}	58–73, 66 ± 4^{p}
c_1	15–23, 18 ± 2^{ac}	11–19, 15 ± 2^{o}	17–31, 23 ± 3^{p}
c_2	34–74, 58 ± 9^{ah}	44–70, 55 ± 6^{t}	55–69, 62 ± 4^{p}
c_3	19–50, 37 ± 7^{ai}	34–47, 39 ± 4^{t}	36–46, 41 ± 2^{p}
c_p	32–65, 54 ± 8^{ai}	46–63, 53 ± 4^{t}	57–70, 62 ± 4^{p}
d_1	10–26, 15 ± 3^{ah}	7–18, 13 ± 3^{t}	15–19, 18 ± 1^{o}
d_2	20–43, 32 ± 6^{ai}	26–49, 36 ± 6^{s}	32–44, 38 ± 4^{p}
e_1	9–19, 13 ± 2^{ai}	7–15, 11 ± 2^{t}	13–21, 17 ± 2^{p}
e_2	18–39, 29 ± 5^{ai}	23–41, 32 ± 6^{t}	31–39, 35 ± 2^{p}
f_2	11–20, 15 ± 2^{ai}	8–17, 12 ± 2^{t}	19–26, 22 ± 2^{p}
h_1	6–18, 12 ± 3^{ai}	5–14, 9 ± 2^{t}	14–17, 16 ± 1^{p}
h_2	14–39, 21 ± 6^{ah}	14–26, 17 ± 3^{t}	21–37, 26 ± 4^{p}
h_3	97–172, 139 ± 18^{ab}	111–164, 136 ± 16^{j}	128–151, 135 ± 7^{k}
1a	85–143, 116 ± 13^{p}	104–142, 118 ± 10^{i}	87–127, 106 ± 15^{j}
4b	26–56, 38 ± 7^{ae}	27–43, 35 ± 5^{t}	27–41, 35 ± 4^{p}
3a	61–116, 88 ± 18^{q}	88–115, 103 ± 9^{k}	76–98, 87 ± 7^{j}
4a	58–117, 92 ± 14^{y}	84–111, 99 ± 8^{h}	59–97, 75 ± 13^{j}
g	9–15, 12 ± 1^{ad}	11–14, 12 ± 1^{s}	10–13, 12 ± 1^{n}
length of attachment organ[3]	45–68, 59 ± 6^{ai}	58–70, 63 ± 3^{t}	55–71, 63 ± 3^{p}
width of attachment organ[4]	50–75, 65 ± 6^{ai}	62–80, 71 ± 4^{t}	65–73, 69 ± 2^{p}
anterior sucker (ad_3)[4]	8–12, 10 ± 1^{ai}	8–12, 9 ± 1^{t}	9–10, 10 ± 0^{p}
median shield (ad_1+ad_2, ad_3)	21–31, 27 ± 2^{ai}	26–32, 29 ± 2^{t}	27–31, 29 ± 1^{p}
anterior lateral conoid (ps_2)	4–7, 5 ± 1^{ai}	5–7, 6 ± 1^{t}	5–6, 6 ± 0^{p}
posterior lateral conoid (ps_1)	4–6, 5 ± 1^{ai}	5–8, 6 ± 1^{t}	5–7, 6 ± 1^{p}
anterior cuticular conoid	3–7, 4 ± 1^{ai}	3–8, 5 ± 1^{t}	3–5, 4 ± 1^{p}
ih	3–6, 4 ± 1^{ai}	3–5, 4 ± 1^{t}	4–6, 5 ± 1^{p}
leg I	117–170, 149 ± 12^{ai}	130–154, 140 ± 7^{t}	128–150, 140 ± 6^{p}
tarsus I	32–47, 40 ± 3^{ai}	35–42, 38 ± 2^{t}	32–41, 36 ± 3^{o}
empodium I	24–35, 31 ± 3^{t}	27–37, 34 ± 3^{t}	25–37, 29 ± 3^{p}
ω_1 I	17–25, 21 ± 2^{x}	18–24, 22 ± 2^{m}	16–23, 19 ± 2^{m}
ω_2 I	6–12, 10 ± 1^{o}	9–11, 10 ± 1^{j}	7–9, 8 ± 1^{c}
ω_3 I	36–46, 41 ± 3^{ah}	41–47, 43 ± 2^{q}	34–41, 38 ± 2^{m}
ε I	3–6, 5 ± 1^{ag}	4–6, 5 ± 1^{t}	4–5, 4 ± 1^{k}
f I	50–80, 66 ± 7^{ag}	60–71, 66 ± 3^{t}	65–75, 69 ± 3^{o}
d I	69–100, 87 ± 6^{af}	66–99, 87 ± 10^{r}	84–98, 91 ± 4^{p}
ra I	14–22, 17 ± 2^{x}	16–20, 18 ± 1^{q}	16–20, 17 ± 1^{p}
la I	16–27, 21 ± 3^{ah}	19–30, 25 ± 3^{t}	20–26, 23 ± 2^{o}
wa I	25–39, 32 ± 3^{ai}	27–33, 30 ± 2^{t}	31–36, 33 ± 1^{p}
gT I	19–34, 26 ± 4^{ae}	21–35, 25 ± 3^{t}	20–30, 25 ± 3^{l}
hT I	17–29, 23 ± 3^{ag}	16–27, 23 ± 2^{r}	22–26, 24 ± 1^{o}
ϕ I	52–62, 58 ± 3^{m}	50–62, 56 ± 3^{n}	52–60, 56 ± 3^{l}
mG I	38–65, 51 ± 6^{ag}	42–67, 51 ± 7^{p}	44–63, 53 ± 4^{p}
cG I	42–108, 78 ± 14^{w}	80–93, 88 ± 4^{i}	76–92, 86 ± 5^{o}
σ I	5–10, 8 ± 1^{ac}	7–11, 9 ± 1^{o}	7–10, 8 ± 1^{k}

(continued)

Table 23. (Continued)

Structure	micheneri (group 1)	micheneri (group 2)	micheneri (group 3)
vF I	57–96, 78 ± 10^{ae}	61–94, 76 ± 10^{r}	69–83, 75 ± 4^{p}
pR I	90–144, 115 ± 14^{w}	82–138, 117 ± 15^{j}	92–127, 102 ± 10^{k}
leg II	116–167, 148 ± 12^{ah}	126–152, 141 ± 8^{t}	128–150, 142 ± 7^{p}
tarsus II	33–44, 39 ± 3^{ai}	32–43, 38 ± 2^{t}	32–40, 36 ± 2^{o}
empodium II	24–37, 31 ± 3^{ai}	22–37, 34 ± 3^{t}	26–38, 31 ± 3^{p}
ω_1 II	23–29, 26 ± 2^{v}	25–30, 27 ± 2^{l}	25–26, 25 ± 0^{h}
f II	56–75, 65 ± 5^{ah}	61–85, 68 ± 5^{t}	62–73, 67 ± 3^{p}
d II	66–103, 87 ± 9^{af}	82–99, 91 ± 5^{r}	82–97, 89 ± 4^{p}
ra II	18–25, 21 ± 2^{x}	18–25, 22 ± 2^{n}	17–25, 20 ± 2^{o}
la II	17–26, 22 ± 2^{ai}	19–28, 24 ± 3^{t}	19–27, 22 ± 2^{p}
wa II	24–41, 33 ± 4^{ah}	26–34, 30 ± 2^{t}	29–35, 32 ± 2^{n}
gT II	13–23, 17 ± 3^{z}	11–17, 14 ± 2^{p}	19–23, 21 ± 1^{h}
hT II	16–32, 23 ± 4^{af}	17–26, 22 ± 2^{s}	24–31, 27 ± 2^{p}
ϕ II	50–66, 60 ± 4^{u}	51–67, 58 ± 4^{p}	53–62, 57 ± 3^{l}
mG II	110–193, 164 ± 19^{ae}	152–238, 199 ± 20^{n}	159–202, 179 ± 14^{o}
cG II	11–20, 16 ± 2^{ai}	11–17, 14 ± 1^{t}	16–22, 18 ± 2^{m}
σ II	7–12, 9 ± 1^{ad}	8–11, 9 ± 1^{l}	8–10, 9 ± 1^{j}
vF II	78–138, 119 ± 15^{ai}	95–148, 123 ± 14^{s}	106–136, 120 ± 8^{o}
pR II	83–150, 126 ± 16^{z}	108–148, 130 ± 13^{n}	92–136, 115 ± 14^{h}
leg III	90–140, 122 ± 12^{ai}	97–133, 113 ± 9^{t}	106–120, 115 ± 4^{p}
tarsus III	27–40, 35 ± 3^{ai}	27–37, 31 ± 3^{t}	30–36, 32 ± 2^{p}
empodium III	23–32, 28 ± 3^{ai}	20–32, 28 ± 3^{t}	20–31, 25 ± 4^{p}
d III	107–184, 144 ± 19^{aa}	131–157, 144 ± 8^{p}	133–153, 143 ± 6^{o}
e III	56–83, 70 ± 7^{af}	61–78, 69 ± 6^{o}	65–76, 70 ± 3^{o}
f III	42–68, 58 ± 6^{ai}	52–76, 62 ± 7^{r}	56–64, 59 ± 2^{p}
s III	12–20, 16 ± 2^{af}	11–17, 14 ± 2^{s}	15–17, 15 ± 1^{o}
kT III	11–20, 14 ± 2^{ae}	10–13, 11 ± 1^{n}	14–18, 16 ± 1^{o}
ϕ III	22–37, 28 ± 4^{ag}	22–28, 25 ± 2^{s}	24–30, 26 ± 2^{n}
nG III	26–77, 58 ± 11^{ag}	53–72, 62 ± 5^{p}	50–70, 60 ± 6^{o}
sR III	43–97, 71 ± 11^{af}	58–86, 72 ± 8^{p}	51–80, 65 ± 7^{p}
leg IV	62–98, 83 ± 7^{ai}	60–82, 72 ± 6^{t}	70–83, 79 ± 3^{p}
tarsus IV	18–28, 23 ± 2^{ai}	15–22, 19 ± 2^{t}	17–26, 23 ± 2^{p}
d IV	308–428, 371 ± 30^{x}	355–431, 400 ± 25^{i}	363–441, 396 ± 25^{m}
e IV	2–10, 7 ± 2^{p}	4–8, 6 ± 2^{d}	
f IV	5–15, 7 ± 3^{o}	6–7, 6 ± 1^{b}	3–5, 4 ± 1^{c}
w IV	4–18, 11 ± 3^{ad}	9–14, 11 ± 1^{s}	7–12, 10 ± 2^{p}
s IV	4–11, 8 ± 2^{af}	3–7, 5 ± 1^{q}	2–6, 4 ± 1^{o}
ϕ IV	7–11, 9 ± 1^{j}	6–10, 8 ± 1^{l}	4–6, 5 ± 2^{b}
vF IV	25–103, 55 ± 21^{ah}	23–43, 30 ± 5^{q}	31–62, 46 ± 8^{o}

Superscript: 1 = excluding bases of f_2; 2 = from free end to outer posterior edge of coxa IV; 3 = medial horn-posterior sclerotized end; 4 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10 . . . ai = 35. hyst=hysterosomal.

Table 24. Measurements of four species of *Chaetodactylus* (range, mean ± SD).

Structure	**rozeni**	**claudus**	**hopliti**	**krombeini**
idiosoma, length	257–320, 292.4 ± 18.5[j]	331–378, 355.9 ± 18.3[j]	292–359, 327.7 ± 22.3[j]	329–376, 341.3 ± 13.5[j]
idiosoma, width	217–259, 238.9 ± 14.1[j]	262–339, 306.1 ± 22.1[j]	261–348, 309.3 ± 27[j]	261–326, 287.2 ± 21.2[j]
prodorsal shield, length	61–78, 68.9 ± 5.2[j]	86–101, 94.1 ± 4.3[j]	76–97, 85.8 ± 6.9[j]	87–100, 92.9 ± 4.5[j]
prodorsal shield, width	138–164, 151.6 ± 9.5[j]	156–176, 164.2 ± 6.8[j]	158–207, 183.7 ± 15.7[j]	178–200, 185.2 ± 7.5[j]
hyst shield, length	161–195, 179.1 ± 13.9[j]	183–209, 195.6 ± 8.3[j]	161–211, 188 ± 19[j]	175–209, 185 ± 10.3[j]
hyst shield, width anterior	172–211, 195.9 ± 12.7[j]	220–251, 237.5 ± 10.8[j]	203–264, 240.2 ± 18.2[j]	217–256, 230.4 ± 14.5[j]
hyst shield, width at f_2 level[1]	101–128, 117.7 ± 8.5[j]	119–142, 126 ± 6.7[j]	105–134, 115.8 ± 9.4[j]	109–133, 121.2 ± 8.2[j]
length of free palpi	8–11, 9.7 ± 0.8[j]	9–11, 10.1 ± 0.6[j]	8–12, 10.5 ± 1.4[j]	8–11, 9.7 ± 1.1[j]
width of free palpi, base	5–7, 6.4 ± 0.6[j]	7–9, 8 ± 0.8[j]	8–10, 8.5 ± 0.8[j]	7–9, 7.6 ± 0.5[j]
gnathosomal solenidion	8–12, 10.3 ± 1.3[i]	16–20, 17.6 ± 1.2[j]	16–21, 18.6 ± 1.7[j]	19–23, 21.5 ± 1.5[j]
sternum	41–56, 49.8 ± 4.5[j]	46–64, 53.8 ± 6[j]	39–55, 48.4 ± 5.1[j]	62–73, 65.5 ± 3.3[j]
apodeme II	63–75, 68.7 ± 3.4[j]	75–94, 82.5 ± 5.6[j]	68–90, 77.5 ± 8.2[j]	78–92, 85.7 ± 4.6[j]
apodeme III	48–57, 52.9 ± 3.2[j]	71–88, 79.8 ± 6.8[j]	62–78, 69.9 ± 4.5[j]	69–76, 72.5 ± 2.2[j]
apodeme IV	52–67, 60.4 ± 5.3[j]	72–90, 76.2 ± 5.2[j]	58–76, 66.1 ± 5.4[j]	70–77, 72.3 ± 2.3[j]
posterior apodeme IV[2]	12–25, 19.3 ± 4.3[i]	20–39, 30.4 ± 6[j]	31–41, 36.3 ± 3.5[j]	23–36, 31 ± 4[j]
vi	10–18, 12.3 ± 2.2[j]	10–14, 12.5 ± 1.2[j]	10–20, 14.8 ± 2.6[j]	14–18, 15.4 ± 1.3[j]
si	20–27, 23.4 ± 3[j]	37–52, 43.8 ± 4.8[j]	73–105, 86.1 ± 9.5[j]	67–86, 77.6 ± 6[j]
se	46–59, 52.4 ± 3.9[j]	55–71, 63.2 ± 5.8[j]	62–87, 72.9 ± 7[j]	66–75, 69.7 ± 2.9[j]
c_1	17–25, 20.7 ± 2.6[h]	26–35, 30.6 ± 2.7[j]	58–77, 67 ± 6.3[j]	56–67, 60.8 ± 3.8[i]
c_2	39–54, 46.1 ± 4.8[i]	50–74, 58.8 ± 7.2[j]	70–94, 78.5 ± 7.7[j]	70–83, 76.3 ± 4.1[j]
c_3	27–39, 34.9 ± 4[j]	29–43, 35.7 ± 4.8[j]	27–44, 35.5 ± 6.3[j]	33–51, 44.5 ± 5.5[j]
c_p	38–51, 44.9 ± 4.5[j]	60–74, 65.2 ± 4.4[j]	73–100, 84.6 ± 9.3[j]	70–86, 79.6 ± 5.9[j]
d_1	14–20, 17.3 ± 2.3[j]	29–36, 32 ± 2.1[j]	55–73, 60.5 ± 6.6[j]	48–67, 55.3 ± 6.2[j]
d_2	23–29, 25.6 ± 2.1[j]	27–39, 31.7 ± 3.3[j]	48–71, 56.8 ± 7.6[j]	45–58, 51 ± 3.7[i]
e_1	12–18, 14.9 ± 1.9[g]	25–29, 27.1 ± 1.6[j]	36–55, 44.3 ± 6.7[i]	31–42, 35.9 ± 3.5[i]
e_2	19–24, 22 ± 1.9[i]	24–30, 27 ± 2.1[j]	39–52, 45.4 ± 5.1[j]	34–42, 39.2 ± 2.3[j]
f_2	13–17, 14.6 ± 1.4[i]	24–30, 26.6 ± 2.2[j]	31–39, 34.7 ± 3.3[j]	20–30, 25.9 ± 3.1[j]
h_1	9–16, 13.7 ± 2.8[h]	20–27, 24.1 ± 2.1[j]	29–41, 32.7 ± 4.2[j]	23–28, 25.6 ± 1.4[j]
h_2	13–24, 19.1 ± 3.4[j]	35–45, 39.2 ± 3.5[j]	33–47, 38.6 ± 4.7[j]	25–33, 29.3 ± 2.7[j]
h_3	50–70, 60.4 ± 6[i]	20–26, 23.5 ± 2.2[j]	26–41, 34.5 ± 5.1[j]	27–35, 30.7 ± 3[j]
1a	78–101, 85.8 ± 10.1[e]	107–144, 121.8 ± 15.3[f]	62–89, 74.4 ± 8.7[i]	73–83, 78 ± 6.6[b]
4b	25–39, 31.6 ± 4.6[j]	62–82, 71.3 ± 6.9[i]	50–89, 61.6 ± 11[i]	69–86, 77.8 ± 5.3[i]
3a	61–80, 67.9 ± 6.4[h]	112–138, 122.8 ± 11.5[e]	66–84, 72.5 ± 6.4[i]	69–86, 75.7 ± 5.5[h]
4a	56–70, 62.3 ± 6[f]	113–135, 124 ± 15.6[b]	64–112, 83 ± 15.9[j]	70–125, 87.5 ± 15.9[i]
g	11–17, 13.9 ± 2.3[i]	10–14, 11.9 ± 1[j]	10–13, 11.9 ± 1.2[j]	12–15, 13.1 ± 0.9[i]
length of attachment organ[3]	45–67, 53.4 ± 7.3[j]	53–65, 58.7 ± 3.4[j]	45–53, 49.1 ± 2.4[j]	49–55, 52.1 ± 2[j]
width of attachment organ[4]	62–81, 72.7 ± 5.2[j]	61–72, 66.6 ± 3.6[j]	58–76, 67.3 ± 5.3[j]	69–80, 73.4 ± 3.5[j]
anterior sucker (ad_3)[4]	9–12, 10.5 ± 0.8[j]	9–10, 9.6 ± 0.5[j]	7–9, 7.9 ± 0.6[j]	8–10, 9.4 ± 0.6[j]
median shield (ad_1+ad_2, ad_3)	22–29, 26 ± 2.3[j]	25–31, 27.5 ± 1.9[j]	11–14, 12 ± 1[j]	27–31, 28.7 ± 1.5[j]
anterior lateral conoid (ps_2)	6–8, 6.8 ± 0.7[j]	5–7, 5.8 ± 0.7[j]	5–8, 5.8 ± 1[j]	6–8, 7 ± 0.7[j]
posterior lateral conoid (ps_1)	6–8, 6.9 ± 0.6[j]	5–7, 5.8 ± 0.7[j]	5–7, 5.9 ± 0.9[j]	6–9, 7 ± 0.9[j]
anterior cuticular conoid	3–8, 5.5 ± 1.7[j]	2–4, 3 ± 0.5[j]	3–6, 4.4 ± 1[j]	3–5, 4.4 ± 0.6[j]
ih	5–6, 5.6 ± 0.7[j]	3–5, 4.3 ± 0.8[j]	4–6, 4.7 ± 0.8[j]	4–8, 5.7 ± 1.1[i]
leg I	117–144, 130.1 ± 9.8[j]	145–168, 159 ± 6.7[j]	128–164, 150.8 ± 11.2[j]	142–161, 151.4 ± 6.2[j]
tarsus I	30–41, 35 ± 3.8[j]	43–49, 45 ± 2.4[j]	35–42, 39.3 ± 2.2[j]	33–39, 36 ± 2.2[j]
empodium I	17–28, 21.8 ± 3.4[j]	31–39, 35.7 ± 2.4[j]	23–33, 29.5 ± 2.5[j]	25–33, 29.2 ± 2.3[j]
ω_1 I	16–21, 18.5 ± 1.8[g]	25–28, 26.1 ± 1[i]	20–23, 21.3 ± 1.2[j]	22–27, 24.1 ± 1.5[j]
ω_2 I	8–11, 9.3 ± 1.3[f]	16–21, 17.8 ± 1.3[i]	13–16, 14.3 ± 1[j]	11–18, 14.6 ± 2.2[g]
ω_3 I	31–40, 35.2 ± 3[j]	50–56, 52.8 ± 1.7[j]	37–42, 39.5 ± 2.1[j]	40–46, 42.9 ± 2[j]
ε I	4–5, 4.6 ± 0.5[f]	5–7, 5.4 ± 0.7[i]	4–5, 4.5 ± 0.4[j]	5–6, 5.7 ± 0.5[g]
f I	48–62, 55.7 ± 4.3[j]	80–97, 86.4 ± 5.8[j]	56–69, 62.5 ± 4.3[j]	59–73, 65.3 ± 5.5[j]
d I	75–91, 80.5 ± 5.3[j]	97–127, 111.3 ± 10.4[j]	78–92, 86.1 ± 4.5[j]	78–106, 90.2 ± 8[j]
ra I	15–20, 17 ± 1.9[j]	17–21, 18.6 ± 1.8[i]	16–22, 18.6 ± 2.1[j]	16–19, 17.5 ± 0.9[j]
la I	16–21, 18.2 ± 1.5[i]	21–29, 25.6 ± 2.6[i]	21–26, 23.1 ± 1.8[i]	25–30, 27.1 ± 1.6[i]
wa I	27–33, 28.9 ± 1.9[j]	36–42, 38 ± 2.2[j]	23–34, 27.2 ± 3.4[j]	19–27, 21.7 ± 2.9[j]
gT I	22–26, 23.5 ± 1.4[h]	29–41, 34.1 ± 4[j]	25–34, 28.9 ± 3.1[j]	27–37, 30.8 ± 3.7[h]
hT I	18–27, 22.1 ± 2.8[i]	29–36, 32.7 ± 2.2[j]	23–33, 29.6 ± 3.3[j]	25–33, 29.1 ± 2.4[j]
ϕ I	58–61, 58.5 ± 1.2[h]	68–73, 70.8 ± 2.1[d]	48–61, 54 ± 3.8[j]	55–69, 59.5 ± 5.2[f]
mG I	37–55, 46.9 ± 6.6[i]	85–118, 100.1 ± 11.4[j]	87–115, 105.7 ± 11.6[h]	76–108, 94.5 ± 8.6[j]
cG I	53–67, 57.7 ± 5.2[i]	150–178, 160.6 ± 10.3[h]	139–172, 155.8 ± 10.8[g]	136–198, 162.1 ± 22.1[i]
σ I	7–9, 8.1 ± 0.7[i]	21–28, 24.3 ± 1.7[j]	21–31, 24.5 ± 2.7[j]	25–34, 29.4 ± 3.5[j]

(continued)

Table 24. (Continued)

Structure	rozeni	claudus	hopliti	krombeini
vF I	52–66, 58.3 ± 4^{j}	102–130, 112.8 ± 9.3^{j}	67–97, 82.4 ± 8.9^{j}	72–98, 83.8 ± 10.2^{i}
pR I	82–120, 97.6 ± 13.5^{g}	104–145, 124.7 ± 17.1^{g}	87–120, 99.6 ± 11.8^{g}	106–133, 115.4 ± 7.8^{i}
leg II	115–143, 131.2 ± 10.3^{j}	141–163, 156.7 ± 6.5^{j}	128–161, 148.9 ± 10.6^{j}	142–158, 148.2 ± 4.5^{j}
tarsus II	31–40, 34.7 ± 3.3^{j}	41–48, 44.4 ± 2.2^{j}	36–41, 38.3 ± 1.6^{j}	34–39, 37.1 ± 1.8^{j}
empodium II	20–28, 23.9 ± 2.8^{j}	35–40, 36.8 ± 1.4^{j}	22–33, 30.2 ± 3.3^{j}	25–34, 29.4 ± 2.4^{j}
ω_1 II	18–25, 21.9 ± 2.3^{h}	30–36, 33.5 ± 2.2^{j}	25–29, 27 ± 1.1^{j}	27–32, 29.3 ± 1.7^{j}
f II	49–65, 56.8 ± 5.3^{i}	75–96, 83.1 ± 6.7^{j}	53–67, 61.7 ± 4.6^{j}	53–73, 62.7 ± 6.4^{j}
d II	75–90, 82.7 ± 5.7^{j}	103–127, 114.6 ± 7.2^{j}	80–102, 89.8 ± 7.5^{j}	75–98, 87.2 ± 7^{j}
ra II	18–21, 18.9 ± 1.3^{i}	19–22, 20.4 ± 0.8^{h}	16–27, 19 ± 3.1^{j}	16–21, 18.7 ± 1.5^{j}
la II	18–21, 19.5 ± 1.2^{h}	22–28, 25.4 ± 1.8^{j}	20–28, 24.6 ± 2.1^{j}	27–32, 28.2 ± 2^{j}
wa II	30–34, 31.4 ± 1.7^{i}	36–42, 38.1 ± 2^{j}	25–34, 28.3 ± 3.4^{j}	19–23, 20.7 ± 1.5^{j}
gT II	17–23, 20.3 ± 2.1^{f}	15–24, 18.8 ± 2.4^{j}	19–34, 26.4 ± 6.2^{e}	24–36, 29.4 ± 4.9^{f}
hT II	21–34, 27.1 ± 4.2^{i}	26–36, 30.8 ± 3.6^{j}	25–40, 32.1 ± 4.5^{j}	27–39, 32.4 ± 3.7^{j}
ϕ II	53–62, 58 ± 3.5^{e}	70–75, 72.3 ± 2^{f}	55–63, 58.7 ± 3.2^{j}	59–70, 64 ± 3.9^{f}
mG II	151–184, 172.6 ± 11.1^{h}	180–237, 201.9 ± 19.5^{j}	176–211, 193.6 ± 10.2^{h}	164–234, 195.3 ± 20.9^{j}
cG II	12–15, 13.3 ± 1^{j}	16–27, 20.5 ± 3.6^{j}	12–21, 16.8 ± 2.7^{j}	12–18, 16.1 ± 2^{j}
σ II	6–10, 7.9 ± 1.3^{h}	16–19, 17.2 ± 1.3^{i}	11–14, 12.7 ± 0.9^{j}	15–21, 17.8 ± 2.3^{g}
vF II	66–103, 85.3 ± 11.7^{j}	117–161, 139.7 ± 14.3^{j}	101–120, 110.9 ± 7.3^{j}	90–131, 108.9 ± 14.9^{j}
pR II	85–102, 91.5 ± 5.7^{f}	124–166, 138.6 ± 13.9^{i}	110–129, 122.1 ± 8.5^{f}	94–136, 112.5 ± 12.7^{i}
leg III	93–118, 107.8 ± 9.4^{j}	121–142, 133.3 ± 7.1^{j}	112–136, 126.5 ± 9^{j}	108–135, 121.1 ± 7.8^{i}
tarsus III	27–33, 30.4 ± 2.3^{j}	40–43, 41.4 ± 0.9^{j}	33–41, 37.9 ± 2.7^{j}	28–40, 33.8 ± 3.6^{i}
empodium III	16–24, 20.7 ± 2.8^{j}	25–36, 31.4 ± 4.3^{j}	27–30, 28.2 ± 1.4^{j}	20–29, 25.2 ± 3.4^{j}
d III	119–159, 140.7 ± 15.4^{g}	160–207, 180.6 ± 17.6^{i}	148–176, 161.5 ± 10.4^{i}	125–158, 141.3 ± 10.6^{j}
e III	51–68, 59.8 ± 4.8^{h}	80–110, 92.3 ± 9^{j}	61–73, 66.4 ± 3.8^{h}	61–75, 68.3 ± 5.9^{h}
f III	41–56, 48.9 ± 4.9^{j}	66–92, 79 ± 8.7^{j}	58–66, 61.4 ± 3^{h}	50–64, 58.9 ± 3.6^{j}
s III	14–22, 17.4 ± 2.3^{j}	27–36, 31.6 ± 2.3^{j}	19–28, 22.6 ± 3.3^{i}	12–20, 15.9 ± 2.5^{j}
kT III	16–20, 18.1 ± 1.3^{g}	26–36, 32.2 ± 3.2^{i}	18–31, 25 ± 5.1^{i}	20–35, 26.8 ± 5^{h}
ϕ III	17–24, 20.6 ± 2.8^{j}	26–33, 28.6 ± 2.1^{j}	22–29, 25.5 ± 2.4^{j}	24–30, 26.5 ± 1.6^{j}
nG III	37–55, 46.4 ± 5.5^{j}	119–168, 140 ± 13.8^{j}	114–137, 122.3 ± 6.9^{j}	86–112, 98.9 ± 8.9^{j}
sR III	39–62, 51.6 ± 7.8^{h}	101–131, 111.6 ± 11.1^{h}	78–117, 89.9 ± 14.4^{j}	76–106, 87.5 ± 9.1^{j}
leg IV	59–71, 64.9 ± 4.8^{j}	99–112, 105.3 ± 3.9^{j}	86–112, 98.9 ± 7.7^{j}	90–112, 103.4 ± 7.1^{j}
tarsus IV	17–22, 19.5 ± 1.5^{j}	38–41, 39.5 ± 1.1^{j}	25–36, 30.2 ± 3^{j}	30–36, 32.8 ± 2.2^{j}
d IV	359–392, 373.2 ± 14.1^{d}	420–523, 473.3 ± 37.7^{g}	348–493, 406 ± 49.8^{g}	410–505, 455.5 ± 34.3^{g}
e IV	*3a*	53–74, 60.2 ± 5.8^{j}	212–323, 275.6 ± 33^{j}	229–340, 286.2 ± 38.4^{i}
f IV	3–4, 3.6 ± 0.2^{b}	46–71, 59.2 ± 8^{j}	218–309, 267.2 ± 28.6^{j}	197–324, 269.1 ± 50.4^{j}
w IV	6–9, 7.6 ± 1.2^{j}	12–18, 14.3 ± 2.1^{j}	27–40, 32.2 ± 4.8^{j}	22–43, 32.9 ± 6.4^{j}
s IV	4–6, 4.7 ± 1.2^{b}	13–17, 14.8 ± 1.6^{j}	29–43, 34.8 ± 4.4^{j}	28–44, 35.9 ± 6.2^{j}
ϕ IV	5–6, 5.5 ± 0.7^{b}	8–13, 10.7 ± 1.5^{h}	11–13, 12.3 ± 1^{j}	11–14, 12.7 ± 1.1^{d}
vF IV	20–27, 23.3 ± 2.8^{f}	80–125, 102.9 ± 14.6^{j}	89–117, 100.9 ± 9.8^{j}	83–133, 100.5 ± 16.3^{j}

Superscript: 1 = excluding bases of f_2; 2 = from free end to outer posterior edge of coxa IV; 3 = medial horn-posterior sclerotized end; 4 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10. hyst = hysterosomal.

Table 25. Measurements of four species of *Sennertia* (range, mean ± SD).

Structure	**haustrifera**	**recondita**	**sodalis**	**argentina**
idiosoma, length	449–598, 521.2 ± 49.9[j]	476–623, 550.7 ± 47.1[j]	420–481, 448 ± 22[j]	340–419, 380.8 ± 23.4[j]
idiosoma, width	281–367, 319 ± 29.7[j]	291–363, 331.4 ± 23.7[j]	270–335, 301.3 ± 22.3[j]	239–324, 266.1 ± 24.4[i]
hyst shield, length	331–454, 402.1 ± 38[j]	350–460, 424.1 ± 32.8[j]	338–390, 361.1 ± 19.8[j]	181–215, 198.7 ± 11.1[j]
hyst shield, width anterior	220–316, 271.6 ± 29.1[j]	230–295, 274.4 ± 19.9[j]	235–300, 259 ± 22.9[j]	80–100, 92.4 ± 7.3[j]
hyst shield, width at f_2 level[1]	197–282, 243.7 ± 25.2[j]	205–240, 225.3 ± 13.2[j]	163–218, 188.6 ± 15.5[j]	128–158, 143.5 ± 9.5[j]
gnathosomal solenidion	4–5, 4.4 ± 0.4[j]	5–8, 5.9 ± 0.8[j]	2–3, 2.6 ± 0.7[j]	1–1, 0.9 ± 0.1[i]
sternum	29–41, 32.8 ± 3.7[j]	35–63, 50.9 ± 9.9[j]	28–44, 36 ± 4.9[j]	27–33, 29.8 ± 1.8[j]
apodeme II	83–118, 101.2 ± 10.4[j]	87–112, 104.6 ± 7.7[j]	90–106, 96.4 ± 6[j]	68–78, 72.5 ± 3[j]
posterior apodeme II	90–123, 107.7 ± 11.1[j]	80–112, 94.9 ± 9.1[j]	64–101, 83.4 ± 13.3[j]	46–61, 54.1 ± 4.1[j]
apodeme III	39–67, 54.9 ± 8.9[j]	40–54, 48.1 ± 4.1[j]	35–47, 40.6 ± 3.7[j]	32–39, 35.8 ± 2.3[j]
apodeme IV	71–99, 87.7 ± 8.6[j]	81–105, 94.9 ± 8.5[j]	71–82, 75.4 ± 3.7[j]	61–70, 66.2 ± 2.9[j]
vi	6–10, 8.4 ± 1.2[j]	8–11, 9.1 ± 1.2[j]	7–10, 8.4 ± 1.5[j]	8–13, 10.7 ± 1.8[j]
si	45–63, 54.8 ± 5.3[j]	46–58, 52.5 ± 4.1[j]	37–45, 42.1 ± 2.3[j]	75–92, 86.2 ± 5.3[j]
se	50–71, 63.5 ± 6.7[j]	57–74, 65.7 ± 4.7[j]	53–65, 59.3 ± 3.7[j]	44–55, 49.8 ± 3.1[j]
c_1	6–12, 8.5 ± 1.8[i]	5–11, 7.7 ± 1.9[j]	5–8, 7 ± 1[j]	3–8, 5.3 ± 1.3[j]
c_2	51–80, 67.2 ± 8.1[j]	56–68, 64.4 ± 3.7[j]	54–65, 58.8 ± 3.6[j]	66–118, 86.4 ± 18.4[j]
c_3	21–31, 26 ± 3.7[j]	33–44, 39.5 ± 3.8[j]	27–39, 30 ± 3.8[j]	23–30, 26.4 ± 2.2[j]
c_p	57–91, 79.3 ± 9.3[j]	72–84, 78.1 ± 3.8[j]	64–77, 70.5 ± 3.4[j]	82–102, 95 ± 6.9[j]
d_1	7–12, 8.8 ± 1.6[j]	3–12, 8.2 ± 2.7[j]	6–12, 7.7 ± 1.6[j]	8–16, 12.5 ± 2[j]
d_2	55–83, 71 ± 8.1[j]	60–75, 69.2 ± 5.5[j]	59–68, 63.2 ± 3.8[j]	91–108, 99.9 ± 5.8[j]
e_1	6–10, 8.1 ± 1.5[j]	7–9, 7.7 ± 0.7[j]	6–7, 6.3 ± 0.6[h]	5–10, 7.6 ± 1.4[j]
e_2	56–82, 71.6 ± 7.2[j]	60–81, 68.8 ± 6.8[j]	56–67, 61.8 ± 3.9[j]	67–86, 76.7 ± 7.3[j]
f_2	7–11, 9 ± 1.2[j]	5–11, 8 ± 1.7[j]	6–8, 6.8 ± 1[j]	6–8, 7 ± 0.7[i]
h_1	5–8, 6.5 ± 1[j]	6–8, 7.2 ± 0.8[j]	5–9, 6.7 ± 1.2[j]	7–10, 8.4 ± 0.8[j]
h_2	9–15, 11.2 ± 1.6[j]	10–14, 11.7 ± 1.3[j]	10–13, 11.6 ± 0.9[j]	4–7, 5.3 ± 0.7[i]
h_3	115–193, 155.4 ± 29.9[h]	113–153, 131.1 ± 12.5[j]	108–132, 121.9 ± 7.4[i]	73–95, 85.1 ± 7.1[h]
1a	105–158, 132.7 ± 20.3[f]	113–151, 130.3 ± 12.7[h]	93–118, 101.5 ± 11.8[d]	17–25, 21.9 ± 2[j]
4b	8–11, 9.5 ± 1[j]	27–36, 31.4 ± 2.9[j]	22–31, 25.7 ± 3[j]	14–16, 14.8 ± 0.8[j]
3a	97–190, 137.9 ± 29.5[h]	87–177, 134.9 ± 28[h]	129–150, 134.2 ± 6.4[i]	22–27, 24.7 ± 1.2[j]
4a	25–36, 30.5 ± 3.7[j]	31–41, 37.6 ± 3.6[j]	21–30, 25.2 ± 2.5[j]	25–30, 27.2 ± 1.6[j]
g	18–27, 22.7 ± 2.7[j]	22–27, 24.5 ± 1.6[j]	17–23, 20.3 ± 1.6[j]	15–20, 17.3 ± 1.3[j]
length of attachment organ[2]	93–146, 124.1 ± 16.1[j]	82–105, 96.7 ± 6.1[j]	80–89, 83.4 ± 3.4[j]	58–72, 66.3 ± 4.6[j]
width of attachment organ[3]	134–227, 184.1 ± 26.4[j]	120–155, 135.1 ± 10.4[j]	102–122, 112.8 ± 6.4[j]	79–97, 88.1 ± 4.9[j]
anterior sucker (ad_3)[3]	20–27, 23.6 ± 2.3[j]	23–35, 28.9 ± 3.2[j]	19–23, 21.2 ± 1.2[j]	32–38, 35.4 ± 2[j]
median shield (ad_1+ad_2, ad_3)	44–85, 67.4 ± 11.6[j]	27–33, 30.8 ± 1.7[j]	25–29, 26.9 ± 1.2[j]	27–34, 30.3 ± 2.3[j]
anterior lateral conoid (ps_2)	21–32, 26.5 ± 2.8[j]	19–24, 22.4 ± 1.5[j]	20–23, 21.6 ± 0.9[j]	11–13, 11.8 ± 0.8[j]
posterior lateral conoid (ps_1)	15–25, 20.2 ± 2.8[j]	16–21, 19.7 ± 1.3[j]	17–22, 19.8 ± 1.5[j]	9–13, 10.3 ± 1.1[j]
leg I	207–272, 241.3 ± 17.8[j]	208–260, 234.1 ± 16.3[j]	201–230, 216.9 ± 11.7[j]	146–167, 158 ± 6.3[j]
tarsus I	57–74, 67 ± 5.1[j]	55–71, 65 ± 5.3[j]	60–71, 64 ± 4[j]	37–46, 41 ± 2.5[j]
empodium I	20–26, 23.3 ± 1.8[j]	18–27, 23.1 ± 3[j]	20–26, 22.6 ± 2.1[j]	23–29, 26.6 ± 2[h]
ω_1 I	20–23, 21.1 ± 1[g]	19–28, 22.6 ± 3.2[g]	20–23, 20.9 ± 0.8[j]	15–17, 15.9 ± 1[h]
ω_2 I		11–17, 13.6 ± 2[i]	9–12, 10.3 ± 1.3[e]	8–11, 8.9 ± 1.1[f]
ω_3 I	43–52, 47.8 ± 3.3[j]	49–53, 50.5 ± 1.6[i]	38–46, 43 ± 2.6[j]	24–31, 27.1 ± 2.2[j]
ε I	5–7, 6 ± 0.6[j]	5–8, 5.8 ± 0.9[j]	4–6, 5.2 ± 0.8[j]	5–6, 5.2 ± 0.2[i]
f I	52–70, 63.1 ± 6.8[i]	59–73, 66.1 ± 4.4[j]	45–67, 56.2 ± 6.7[j]	33–43, 38.5 ± 3.6[h]
d I	78–100, 90.3 ± 6.5[j]	78–123, 98.5 ± 11.8[j]	78–93, 86.2 ± 5.1[j]	103–140, 126.3 ± 12.1[j]
ra I	16–21, 19 ± 1.7[j]	13–24, 18.8 ± 3.3[i]	14–19, 16.2 ± 1.7[h]	16–20, 17.4 ± 1.4[j]
la I	9–13, 10.3 ± 1.1[j]	10–13, 11.6 ± 1.1[j]	8–12, 10.4 ± 1.2[j]	5–6, 5.2 ± 0.3[j]
wa I	11–16, 13 ± 1.2[j]	12–16, 13.6 ± 1.5[j]	9–12, 10 ± 1.2[j]	13–18, 15.9 ± 1.4[j]
gT I	27–39, 31.7 ± 4[i]	16–31, 24.8 ± 6[h]	19–31, 24.2 ± 4[j]	18–21, 19.1 ± 1.1[j]
hT I	25–38, 31.2 ± 3.6[j]	24–30, 27.2 ± 1.7[j]	17–24, 19.7 ± 2.2[j]	13–18, 15.2 ± 1.2[j]
ϕ I	110–130, 120.6 ± 7.1[g]	109–115, 111.9 ± 2.7[g]	107–121, 113.3 ± 5.2[f]	
mG I	49–75, 64.8 ± 7.7[j]	49–67, 59.5 ± 6.7[j]	51–55, 52.3 ± 1.4[j]	29–38, 33.3 ± 2.5[j]
cG I	15–21, 17.5 ± 1.8[j]	18–23, 20.8 ± 2.1[j]	12–21, 15.4 ± 2.5[j]	12–15, 12.9 ± 1[j]
σ I	12–16, 13.4 ± 1.4[j]	12–15, 13.1 ± 1[j]	11–13, 11.8 ± 0.9[j]	17–20, 18.8 ± 1[j]
vF I	58–84, 71.6 ± 7.5[j]	75–93, 86.1 ± 5.7[j]	63–74, 67.5 ± 4.1[i]	50–77, 62.2 ± 10.6[j]
pR I	130–165, 145.1 ± 13.2[g]	110–183, 147.8 ± 20.1[i]	100–143, 120.4 ± 15.7[j]	12–15, 13.1 ± 1.2[j]
leg II	201–260, 234 ± 17.4[j]	202–249, 225.7 ± 14.2[j]	200–229, 214.8 ± 10.7[j]	144–163, 156.5 ± 5.3[j]
tarsus II	57–70, 63.9 ± 4.4[j]	54–68, 62.3 ± 4.3[j]	58–70, 63.6 ± 4[j]	40–50, 43.5 ± 2.9[j]
empodium II	20–25, 22.7 ± 1.5[j]	18–28, 22.8 ± 3.3[j]	22–26, 23.7 ± 1.7[j]	25–28, 26.4 ± 1.4[g]
ω_1 II	25–28, 26.2 ± 1.2[i]	23–28, 25.2 ± 1.8[h]	24–27, 25.1 ± 1.2[j]	16–20, 17.9 ± 1.2[i]

(continued)

Table 25. (Continued)

Structure	**haustrifera**	**recondita**	**sodalis**	**argentina**
f II	57–75, 67.2 ± 5.5^{j}	52–73, 62 ± 6.9^{j}	49–69, 60.5 ± 7.1^{j}	38–49, 43.4 ± 2.9^{j}
d II	77–99, 87.7 ± 6.9^{i}	85–115, 99 ± 10.4^{j}	68–94, 82.4 ± 7.8^{j}	126–155, 143.6 ± 9.3^{j}
ra II	16–26, 21.4 ± 2.8^{j}	16–22, 19.1 ± 2.2^{g}	16–17, 16.6 ± 0.5^{e}	17–21, 19 ± 1.1^{j}
la II	8–13, 10.2 ± 1.7^{j}	8–13, 11 ± 1.8^{j}	8–12, 9.8 ± 1.2^{j}	4–7, 5.2 ± 1^{j}
wa II	11–14, 12.4 ± 0.8^{i}	11–16, 13.3 ± 1.3^{j}	10–12, 10.5 ± 0.8^{j}	17–19, 17.7 ± 0.8^{j}
gT II	18–33, 25.4 ± 4.6^{g}	17–30, 23.7 ± 4.4^{i}	21–28, 24.5 ± 2.1^{j}	20–25, 22 ± 1.8^{j}
hT II	25–32, 28.7 ± 1.9^{i}	28–35, 31.6 ± 2.1^{j}	19–26, 21.9 ± 2.1^{j}	17–22, 18.6 ± 1.5^{j}
ϕ II	85–118, 109.6 ± 9.7^{j}	90–110, 101 ± 6.8^{j}	90–105, 95.5 ± 5.3^{j}	
mG II	59–90, 77.9 ± 9.9^{j}	58–80, 71.7 ± 7.9^{j}	57–73, 67 ± 4.7^{j}	68–88, 75.5 ± 6.3^{j}
cG II	11–17, 14 ± 2.3^{j}	12–16, 14.4 ± 1.1^{j}	10–13, 11.5 ± 1.2^{j}	10–15, 13.2 ± 1.8^{j}
σ II	9–10, 9.6 ± 0.6^{j}	8–10, 9.1 ± 0.9^{i}	7–10, 8.6 ± 1^{j}	10–15, 12.7 ± 1.6^{i}
vF II	64–100, 80.4 ± 10^{j}	75–94, 86.7 ± 6.4^{j}	73–91, 81 ± 6.5^{j}	60–75, 67.4 ± 4^{j}
pR II	115–180, 138.6 ± 22.8^{i}	125–167, 143.9 ± 12^{j}	110–138, 122.4 ± 10.7^{g}	14–17, 14.9 ± 0.9^{j}
leg III	139–188, 163.6 ± 15.7^{j}	146–168, 158 ± 7.6^{j}	136–165, 152.4 ± 9.7^{j}	134–153, 143.9 ± 6.9^{j}
tarsus III	40–56, 47.6 ± 5^{j}	42–51, 46.3 ± 3.8^{j}	42–55, 48.5 ± 4.5^{j}	45–57, 50.4 ± 3.9^{j}
empodium III	17–29, 23.2 ± 3.3^{j}	18–23, 20.9 ± 1.7^{j}	16–25, 20.6 ± 2.8^{j}	24–30, 28.2 ± 1.9^{i}
d III	170–214, 198.5 ± 16.9^{f}	127–204, 171.2 ± 28.4^{i}	101–213, 157.1 ± 29.6^{i}	215–282, 250.8 ± 21.1^{i}
e III	65–103, 84.8 ± 10.2^{j}	73–95, 84 ± 7.5^{j}	60–91, 70.4 ± 10.3^{j}	125–162, 141.3 ± 13^{j}
f III	47–72, 58.9 ± 8.5^{j}	42–65, 55.5 ± 6.8^{j}	45–62, 52.2 ± 5.4^{j}	107–128, 117.7 ± 5.2^{j}
s III	12–13, 12.5 ± 0.4^{j}	8–11, 9.7 ± 1^{j}	9–11, 10.2 ± 0.8^{j}	16–19, 17.2 ± 0.9^{j}
kT III	12–16, 14.3 ± 1.7^{f}	12–15, 12.9 ± 1.3^{h}	10–16, 12.3 ± 1.9^{h}	19–25, 22 ± 1.6^{j}
ϕ III	25–38, 31 ± 4.2^{j}	19–29, 24.5 ± 2.8^{i}	25–31, 27.4 ± 2.4^{j}	23–30, 26.2 ± 2^{j}
nG III	18–24, 21.3 ± 2.1^{j}	16–21, 18 ± 1.4^{j}	13–20, 15.5 ± 2.5^{j}	25–35, 29.6 ± 3.1^{j}
σ III	6–8, 6.9 ± 0.9^{j}	5–8, 6.3 ± 0.8^{i}	5–7, 5.5 ± 0.5^{j}	9–12, 10.6 ± 1^{j}
sR III	115–145, 132.4 ± 9.2^{j}	102–145, 126.5 ± 15.2^{h}	94–133, 115.4 ± 12.8^{i}	15–18, 16.1 ± 1.1^{j}
leg IV	68–82, 73.3 ± 4.3^{j}	73–85, 79.2 ± 3.4^{j}	58–71, 65.6 ± 4.3^{j}	115–135, 125 ± 5.8^{j}
tarsus IV	12–17, 14 ± 1.3^{j}	15–19, 16.5 ± 1.3^{j}	12–14, 13.2 ± 0.7^{j}	35–45, 39.7 ± 3.1^{j}
d IV	339–410, 377.4 ± 28.6^{h}	303–422, 362.7 ± 42^{j}	265–392, 331.8 ± 37.2^{j}	654–827, 719.3 ± 65.4^{f}
e IV	3–6, 4.4 ± 1.1^{j}	4–7, 5.7 ± 0.8^{j}	4–5, 4.7 ± 0.4^{j}	10–13, 11.6 ± 1.4^{j}
f IV	4–7, 5.3 ± 1.1^{j}	6–8, 7.1 ± 0.7^{j}	4–5, 4.7 ± 0.5^{j}	12–14, 12.6 ± 0.6^{j}
w IV	7–11, 8.5 ± 1.4^{j}	7–10, 8.3 ± 1^{j}	6–8, 7 ± 0.4^{j}	11–16, 13.4 ± 1.3^{j}
s IV	3–7, 4.5 ± 1.2^{j}	4–7, 5.2 ± 1^{g}	3–5, 3.7 ± 0.6^{i}	4–9, 6.2 ± 1.9^{j}
vF IV	16–24, 18.6 ± 2.7^{j}	19–26, 21.8 ± 2.9^{j}	12–15, 13.4 ± 0.8^{j}	16–24, 19.8 ± 2.3^{j}

Superscript: 1 = excluding bases of f_2; 2 = medial horn-posterior sclerotized end; 3 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10. hyst = hysterosomal.

Table 26. Measurements of four species of *Sennertia* (range, mean ± SD).

Structure	hurdi	lucrosa	faini	segnis
idiosoma, length	272–295, 284.1 ± 8.3[j]	281–348, 315.6 ± 15[bk]	294–345, 325.9 ± 20.2[f]	451–550, 491.5 ± 36[j]
idiosoma, width	233–272, 246.8 ± 11.5[j]	252–326, 283.2 ± 24[j]	273–298, 285.5 ± 17.7[b]	405–534, 462.3 ± 41.3[j]
hyst shield, length	154–177, 166.4 ± 5.9[j]	167–196, 179.3 ± 9.7[j]	174–175, 174.5 ± 0.7[b]	231–276, 246.5 ± 14[j]
hyst shield, width anterior	75–83, 78.6 ± 3[j]	107–133, 120.5 ± 8.1[j]	116–122, 118.8 ± 3.9[b]	165–230, 190 ± 21.4[j]
hyst shield, width at f_2 level[1]	81–92, 88.2 ± 3.3[j]	121–141, 131.5 ± 7.8[j]	122–125, 123.3 ± 1.8[b]	200–263, 225.9 ± 20.1[j]
gnathosomal solenidion	3–5, 3.5 ± 0.6[j]	5–6, 5.6 ± 0.5[j]	6–7, 6.3 ± 0.6[b]	4–8, 6.5 ± 1.2[j]
sternum	28–35, 31.7 ± 2.2[j]	29–41, 34.8 ± 4[j]	35–38, 36.3 ± 1.8[b]	48–73, 57.7 ± 7[j]
apodeme II	65–74, 69 ± 2.8[j]	62–85, 72.1 ± 5[bt]	71–80, 75.3 ± 3.1[f]	106–135, 118.8 ± 10[j]
posterior apodeme II	45–55, 49.7 ± 2.7[j]	44–55, 47.8 ± 3.7[j]	45–47, 46 ± 1.4[b]	62–86, 74.3 ± 8[j]
apodeme III	29–38, 34.3 ± 2.6[j]	36–45, 40 ± 2.7[j]	37–39, 38 ± 1.4[b]	57–76, 64.8 ± 6.1[j]
apodeme IV	59–68, 62.8 ± 2.9[j]	64–77, 69.7 ± 4.1[j]	67–75, 71 ± 5.7[b]	92–122, 109.7 ± 10.3[j]
vi	6–11, 7.6 ± 1.9[j]	7–11, 9 ± 1[j]	9–12, 10.3 ± 2.5[b]	8–11, 9.2 ± 1.2[j]
si	49–67, 56.1 ± 6.3[j]	38–52, 44.6 ± 4.6[j]	41 ± 0[b]	47–66, 57.6 ± 5.7[j]
se	75–90, 80.5 ± 5.4[j]	58–76, 66.9 ± 4.8[j]	62.5 ± 0[b]	91–102, 97.1 ± 4[j]
c_1	50–61, 54.9 ± 3.7[j]	43–53, 46.9 ± 3.4[j]	44–46, 44.9 ± 0.8[b]	47–62, 55.5 ± 5.2[j]
c_2	72–86, 78.8 ± 4.4[j]	65–84, 73 ± 5.4[j]	60–67, 63.5 ± 4.9[b]	92–110, 99.4 ± 5.8[j]
c_3	39–49, 44.6 ± 3.7[j]	23–29, 27.1 ± 1.7[j]	27–27, 26.8 ± 0.4[b]	24–42, 30.9 ± 5.1[j]
c_p	82–97, 88.7 ± 4.9[j]	62–75, 68.7 ± 3.7[j]	60–68, 64 ± 5.7[b]	91–109, 101.2 ± 6.4[j]
d_1	20–28, 23.1 ± 2.2[j]	24–50, 37 ± 4.6[bt]	24–32, 27.3 ± 2.8[f]	48–69, 59.8 ± 7.2[j]
d_2	74–89, 79.6 ± 4.5[j]	60–76, 68.8 ± 5.2[j]	61–65, 63 ± 2.8[b]	86–101, 95.4 ± 4.8[j]
e_1	11–24, 16.3 ± 4[j]	28–38, 31.6 ± 3.8[j]		57–68, 62.6 ± 4.2[j]
e_2	69–81, 75.2 ± 3.8[j]	56–74, 63.1 ± 6.1[j]	59–60, 59.3 ± 0.4[b]	86–107, 92.9 ± 7[j]
f_2	4–6, 5.1 ± 0.4[i]	7–9, 7.7 ± 0.7[i]	5–8, 6.6 ± 2[b]	7–12, 9.2 ± 1.4[j]
h_1	4–8, 5.5 ± 1.2[j]	6–8, 7.3 ± 0.5[j]	6–8, 6.9 ± 2[b]	7–10, 8.6 ± 1.1[j]
h_2	5–8, 6 ± 0.9[j]	11–15, 13.1 ± 1.1[j]		13–18, 15.4 ± 1.1[j]
h_3	82–95, 88.9 ± 4.2[j]	108–157, 134.4 ± 15.9[j]	137–143, 140 ± 4.2[b]	184–255, 219 ± 22.2[i]
1a	81–106, 91.4 ± 10.1[e]	62–79, 71.4 ± 5.7[i]		112–155, 138.9 ± 16[g]
4b	13–15, 14.6 ± 0.7[j]	15–17, 15.6 ± 0.8[j]	13–17, 15 ± 2.8[b]	21–26, 22.9 ± 1.8[j]
3a	82–92, 87.9 ± 3.5[f]	54–68, 60.5 ± 4.5[j]		105–150, 131.4 ± 16.3[g]
4a	16–25, 21.1 ± 2.7[i]	22–26, 23.4 ± 1.3[j]	24–27, 25 ± 2.1[b]	32–42, 36.6 ± 3.2[j]
g	10–13, 10.9 ± 1[j]	14–17, 15.7 ± 1.1[j]	13–17, 14.5 ± 2.8[b]	17–23, 20.1 ± 1.9[j]
length of attachment organ[2]	30–35, 32.8 ± 1.4[j]	40–48, 44.6 ± 2.3[j]	42–43, 42.3 ± 1.1[b]	48–53, 50.6 ± 1.6[j]
width of attachment organ[3]	46–52, 48.3 ± 1.9[j]	55–62, 59 ± 2.4[j]	53–57, 55 ± 2.8[b]	70–85, 75 ± 4.5[j]
anterior sucker (ad_3)[3]	6–7, 6.4 ± 0.4[j]	13–17, 15 ± 0.9[bt]	11–13, 11.8 ± 0.7[f]	13–14, 13.3 ± 0.4[j]
median shield (ad_1+ad_2, ad_3)	12–14, 12.9 ± 0.7[j]	18–21, 19.3 ± 1[j]	17–20, 18.4 ± 1.6[b]	21–24, 22.6 ± 1.2[j]
anterior lateral conoid (ps_2)	5–6, 5 ± 0.3[j]	4–6, 5 ± 0.3[j]	5–5, 4.8 ± 0.3[b]	5–7, 5.8 ± 0.5[j]
posterior lateral conoid (ps_1)	5–6, 5.3 ± 0.4[j]	4–6, 5.2 ± 0.5[j]	5–5, 5.1 ± 0.1[b]	5–6, 5.6 ± 0.4[j]
leg I	115–136, 127.3 ± 6.3[j]	144–175, 159.3 ± 10.7[j]	148–163, 155.3 ± 11[b]	188–219, 202.4 ± 11.5[j]
tarsus I	36–42, 38.6 ± 1.7[j]	46–55, 50.1 ± 2.7[j]	43–46, 44.5 ± 2.1[b]	55–71, 63.6 ± 5.4[j]
empodium I	28–40, 34.5 ± 3.3[j]	31–40, 35.5 ± 3.6[j]	37–39, 38 ± 1.4[b]	32–47, 38 ± 5.3[j]
ω_1 I	19–20, 19.6 ± 0.5[j]	21–24, 22.5 ± 1.1[j]	22–22, 21.8 ± 0.4[b]	27–30, 28.4 ± 0.9[j]
ω_2 I	11–14, 12.5 ± 0.9[j]	16–21, 18.5 ± 1.4[j]	18–20, 18.9 ± 2[b]	12–15, 13.7 ± 0.9[g]
ω_3 I	56–65, 60.4 ± 2.9[j]	65–80, 70.5 ± 4.5[j]	62–63, 62.5 ± 0.7[b]	70–79, 74.6 ± 3.4[g]
ε I	4–6, 4.9 ± 0.7[i]	5–9, 7 ± 1.2[h]		7–9, 7.4 ± 0.8[g]
f I	75–97, 86.7 ± 6.9[j]	78–95, 88.6 ± 6.3[i]	92–97, 94.5 ± 3.5[b]	95–117, 107.1 ± 7.2[i]
d I	102–128, 116.2 ± 7.7[j]	121–137, 129.1 ± 5.5[i]	127–133, 130 ± 4.2[b]	124–160, 140.7 ± 12[j]
ra I	18–22, 20 ± 1.3[j]	26–32, 28.6 ± 1.7[j]	26–28, 26.8 ± 1.1[b]	33–38, 35 ± 1.8[f]
la I	10–13, 11.2 ± 0.7[j]	13–15, 14 ± 0.8[j]	13–14, 13.7 ± 0.9[b]	19–25, 22.5 ± 2.4[j]
wa I	17–22, 19.5 ± 1.6[j]	15–22, 18.2 ± 1.6[bs]	16–18, 16.9 ± 0.8[e]	25–33, 29.2 ± 2.6[j]
gT I	13–16, 13.6 ± 1[j]	18–25, 21.9 ± 1.9[j]	22–23, 22.7 ± 0.5[b]	32–41, 35.6 ± 2.8[j]
hT I	15–19, 16.8 ± 1.2[j]	17–30, 23.1 ± 2.2[bt]	20–23, 21.2 ± 1.1[f]	34–47, 40.4 ± 3.7[j]
ϕ I	84–88, 86 ± 2.8[b]		94–97, 95.5 ± 2.1[b]	
mG I	41–52, 47.5 ± 3.6[j]	43–57, 51.3 ± 3.7[j]	43–45, 44 ± 1.4[b]	61–86, 71.2 ± 7.4[j]
cG I	13–18, 14.7 ± 1.4[j]	15–28, 20.2 ± 2.4[bt]	15–18, 16.4 ± 1.2[f]	24–38, 29 ± 4.7[j]
σ I	22–24, 23 ± 0.8[j]	43–48, 45.5 ± 1.5[i]	37–43, 40 ± 4.2[b]	40–46, 42.3 ± 1.7[i]
vF I	47–58, 51 ± 3.8[i]	57–66, 62.4 ± 3.1[j]	55–57, 56 ± 1.4[b]	71–84, 77.6 ± 4.4[j]
pR I	70–100, 88 ± 12.6[e]	24–37, 32.8 ± 3.5[j]		42–53, 48.3 ± 3.5[j]
leg II	113–129, 121.7 ± 5.1[j]	138–166, 151 ± 9.6[j]	144–152, 148 ± 5.7[b]	175–219, 198.4 ± 13.1[j]
tarsus II	32–38, 35.7 ± 2.1[j]	41–51, 46.1 ± 3.8[j]	43–43, 42.8 ± 0.4[b]	56–66, 61.3 ± 3.5[j]
empodium II	27–37, 31.3 ± 2.7[j]	27–42, 34.8 ± 3.1[bt]	35–41, 38.3 ± 2.3[f]	32–44, 38 ± 3.8[j]
ω_1 II	23–27, 24.3 ± 1.2[j]	25–28, 26.7 ± 0.9[j]	22–26, 23.9 ± 2.3[b]	30–36, 33 ± 1.9[j]

(continued)

Table 26. (Continued)

Structure	**hurdi**	**lucrosa**	**faini**	**segnis**
f II	76–88, 81.2 ± 4^{j}	83–105, 91.4 ± 6.4^{j}	93–94, 93.5 ± 0.7^{b}	98–117, 109.8 ± 6.6^{i}
d II	107–127, 118.6 ± 7.3^{j}	119–139, 129.9 ± 6.6^{h}	127–136, 131.5 ± 6.4^{b}	128–160, 142.4 ± 11.6^{i}
ra II	17–21, 19.2 ± 1.2^{j}	26–31, 27.9 ± 1.3^{i}	27–27, 26.9 ± 0.6^{b}	30–36, 33.3 ± 2.5^{f}
la II	10–12, 11.2 ± 0.7^{j}	12–15, 14 ± 1.2^{j}	11–12, 11.7 ± 0.5^{b}	20–24, 22.6 ± 1.3^{j}
wa II	16–20, 18.2 ± 1.4^{j}	15–21, 17.7 ± 1.3^{bt}	14–17, 15.9 ± 1.4^{f}	25–33, 27.9 ± 2.6^{j}
gT II	11–14, 12.3 ± 0.9^{j}	18–23, 20 ± 1.3^{j}	17–20, 18.6 ± 1.8^{b}	27–35, 30.1 ± 2.9^{j}
hT II	17–22, 19 ± 2^{j}	20–29, 24.8 ± 1.9^{bt}	19–22, 20.2 ± 1^{f}	39–53, 45.7 ± 4^{j}
ϕ II	70–76, 72.7 ± 3.1^{c}		83–86, 84.3 ± 2.5^{b}	
mG II	105–137, 121.1 ± 9.3^{j}	52–72, 64.9 ± 6^{j}	57–57, 57.2 ± 0.2^{b}	81–104, 94.4 ± 6.7^{j}
cG II	12–16, 13.8 ± 1.3^{i}	13–19, 16.5 ± 1.9^{j}	14–16, 15.2 ± 1.6^{b}	18–26, 22.3 ± 2.5^{j}
σ II	10–13, 11.5 ± 0.8^{j}	14–18, 15.9 ± 1.1^{j}	14–17, 15 ± 2.1^{b}	17–21, 19.5 ± 1.4^{j}
vF II	78–92, 86 ± 4.6^{j}	75–86, 80.1 ± 3.3^{j}	73–76, 74.5 ± 2.1^{b}	79–101, 90.4 ± 7.5^{j}
pR II	94–130, 105.7 ± 11.8^{i}	31–40, 35 ± 3.1^{j}	32–35, 33.3 ± 1.8^{b}	45–55, 49.6 ± 3.6^{g}
leg III	126–144, 132.6 ± 5.1^{j}	124–158, 139.2 ± 10.7^{j}	139–150, 144.5 ± 7.8^{b}	174–194, 183.9 ± 7^{j}
tarsus III	44–52, 47.9 ± 2.2^{j}	41–53, 45.1 ± 3.9^{j}	40–44, 42 ± 2.8^{b}	59–68, 63.2 ± 3^{j}
empodium III	28–36, 33.1 ± 2.5^{j}	29–40, 34.3 ± 3.7^{j}	33–35, 33.8 ± 1.1^{b}	35–39, 37 ± 1.5^{j}
d III	134–168, 151.9 ± 11.1^{j}	160–195, 178.1 ± 10.4^{h}	160–175, 167.5 ± 10.6^{b}	205–265, 236.6 ± 21.6^{i}
e III	80–95, 88 ± 5.8^{j}	97–115, 103.3 ± 5^{j}	102–112, 107 ± 7.1^{b}	112–150, 132.4 ± 10.8^{j}
f III	72–94, 82.2 ± 6.5^{j}	82–95, 89.7 ± 4.5^{j}	87–95, 91 ± 5.7^{b}	108–137, 120.9 ± 9.7^{j}
s III	16–19, 16.7 ± 1.2^{j}	14–17, 15.4 ± 0.8^{j}	13–15, 14 ± 1.4^{b}	15–24, 19.4 ± 2.4^{j}
kT III	9–12, 10.7 ± 0.8^{j}	13–17, 14.5 ± 1.2^{i}	13–16, 14.3 ± 1.8^{b}	17–23, 20.4 ± 2.3^{j}
ϕ III	27–34, 30.1 ± 2.2^{j}	28–33, 30 ± 1.9^{j}	33–37, 35 ± 2.8^{b}	24–31, 27.6 ± 2^{j}
nG III	10–15, 12.5 ± 1.5^{j}	21–26, 23.3 ± 1.8^{j}	19–20, 19.3 ± 0.4^{b}	20–40, 30.2 ± 6.3^{j}
σ III	11–14, 12 ± 0.9^{j}	11–13, 12 ± 0.8^{j}	13–14, 13.7 ± 0.5^{b}	11–14, 12.3 ± 1^{j}
sR III	60–88, 71.5 ± 9.3^{h}	20–25, 22.1 ± 1.5^{j}	23–24, 23.5 ± 0.7^{b}	47–65, 54.5 ± 5.6^{j}
leg IV	59–69, 63.2 ± 3.3^{j}	78–97, 84.4 ± 5.6^{j}	84–100, 92 ± 11.3^{b}	88–106, 93.8 ± 5.5^{j}
tarsus IV	12–17, 14.3 ± 1.5^{j}	19–29, 23.2 ± 2.1^{bt}	25–30, 27.3 ± 1.8^{f}	23–30, 25.7 ± 2^{j}
d IV	540–670, 588.1 ± 45.1^{f}	458–510, 480.3 ± 26.8^{c}		624–793, 725.3 ± 54.6^{g}
e IV	4–7, 5.6 ± 1^{j}	8–11, 9.2 ± 1.1^{j}	8–8, 8.3 ± 0.1^{b}	3–7, 4.9 ± 1^{j}
f IV	4–8, 6.4 ± 1.3^{g}	8–11, 9.4 ± 1.2^{i}		7–8, 7 ± 0.3^{h}
w IV	7–9, 7.6 ± 0.7^{j}	11–26, 16.5 ± 3^{bt}	15–25, 20.9 ± 3.9^{f}	6–10, 8.5 ± 1.3^{j}
s IV	3–6, 4.1 ± 0.8^{i}	4–6, 4.9 ± 0.9^{j}	4–7, 5.5 ± 1.5^{b}	3–5, 3.7 ± 0.7^{i}
vF IV	42–58, 49.5 ± 5.3^{j}	26–40, 31.2 ± 5^{j}	33–35, 33.8 ± 1.8^{b}	50–71, 62.1 ± 6^{j}

Superscript: 1 = excluding bases of f_2; 2 = medial horn-posterior sclerotized end; 3 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10 . . . aa = 27 . . . bk = 63. hyst = hysterosomal.

Table 27. Measurements of three species of *Sennertia* (range, mean ± SD).

Structure	**americana**	**pirata**	**loricata**
idiosoma, length	315–342, 325 ± 9.9[j]	226–277, 253.7 ± 17.5[j]	252–310, 271.2 ± 20.2[j]
idiosoma, width	296–339, 318.6 ± 13.2[j]	197–249, 223 ± 16.6[j]	211–274, 238.7 ± 20.7[j]
hyst shield, length	167–204, 180.3 ± 10.6[j]	171–214, 189.7 ± 13[j]	159–200, 173.9 ± 14.5[j]
hyst shield, width anterior	80–115, 94.1 ± 10.6[j]	102–137, 119.2 ± 11.3[j]	78–103, 87.1 ± 9.2[j]
hyst shield, width at f_2 level[1]	101–117, 108.5 ± 4.9[j]	92–122, 110 ± 10.7[j]	72–89, 78.7 ± 6[j]
gnathosomal solenidion	3–6, 4.7 ± 0.9[j]	2–3, 2.5 ± 0.5[j]	2–3, 2.6 ± 0.4[j]
sternum	24–38, 30.2 ± 5[j]	25–34, 29.2 ± 2.6[j]	33–43, 36.7 ± 2.7[j]
apodeme II	66–84, 72.8 ± 5.3[j]	50–65, 58.4 ± 5.2[j]	60–78, 65.4 ± 6.7[j]
posterior apodeme II	42–54, 46.8 ± 3.5[j]	40–49, 43.9 ± 2.9[j]	38–52, 42.3 ± 4.6[j]
apodeme III	32–44, 37.6 ± 3.8[j]	26–33, 29.2 ± 2.3[j]	30–46, 36 ± 5.2[j]
apodeme IV	63–76, 68.5 ± 3.8[j]	47–59, 53.9 ± 3.7[j]	57–67, 60.4 ± 3.9[j]
vi	7–10, 8.6 ± 0.9[h]	8–10, 9 ± 0.8[j]	8–10, 8.4 ± 0.7[j]
si	49–56, 52.3 ± 2.6[j]	55–77, 63.5 ± 7.1[i]	47–64, 54.4 ± 5.4[j]
se	71–83, 76.2 ± 3.6[j]	54–72, 61.5 ± 5.5[j]	52–67, 58.5 ± 5[i]
c_1	33–48, 39.2 ± 4.2[j]	53–67, 61 ± 5.1[j]	37–54, 44.3 ± 5.5[j]
c_2	60–74, 68.2 ± 4.6[j]	63–79, 71.5 ± 5[j]	55–73, 62.4 ± 6.1[j]
c_3	25–35, 30.5 ± 3.3[j]	29–39, 33.9 ± 3.2[j]	33–43, 37.9 ± 3.4[j]
c_p	74–89, 78.9 ± 4.5[j]	56–75, 64.2 ± 5.5[j]	61–78, 68.6 ± 5.8[j]
d_1	8–13, 9.8 ± 2[j]	6–8, 6.7 ± 0.5[i]	7–10, 8.2 ± 1[j]
d_2	58–72, 63.5 ± 5.1[j]	70–90, 80.3 ± 6.4[j]	56–81, 66.9 ± 7.5[j]
e_1	7–9, 7.4 ± 0.8[j]	6–10, 7.4 ± 0.9[j]	4–8, 5.9 ± 1.1[j]
e_2	52–66, 59 ± 4.2[j]	68–86, 78.7 ± 5.8[j]	50–69, 59 ± 6.2[j]
f_2	4–8, 5.8 ± 1.2[j]	5–7, 6.2 ± 0.9[j]	4–7, 5.7 ± 0.8[j]
h_1	4–8, 5.5 ± 1.2[j]	5–9, 7.4 ± 1.3[j]	4–7, 5.7 ± 1.2[j]
h_2	3–8, 5.3 ± 1.4[j]	8–11, 9.7 ± 0.8[j]	7–9, 8.2 ± 0.8[j]
h_3	72–94, 82.2 ± 6.8[j]	60–77, 68.9 ± 6.4[i]	67–78, 72.3 ± 5.1[d]
1a	81–103, 92.4 ± 6.7[g]	69–107, 89.8 ± 12.5[f]	86–114, 102.2 ± 9.9[h]
4b	14–17, 15.7 ± 1[j]	17–23, 19.5 ± 1.6[j]	15–20, 17.4 ± 1.5[j]
3a	72–81, 78.3 ± 3.2[g]	67–88, 77.7 ± 6.9[j]	75–94, 86.8 ± 8[e]
4a	20–23, 21 ± 1[j]	21–27, 24 ± 1.7[j]	21–25, 22.5 ± 1.6[i]
g	10–14, 11.6 ± 1.3[j]	13–14, 13.5 ± 0.7[j]	10–13, 10.8 ± 0.8[j]
length of attachment organ[2]	34–39, 36.2 ± 1.8[j]	42–54, 48.1 ± 4.1[j]	28–35, 31.1 ± 2.4[j]
width of attachment organ[3]	52–58, 55.9 ± 2[j]	60–74, 68.2 ± 4.7[j]	40–48, 43.4 ± 2.9[j]
anterior sucker (ad_3)[3]	8–9, 8.2 ± 0.3[j]	8–11, 9.7 ± 1[j]	6–8, 6.8 ± 0.5[j]
median shield (ad_1+ad_2, ad_3)	14–18, 16.1 ± 1.3[j]	16–20, 17.8 ± 1.4[j]	11–12, 11.8 ± 0.5[j]
anterior lateral conoid (ps_2)	5–6, 5.6 ± 0.5[j]	9–11, 9.8 ± 0.8[j]	3–5, 4 ± 0.4[j]
posterior lateral conoid (ps_1)	6–7, 6.1 ± 0.6[j]	10–12, 11 ± 0.7[j]	4–5, 4.8 ± 0.3[j]
leg I	142–160, 148.8 ± 5.9[j]	98–126, 109.8 ± 8.8[j]	115–146, 129.9 ± 9.8[j]
tarsus I	44–50, 46.9 ± 1.8[j]	27–36, 32 ± 2.7[j]	35–47, 40.8 ± 3.5[j]
empodium I	28–39, 35 ± 3.8[j]	18–24, 20.5 ± 2.1[j]	35–41, 37 ± 2.2[j]
ω_1 I	20–24, 21.7 ± 1.2[j]	17–20, 18.6 ± 1.1[j]	19–22, 20.4 ± 1.2[j]
ω_2 I	9–15, 12.2 ± 1.7[j]	10–13, 11.4 ± 0.9[i]	11–14, 12.5 ± 1.3[j]
ω_3 I	61–71, 64.7 ± 3.7[i]	44–53, 48.2 ± 3.1[j]	58–68, 63.2 ± 3.4[j]
ε I	4–7, 5.1 ± 1.1[j]	4–6, 4.8 ± 0.6[j]	3–6, 4.5 ± 1.1[g]
f I	71–97, 84.4 ± 6.7[j]	38–53, 46.2 ± 4.6[j]	79–105, 88.8 ± 7.8[j]
d I	111–131, 120.2 ± 6.2[j]	67–92, 79.3 ± 8[j]	109–147, 122.8 ± 13.4[j]
ra I	21–24, 22.7 ± 0.9[j]	14–18, 16.1 ± 1.3[h]	18–26, 22.6 ± 3[h]
la I	13–18, 15.3 ± 1.3[j]	9–13, 11 ± 1[j]	11–14, 12.5 ± 0.9[j]
wa I	17–21, 18.9 ± 1.4[j]	8–10, 9 ± 0.8[j]	16–21, 18.3 ± 1.4[i]
gT I	16–24, 20.3 ± 2.7[h]	12–15, 12.8 ± 1[h]	13–18, 16.2 ± 1.8[j]
hT I	18–23, 20.9 ± 1.5[i]	10–14, 11.2 ± 1.2[j]	16–22, 18.5 ± 1.8[j]
ϕ I		75–93, 81 ± 6.6[f]	95–120, 108.3 ± 12.6[c]
mG I	43–61, 51.2 ± 5.3[j]	39–50, 43.2 ± 3.8[j]	46–62, 51.6 ± 4.9[j]
cG I	12–20, 16.7 ± 3.3[j]	11–16, 13.4 ± 1.6[j]	11–20, 14.7 ± 2.7[j]
σ I	28–35, 31.8 ± 2.1[j]	16–20, 18 ± 1.6[j]	19–25, 20.8 ± 2[j]
vF I	51–71, 60.5 ± 6.2[i]	40–49, 44.8 ± 3.3[j]	46–59, 50.6 ± 4.3[i]
pR I	99–130, 111 ± 9.7[h]	77–89, 83.3 ± 4.5[f]	102–121, 112.3 ± 7[e]
leg II	134–153, 144.6 ± 5.9[j]	101–124, 110.6 ± 8.4[j]	113–139, 122.2 ± 9.6[j]
tarsus II	43–48, 45.3 ± 1.6[j]	31–37, 33.8 ± 2.2[j]	34–42, 37.1 ± 2.9[j]
empodium II	26–37, 32.4 ± 3.7[j]	20–24, 21.9 ± 1.5[j]	31–39, 35.2 ± 2.5[j]
ω_1 II	25–27, 25.8 ± 0.7[j]	21–25, 22.8 ± 1.1[j]	22–28, 24.9 ± 1.6[j]

(continued)

Table 27. (Continued)

Structure	americana	pirata	loricata
f II	77–91, 82.5 ± 4.5^{j}	47–58, 52 ± 4.1^{i}	75–103, 83.3 ± 9^{j}
d II	114–125, 119.1 ± 3.6^{j}	83–105, 95.4 ± 7.5^{j}	110–158, 126.4 ± 17.2^{i}
ra II	20–25, 23 ± 2^{i}	15–20, 16.7 ± 2^{e}	19–27, 22.1 ± 2.9^{g}
la II	13–16, 14.4 ± 0.7^{j}	10–13, 11.3 ± 0.9^{j}	11–16, 12.9 ± 1.5^{j}
wa II	16–20, 18.1 ± 1.4^{j}	8–10, 9 ± 0.8^{j}	17–21, 18.9 ± 1.4^{i}
gT II	16–20, 18.4 ± 1.5^{j}	11–16, 12.1 ± 1.5^{j}	12–17, 14.2 ± 1.7^{j}
hT II	20–31, 25.2 ± 3.8^{j}	10–16, 12 ± 2^{j}	16–27, 21.3 ± 3.2^{j}
ϕ II		65–82, 71.6 ± 6^{g}	78–95, 86.2 ± 7^{e}
mG II	108–143, 125.3 ± 11.4^{j}	76–92, 85.1 ± 5.6^{i}	127–163, 142 ± 13.1^{h}
cG II	11–19, 15 ± 2.8^{i}	11–16, 12.6 ± 1.5^{j}	12–16, 13.8 ± 1.1^{j}
σ II	13–18, 15.3 ± 1.6^{j}	9–11, 10 ± 0.7^{j}	10–12, 11.1 ± 0.8^{j}
vF II	90–109, 96.8 ± 7.3^{j}	62–75, 70.2 ± 4.2^{j}	73–99, 82.4 ± 8.2^{i}
pR II	106–131, 119.7 ± 7.7^{i}	83–94, 87.3 ± 5.9^{c}	115–142, 123.8 ± 10.5^{h}
leg III	126–148, 135.9 ± 7.5^{j}	85–106, 93.2 ± 6.8^{j}	113–145, 125.7 ± 10.2^{j}
tarsus III	44–50, 46.8 ± 1.9^{j}	27–35, 30.4 ± 2.4^{j}	39–52, 45.8 ± 3.7^{j}
empodium III	27–35, 31 ± 2.8^{j}	18–26, 22.3 ± 2.3^{j}	32–38, 33.6 ± 2.2^{i}
d III	144–183, 161.3 ± 14.8^{h}	103–137, 120.4 ± 11.9^{h}	115–149, 133.9 ± 11.2^{g}
e III	84–102, 92.4 ± 5.1^{j}	48–68, 59.8 ± 6^{j}	89–118, 99.1 ± 9.9^{j}
f III	77–97, 85 ± 6.3^{j}	46–62, 53.3 ± 5.2^{j}	75–105, 90.8 ± 8.4^{j}
s III	16–19, 17.5 ± 1.4^{j}	7–8, 7.5 ± 0.5^{j}	16–22, 19.3 ± 2.1^{i}
kT III	13–18, 14.3 ± 1.8^{j}	10–12, 11.1 ± 0.7^{f}	11–13, 11.9 ± 0.4^{j}
ϕ III	25–31, 28.5 ± 2.3^{j}	18–26, 22 ± 2.2^{j}	27–36, 31.4 ± 2.7^{j}
nG III	15–22, 18.2 ± 2.1^{j}	20–26, 23 ± 1.9^{j}	11–16, 13.8 ± 1.6^{j}
σ III	7–12, 9.2 ± 1.5^{j}	6–9, 7.6 ± 0.9^{j}	8–11, 9.1 ± 1^{j}
sR III	71–109, 83.9 ± 11.2^{j}	43–59, 50.5 ± 4.5^{j}	69–85, 77 ± 5.2^{f}
leg IV	71–82, 74.9 ± 3.8^{j}	51–64, 56.9 ± 4.5^{j}	52–61, 55.5 ± 3.1^{j}
tarsus IV	18–22, 19.1 ± 1.3^{j}	11–15, 13.2 ± 1.6^{j}	11–14, 12.4 ± 1.1^{j}
d IV	476–607, 540.4 ± 40.3^{j}	334–412, 369.5 ± 31.8^{f}	581–653, 617 ± 50.9^{b}
e IV	3–6, 4.1 ± 1.2^{j}	4–5, 4.5 ± 0.3^{e}	
f IV	4–5, 4.4 ± 0.4^{i}	6–8, 6.8 ± 0.5^{e}	
w IV	6–9, 7.6 ± 0.8^{j}	9–11, 9.6 ± 0.8^{j}	5–9, 7 ± 0.9^{j}
s IV	3–4, 3.8 ± 0.4^{j}	3–5, 3.9 ± 0.5^{j}	4–7, 5.6 ± 0.9^{g}
vF IV	43–78, 64.7 ± 11.3^{j}	33–47, 41 ± 5.7^{i}	44–56, 50.9 ± 4.6^{i}

Superscript: 1 = excluding bases of f_2; 2 = medial horn-posterior sclerotized end; 3 = excluding transparent margin; letter superscripts indicate number of measurements: a = 1 . . . j = 10. hyst = hysterosomal.

APPENDIX 7. CHAETODACTYLIDAE OF THE WORLD. TAXONOMIC DATABASE

Genera and Subgenera

Achaetodactylus Fain, 1981 (genus) (p. 107)

Afrosennertia Fain, 1981 (subgenus in *Sennertia*)
Orig: *Afrosennertia* Fain, 1981a: 147 (subgenus in *Sennertia*, type species *Sennertia monicae* Fain, 1971, by original designation)
Syn: *Sennertia* (*Afrosennertia*): Fain, 1982: 67; OConnor, 1993a: 362; Kurosa, 2003: 25
Orig: *monicae*-group Fain, 1974a: 215 (*Sennertia*, based on *Sennertia monicae* Fain, 1971)
Orig: *Asiosennertia* Fain, 1981a: 147 (subgenus in *Sennertia*, type species *Sennertia* (*Afrosennertia*) *delfinadoae* Fain, 1981 [sic!], by original designation), synonymized here
Syn: *Sennertia* (*Asiosennertia*): Fain, 1982: 67; Kurosa, 2003: 25

Amsennertia Fain, 1981 (subgenus in *Sennertia*)
Orig: *Amsennertia* Fain, 1981a: 147 (subgenus in *Sennertia*, type species *Sennertia frontalis* Vitzthum, 1941 by original designation)
Syn: *Sennertia* (*Amsennertia*): Alzuet & Abrahamovich, 1987: 345; Lombert *et al*., 1987: 113; Alzuet & Abrahamovich, 1989: 236; Alzuet & Abrahamovich, 1990: 627; OConnor, 1993a: 362; Kurosa, 2003: 25

Centriacarus Klimov & OConnor (genus) (p. 99)

Chaetodactylus Rondani, 1866 (genus) (p. 108)
Syn: *Spinodactylus* Fain, 1981 (subgen. in *Chaetodactylus*), synonymized here

Roubikia OConnor, 1993 (genus) (p. 100)

Sennertia Oudemans, 1905 (genus) (p. 145)

Sennertia Oudemans, 1905 (subgenus in *Sennertia*)
Syn: *Sennertia* (*Sennertia*): Fain, 1981a: 146; Fain, 1982: 67; Lombert *et al*., 1987: 113; OConnor, 1993a: 362; Vicidomini, 1996: 71; Haitlinger, 1999: 57; Haitlinger, 2000: 18; Fain & Pauly, 2001: 131
Orig: *Eosennertia* Kurosa, 2003: 25 (subgenus in *Sennertia*, type species *Sennertia* (*Eosennertia*) *bifida* Kurosa, 2003, by original designation), synonymized here

Spinosennertia Fain, 1981 (subgenus in *Sennertia*)
Orig: *Spinosennertia* Fain, 1981a: 147 (subgenus in *Sennertia*, type species *Sennertia argentina* Vitzthum, 1941, by original designation)
Syn: *Sennertia* (*Spinosennertia*): Alzuet & Abrahamovich, 1987: 350; OConnor, 1993a: 362; Haitlinger, 1999: 57; Kurosa, 2003: 25

Species Groups

americana-group, new (*Sennertia*, subgenus *Amsennertia*, based on *Sennertia americana* Delfinado a& Baker, 1976) (p. 147)
Syn: *Amsennertia* Fain, 1981a: 147 (subgenus in *Sennertia*) (part.)

claviger-group, new (*Chaetodactylus*, *Chaetodactylus claviger* Oudemans, 1928)
Orig: *Spinodactylus* Fain, 1981b: 2 (subgenus in *Chaetodactylus*, type species *Chaetodactylus claviger* Oudemans, 1928, by original designation)
Syn: *Chaetodactylus* (*Spinodactylus*): OConnor, 1993a: 354

cerambycina-group (*Sennertia*, subgenus *Sennertia*) (p. 147)
Orig: *cerambycina*-group Fain, 1974a: 216 (*Sennertia*, subgenus *Sennertia*, based on *Sennertia cerambycina* (Scopoli, 1763))
Syn: *cerambycina*-group Fain, 1981a: 147: Fain, 1982: 70
Orig: *Eosennertia* Kurosa, 2003: 25 (subgenus in *Sennertia*, type species *Sennertia* (*Eosennertia*) *bifida* Kurosa, 2003, by original designation), synonymized here

devincta-group Klimov & OConnor in Klimov *et al*., 2007b (*Sennertia*, ?subgenus *Amsennertia*, based on *Sennertia devincta* Klimov and OConnor, 2007 (p. 147)

ignota-group, new (*Sennertia*, subgenus *Amsennertia*, based on *Sennertia ignota* Delfinado & Baker, 1976) (p. 147)
Syn: *Amsennertia* Fain, 1981a: 147 (subgenus in *Sennertia*) (part.)

faini-group, new (*Sennertia*, subgenus *Amsennertia*, based on *Sennertia faini* Baker & Delfinado-Baker, 1983 (p. 147)
Syn: *Amsennertia* Fain, 1981a: 147 (subgenus in *Sennertia*) (part.)

frontalis-group, new (*Sennertia*, subgenus *Amsennertia*, based on *Sennertia frontalis* Vitzthum, 1941) (p. 147)
Syn: *Amsennertia* Fain, 1981a: 147 (subgenus in *Sennertia*) (part.)

horrida-group Fain, 1981 (*Sennertia*, unranked) (p. 147)
Orig: *horrida*-group Fain, 1981a: 146 (*Sennertia*, subgenus *Sennertia*, based on *Sennertia horrida* (Vitzthum, 1912)) (part.)
Syn: *horrida*-group: Klimov *et al*., 2007b: 124 (redefined)

japonica-group Fain, 1981 (*Sennertia*, subgenus *Sennertia*) (p. 147)
Orig: *japonicus*-group Fain, 1981a: 146 (*Sennertia*, subgenus *Sennertia*, based on *Sennertia japonicus* (Oudemans, 1901) (=*Sennertia japonica* (Oudemans, 1900))

loricata-group, new (*Sennertia*, subgenus *Amsennertia*, based on *Sennertia loricata* sp. n.) (p. 147)

surinamensis-group, new (*Sennertia*, unranked, based on *Sennertia surinamensis* Fain and Lukoschus, 1971) (p. 147)
Syn: *horrida*-group Fain, 1981a: 146 (*Sennertia*, subgenus *Sennertia*) (part.)

zhelochovtsevi-group, new (*Sennertia*, unranked, based on *Sennertia zhelochovtsevi* Zachvatkin, 1941) (p. 147)
Syn: *horrida*-group Fain, 1981a: 146 (*Sennertia*, subgenus *Sennertia*) (part.)

Species and Subspecies

1. **Achaetodactylus ceratinae** (Fain, 1974)
Orig: *Chaetodactylus ceratinae* Fain, 1974a: 214 (holotype and 80 paratype HDNs in MRAC)
Host: *Ceratina* (*Hirashima*) *lativentris*
Distr: Kenya
Note: short description of HDN

Syn: *Chaetodactylus* (*Achaetodactylus*) *ceratinae*: Fain, 1981b: 4, Figs. 1,2,9
Host: *Ceratina lativentris* (type host, Kenya, Tanzania*), Ceratina* (*Hirashima*) *nigriceps* (as *Ceratina apaca* = *lapsus* for *Ceratina opaca*) (South Africa)
Distr: Kenya: Nairobi (type locality), Tanzania (Ngurdoto Crater National Park, Mto wa Mbu), South Africa: KwaZulu-Natal (Salt Rock)
Note: redescription of HDN, included in key, subgeneric assignment, emendation of paratype repository (IRSNB) and type locality, unjustified paratype assignment (from Tanzania and South Africa), year of description inconsistently indicated as 1974 and 1976

Syn: *Achaetodactylus ceratinae*: Klimov *et al*., 2007a: 1371
Host: *Ceratina nigriceps*
Distr: South Africa
Note: HDN included in morphological phylogenetic analysis

Orig: *Achaetodactylus ceratinae*: Klimov *et al*., 2007b: 120, Fig. 1*C*
Host: *Ceratina nigriceps*

Distr: South Africa: KwaZulu-Natal
Note: record from axillar acarinarium

2. **Achaetodactylus decellei** (Fain, 1974)
Orig: *Chaetodactylus decellei* Fain, 1974a: 215 (holotype and 12 paratype HDNs in MRAC)
Host: *Ceratina* sp. (n° 205 B) (type host), *Ceratina spilota* (Cameroon), *Ceratina* (*Propithitis*) *aereola* (Democratic Republic of the Congo), *Ceratina excavata* (Tanzania)
Distr: Tanzania: Arusha National Park ("de Ngurdoto, Nat. Park") (type locality), Tanzania, Cameroon, Democratic Republic of the Congo
Note: short description of HDN

Syn: *Chaetodactylus* (*Ochaetodactylus*) *decellei*: Fain, 1981b: 8, Figs. 7,8,12
Host: *Ceratina* sp. (n° 205 B) (type host), *Ceratina spilota* (Cameroon), *Ceratina aereola* (Democratic Republic of the Congo), *Ceratina excavata* (Tanzania)
Distr: Tanzania: Ngurdoto Crater National Park (type locality), Cameroon; Democratic Republic of the Congo
Note: redescription of HDN, included in key, subgeneric assignment, emendation of paratype repository (IRSNB)

Syn: *Ochaetodactylus decellei*: Klimov *et al*., 2007a: 1371
Host: *Ceratina* sp., *Ceratina spilota*, *Ceratina aereola*, *Ceratina excavata*
Distr: Tanzania: Ngurdoto Crater National Park (type locality), Cameroon; Democratic Republic of the Congo
Note: HDN included in morphological phylogenetic analysis

3. **Achaetodactylus leleupi** (Fain, 1974)
Orig: *Chaetodactylus leleupi* Fain, 1974a: 214 (holotype and 40 paratype HDNs in MRAC)
Host: *Ceratina ruwenzorica*
Distr: Kenya: Nairobi (type locality)
Note: short description of HDN

Syn: *Chaetodactylus* (*Achaetodactylus*) *leleupi*: Fain, 1981b: 4, Figs. 3, 4, 10.
Host: *Ceratina ruwenzorica* (type host), *Ceratina diloloensis* (Kenya), *Ceratina spilota* (Cameroon)
Distr: Kenya: Nairobi Area (Karen) (type locality), Cameroon (Bambui)
Note: redescription of HDN, included in key, year of description inconsistently indicated as 1974 and 1976, emendation of paratype repository (IRSNB) and type locality

Syn: *Chaetodactylus (Achaetodactylus) leleupi*: Fain & Pauly, 2001: 131, Figs 22–23
Host: *Ceratina ruwenzorica* (type host, Kenya), *Ceratina* (*Hirashima*) *nigriceps* (Tanzania), *Ceratina* (*Hirashima*) *lativentris* (Tanzania).
Distr: Kenya: Nairobi (type locality), Tanzania (Kilimanjaro)
Notes: mention, indication of phoresy inside a pouch of 1st metasomal tergite of *Ceratina nigriceps* female (SEM photo).

Syn: *Achaetodactylus leleupi*: Klimov *et al*., 2007a: 1371
Host: *Ceratina diloloensis*
Distr: Democratic Republic of the Congo
Note: HDN included in morphological phylogenetic analysis

4. **Centriacarus guahibo** Klimov & OConnor, 2007 (p. 100)
Orig: *Centriacarus guahibo* Klimov & OConnor, 2007: 817, Figs 5–6 (holotype in AMNH, paratypes in AMNH, OSU, UMMZ)
Host: *Centris* sp.
Distr: Venezuela: Territorio Amazonas
Note: description of HDN

Syn: *Centriacarus guahibo*: Klimov *et al*., 2007a: 1371
Host: *Centris* sp.
Distr: Venezuela
Note: HDN included in morphological phylogenetic analysis

5. **Centriacarus turbator** (p. 100)

6. **Chaetodactylus abditus** Klimov & OConnor, 2004 (p. 124)

7. **Chaetodactylus anthidii** (Oudemans, 1911) (p. 110)
Orig: *Trichotarsus anthidii* Oudemans, 1911a: 165 (holotype not designated, syntypes in RMNH (Buitendijk, 1945))
Host: *Rhodanthidium sticticum* (as *Anthidium sticticum*)
Distr: Tunisia
Note: description of HDN

Syn: *Trichotarsus anthidii*: Vitzthum, 1919: 31
Host: *Rhodanthidium sticticum* (as *Anthidium sticticum*)
Distr: Tunisia
Note: mention, comparison with *Trichotarsus ludwigi*

Syn: *Chaetodactylus anthidii*: Oudemans, 1924: 328
Note: comparison with *Chaetodactylus claviger*

Syn: *Chaetodactylus anthidii*: Zachvatkin, 1941: 398
Host: *Rhodanthidium sticticum* (as *Anthidium sticticum*)
Distr: Tunisia
Note: mention, included in key

Syn: *Chaetodactylus* (*Chaetodactylus*) *anthidii*: Fain, 1981b: 2
Note: subgeneric assignment, included in key

Syn: *Chaetodactylus* (*Chaetodactylus*) *anthidii*: OConnor, 1993a: 62
Note: genus-level character acquisition

8. **Chaetodactylus antillarum** sp. n. (p. 113)

9. **Chaetodactylus birulai** Zachvatkin, 1941 (p. 109)
Orig: *Chaetodactylus birulai* Zachvatkin, 1941: 396, Fig. 680 (lectotype and 2 paralectotype HDNs in ZIN, designated here)
Host: *Chelostoma florisomne* (as *Chelostoma florisomnis*)
Distr: Russia: Kirovskaya Oblast'
Note: description of HDN

Syn: *Chaetodactylus* sp. Lith, 1957: 198
Host: *Chelostoma florisomne*
Distr: Netherlands
Note: observation on biology in host nest, report of killing bee larvae

Syn: *Chaetodactylus birulai*: Samšiňák, 1973: 404, Figs 1–2

Host: *Chelostoma florisomne*
Note: comparison with *Chaetodactylus poetae*

Orig: *Chaetodactylus poetae* Samšiňák, 1973: 401 (holotype and unspecified number of paratype HDNs in "Parasitologischen Institutes in Praha, Nr. 1555" (not found in PARU, F. Dusbábek, pers. comm.); **syn. n.**, see p. 109)
Host: *Chelostoma florisomne* (type host), also found phoretic on cleptoparasites: *Sapyga quinquepunctata*, *Sapyga clavicornis* (Hymenoptera: Sapygidae).
Distr: Czech Republic: Sobotka
Note: description of HDN, host used galleries of the beetle *Hylotrupes bajulus* (Linnaeus, 1758) (Cerambycidae)

Syn: *Chaetodactylus birulai*: Fain, 1974a: 213
Note: comparison with *Chaetodactylus dalyi*

Syn: *Chaetodactylus* (*Chaetodactylus*) *birulai*: Fain, 1981b: 2
Note: included in key, subgeneric assignment

Syn: *Chaetodactylus* (*Chaetodactylus*) *poetae*: Fain, 1981b: 2
Note: included in key, subgeneric assignment

Syn: *Chaetodactylus* (*Chaetodactylus*) *birulai*: Kurosa, 1987: 373
Note: comparison with *Ch. hirashimai*

Syn: *Chaetodactylus* (*Chaetodactylus*) *poetae*: Kurosa, 1987: 373
Note: comparison with *Ch. hirashimai*

10. **Chaetodactylus chrysidis** Fain & Baugnée, 1996 (p. 110)
Orig: *Chaetodactylus chrysidis*: Fain & Baugnée, 1996: 23, Figs 1–6 (holotype and unspecified number of paratype HDNs in IRSNB)
Host: *Chrysura trimaculata* (Hymenoptera, Chrysididae), host of *Osmia aurulenta* and *O. bicolor*
Distr: Belgium: "Treignes-Saumières"
Note: description of HDN

Syn: *Chaetodactylus chrysidis*: Van Asselt, 2000: 225
Host: *Chrysura trimaculata*

Orig: *Chaetodactylus chrysidis aurulenticola* Fain & Baugnée, 1996: 28 (holotype and 16 paratype HDNs in IRSNB; **syn. n.** see p. 110)
Host: *Osmia aurulenta*
Distr: Belgium: "Treignes-Rivelottes"
Note: description of HDN

Syn: *Chaetodactylus chrysidis aurulenticola*: Van Asselt, 2000: 225
Host: *Osmia aurulenta*

Syn: *Chaetodactylus osmiae*: Fain *et al*., 1992 (misidentification)
Host: *Osmia aurulenta*
Distr: Belgium

11. **Chaetodactylus claudus** sp. n. (p. 117)

12. **Chaetodactylus claviger** Oudemans, 1924 (p. 111)
Orig: *Chaetodactylus claviger* Oudemans, 1924: 328 (holotype not designated, syntype HDNs in RMNH (Buitendijk, 1945))
Host: *Osmia tricornis*
Distr: Italy: Promontorio del Gargano ("Monte Gargano, Apulië")
Note: short description of HDN

Syn: *Trichodactyle Osmiae*: Donnadieu, 1868: 84: Figs 2, 5, 6, 8, 10 (misidentification)
Host: *Osmia*
Distr: France
Note: description of HDN

Syn: *Trichodactylus osmiae*: Murray, 1877: 252 (part.), Fig. "*Trichodactylus osmiae*"
Hosts: *Osmia*
Note: mention, character discussion

Syn: *Chaetodactylus claviger*: Zachvatkin, 1941: 396, Fig. 681
Host: *Osmia tricornis*
Distr: Italy

Syn: *Chaetodactylus* (*Spinodactylus*) *claviger*: Fain, 1981b: 2 (part., excluding *Chaetodactylus krombeini*)
Note: included in key, subgeneric assignment, considered as tentative senior synonym of *Chaetodactylus krombeini*, year of species description indicated as 1928

Syn: *Chaetodactylus osmiae*: Abou Senna, 1997: 667, Fig. 3 (misidentification).
Host: *Apis mellifera*
Distr: Egypt
Note: collected from workers

13. **Chaetodactylus azteca** sp. n. (p. 127)

14. **Chaetodactylus dalyi** (Fain, 1974) (p. 111)
Orig: *Chaetodactylus dalyi* Fain, 1974a: 213 (holotype and 3 paratype HDNs in MRAC)
Host: *Ceratina* (*Pithitis*) *turneri* (type host, South Africa), *Ceratina* sp. (Mozambique, "Transvaal")
Distr: South Africa: "Natal" (type locality), Limpopo ("Transvaal"); Mozambique
Note: short description of HDN

Syn: *Chaetodactylus* (*Chaetodactylus*) *dalyi*: Fain, 1981b: 6, Figs. 5,6,11
Host: *Ceratina* (*Pithitis*) *turneri* (type host, South Africa), *Ceratina* sp. (Zimbabwe, "Sta Lucia")
Distr: South Africa: "Natal" (type locality), KwaZulu-Natal (Saint Lucia "Sta Lucia, Natal"), Zimbabwe
Note: redescription of HDN, included in key, inconsistency with original locality data, emendation of paratype repository (IRSNB)

Syn: *Chaetodactylus dalyi*: Klimov & OConnor, 2007: 826.
Note: Remark on morphology

15. **Chaetodactylus dementjevi** Zachvatkin, 1941 (p. 103)
Orig: *Chaetodactylus dementjevi* Zachvatkin, 1941: 399, Fig. 682 (holotype not designated, one syntype HDN (Uzbekistan) found in ZIN)
Host: *Megachile bombycina*, *Megachile ligniseca*, also on *Vespula germanica* (Vespidae) (Uzbekistan)
Distr: Russia: Leningradskaya Oblast', Yaroslavskaya Oblast'; Kazakhstan: Shyghys Qazaqstan (Ust'-Kamenogorsk); Uzbekistan: Toshkent (Gora Aktash)
Note: description of HDN

Syn: *Chaetodactylus* (*Achaetodactylus*) *dementjevi*: Fain, 1981b: 2
Note: provisionally included in *Achaetodactylus*

16. **Chaetodactylus furunculus** sp. n. (p. 116)

17. **Chaetodactylus gibbosi** Klimov & OConnor, 2004 (p. 124)

18. **Chaetodactylus hirashimai** Kurosa, 1987 (p. 110)
Orig: *Chaetodactylus* (*Chaetodactylus*) *hirashimai* Kurosa, 1987: 374, Figs 1–8 (holotype in NSMT, paratype HDNs in author's collection, distributed to "certain foreign museums", UMMZ (6)).
Host: *Osmia* (*Osmia*) *excavata* (type host), *Osmia* (*Osmia*) *cornifrons*,
Osmia (*Osmia*) *pedicornis* and *Osmia* (*Helicosmia*) *imaii*
Distr: Japan: Honshu (Nara Pref., Nara-shi, Furuichi-chô) (type locality) (Nara Pref., Nara-shi, Furuichi-cho - type locality), Kyushu
Note: description of HDN

Syn: *Saproglyphus* sp. Hirashima, 1957: 200, Fig. 3 (photo on host)
Host: *Osmia* (*Osmia*) *excavata*
Distr: Japan
Note: brief observations on host mortality by mite

Syn: *Chaetodactylus* sp. Krombein, 1962: 239
Host: *Osmia* (*Osmia*) *excavata*
Distr: Japan
Note: assignment to genus *Chaetodactylus* of *Saproglyphus* sp. sensu Hirashima (1957)

Syn: *Chaetodactylus hirashimai*: Qu *et al*., 2002: 121
Distr: Japan: Honshu, Kyushu

19. **Chaetodactylus hopliti** sp. n. (p. 137)

20. **Chaetodactylus kouboy** sp. n. (p. 121)

21. **Chaetodactylus krombeini** Baker, 1962 (p. 141)

22. **Chaetodactylus lassulus** Klimov & OConnor, 2007 (p. 111)
Orig: *Chaetodactylus lassulus* Klimov & OConnor, 2007: 824, Figs 12–13 (holotype in KU, paratypes in AMNH, CAS, KU, OSAL, UMMZ)
Host: *Trichothurgus dubius* (type host), *T. herbsti*
Distr: Chile: Coquimbo (type locality), Región Metropolitana
Note: description of HDN

23. **Chaetodactylus lithurgi** Klimov & OConnor, 2004 (p. 121)

24. **Chaetodactylus ludwigi** (Trouessart, 1904) (p. 111)
Orig: *Trichotarsus Ludwigi* Trouessart, 1904a: 234, Figs a, a' (holotype not designated, syntypes in MNHN and ZSMC (Fain & Pauly, 2001))
Host: *Lithurgus* (*Lithurgus*) *atratus* (as *Megachile lonalap*) [nest in trunk of *Hibiscus* ("*Hybiscus*") with pollen of this plant].
Distr: Federated States of Micronesia: Pohnpei Is. ("Carolines Islands: Ponapé") (type locality)
Note: description of inert HDNs, mention of presence of feeding instars and two forms of HDNs. Immobile HDN is erroneously stated to have female external genital organs and is inseminated by adult males

Syn: *Trichotarsus Ludwigi*: Ludwig, 1904: 216, Figs a, a'
Host: *Lithurgus* (*Lithurgus*) *atratus* (as *Megachile lonalap*) [nest in trunk of *Hibiscus* with pollen of this plant].
Distr: Federated States of Micronesia: Pohnpei Is. ("Ponape (Karolinen)")
Note: review of Trouessart's (1904a,b) works where development of two deutonymphal forms of *Ch. ludwigi* and *Ch. osmiae* is discussed.

Syn: *Trichotarsus ludwigi*: Trouessart, 1904b: 365
Note: mention, Immobile HDN is erroneously stated to have female external genital organs and is inseminated by adult males

Syn: *Trichotarsus Ludwigi*: Vitzthum, 1912b: 184
Host: *Lithurgus* (*Lithurgus*) *atratus* (as *Lithurgus dentipes*)
Distr: Federated States of Micronesia: Pohnpei Is. ("Karolinen-Insel Ponape")
Note: mention of two deutonymphal forms, emendation of host name

Syn: *Tricholarsus Ludwigi* [sic!]: Vitzthum, 1912d: 292

Syn: *Chaetodactylus ludwigi*: Zachvatkin, 1941: 42
Host: *Lithurgus* (*Lithurgus*) *atratus* (as *Lithurgus dentipes*)
Note: mention

Syn: *Trichotarsus ludwigi*: Knülle, 1959: 385
Note: short note on leg morphology of inert HDN

Syn: *Chaetodactylus ludwigi*: Baker, 1962a: 229
Note: mention

Syn: *Chaetodactylus ludwigi*: Baker, 1987: 65
Note: mention

Chaetodactylus ludwigi: OConnor, 1993a: 353
Note: mention

Syn: *Chaetodactylus* (*Chaetodactylus*) *ludwigi*: Fain & Pauly, 2001: 128, Figs 1–4, 18–21.
Host: *Lithurgus* (*Lithurgus*) *atratus* (type host, Federated States of Micronesia, India) (as *Lithurgus dentipes*, part.), *Lithurgus pullatus* (Madagascar), *Lithurgus scabrosus* (Java; Moorea Is, near Tahiti; New Caledonia)
Distr: Federated States of Micronesia: Pohnpei Is. ("Eastern Caroline Isles: Ponape") (type locality); New Caledonia;

French Polynesia: Moorea Is; Indonesia ("Java: Soekaboemi"); India; Madagascar.
Note: examining type series (MNHN and in ZSMC); redescription (HDN); distinct groups different by sizes; SE pictures on host.

Syn: *Chaetodactylus ludwigi*: Pauly & Munzinger, 2003: 160.
Host: *Lithurgus scabrosus* (New Caledonia)
Distr: New Caledonia; Federated States of Micronesia (type locality); French Polynesia; Indonesia; South India.
Note: mention

Syn: *Chaetodactylus ludwigi*: Klimov & OConnor, 2007: 826.
Note: Remark on morphology

Syn: *Chaetodactylus ludwigi*: Klimov *et al*., 2007a: 1371.
Host: *Lithurgus* (*Lithurgus*) *atratus* (also as *Lithurgus dentipes*), *Lithurgus scabrosus*
Distr: Federated States of Micronesia; New Caledonia; French Polynesia; Indonesia; South India.
Note: HDN included in morphological phylogenetic analysis

25. **Chaetodactylus melitomae** Klimov & OConnor, 2007 (p. 113)

26. **Chaetodactylus micheneri** sp. n. (p. 127)

27. **Chaetodactylus nipponicus** Kurosa, 1987 (p. 110)
Orig: *Chaetodactylus* (*Chaetodactylus*) *nipponicus* Kurosa, 1987: 377, Figs. 9–15 (holotype in NSMT; paratype HDNs in author's collection, distributed to "certain foreign museums", UMMZ (3)).
Host: *Osmia (Osmia) excavata* (type host), *Osmia (Osmia) cornifrons*, *Osmia (Osmia) taurus*, *Osmia (Osmia) pedicornis*
Distr: Japan: Honshu (Aomori Pref., Hiraka-machi, Minami-Tsugaru-gun - type locality), Tsushima Is.
Note: description of HDN

Syn: *Chaetodactylus* sp. Yamada *et al*., 1971: 32
Host: *Osmia cornifrons*
Distr: Japan: Honshu
Note: report of damage to host in artificial colonies

Syn: *Chaetodactylus* sp. No. 2 Maeta, 1978: 141
Host: *Osmia cornifrons*
Distr: Japan: Honshu
Note: report of damage to host in artificial colonies

Syn: *Chaetodactylus nipponicus*: Van Asselt, 2000: 221
Note: considered as close or identical with *Chaetodactylus osmiae*

Syn: *Chaetodactylus nipponicus*: Bosh & Kemp, 2001: 62
Host: *Osmia cornifrons*
Distr: Japan

Syn: *Chaetodactylus nipponicus*: Qu *et al*., 2002: 121
Host: *Osmia cornifrons*
Distr: Japan: Honshu
Note: study on infestation patterns

Syn: *Chaetodactylus nipponicus*: Qu *et al*., 2003: 55
Host: *Osmia cornifrons*
Distr: northern and central Japan
Note: study of reproductive biology

28. **Chaetodactylus osmiae** (Dufour, 1839) (p. 110)
Orig: *Trichodactylus osmiae* Dufour, 1839: 276, Fig. 8.3 (holotype not designated, syntypes presumed lost)
Host: *Osmia rufa* (as *Osmia bicornis* and *Osmia fronticornis*)
Distr: France
Note: description of HDN

Syn: *Trichodactylus osmiae*: Gervais, 1844: 266 (part.), Fig. 34–10
Host: *Osmia rufa* (as *Osmia bicornis* and *Osmia fronticornis*)
Distr: France (Département des Landes)
Note: short description, not distinguished from *Sennertia cerambycina*

Syn: *Chaetodactylus osmiae*: Rondani, 1866: 183
Host: *Osmia*, *Xylocopa*, *Apis mellifera*
Distr: France, (?) Italy

Syn: *Trichodactylus osmiae*: Murray, 1877: 252 (part.), Fig. *Trichodactylus osmiae* Dufour.
Hosts: *Osmia*
Note: mention, character discussion

Syn: *Trichodactylus osmiae*: Mégnin, 1880: 147
Note: mention; evidence presented that *Trichodactylus* may be a developmental stage of other free-living Astigmata

Syn: *Trichotarsus osmiae*: Canestrini, 1888a: 395
Host: *Osmia rufa* (as *Osmia bicornis*, *Osmia fronticornis*)

Syn: *Trichotarsus Osmiae*: Canestrini, 1888b: 23
Host: *Osmia rufa* (as *Osmia bicornis* and *O. fronticornis*)

Syn: *Trichotarsus Osmiae*: Berlese, 1897: 105, Figs 4.*6*
Host: *Osmia* spp., *Andrena* spp., *Megachile* sp.
Distr: France, Italy.
Note: authorship cited as "(Dufour, 1832) Canestrini"; HDN included in key

Syn: *Trichotarsus osmiae*: Canestrini & Kramer, 1899: 149.
Host: *Osmia rufa*
Dist: France
Note: redescription of HDN, females and HDNs included in key

Syn: *Trichotarsus osmiae*: Giard, 1900: 377
Host: *Osmia rufa*
Distr: Belgium: Luxembourg
Note: included in key, not distinguished from *Ch. claviger*

Syn: *Trichotarsus osmiae*: Oudemans, 1900: 117
Note: comparison with HDNs of *Trichotarsus japonicus* and *Trichotarsus alfkeni*

Syn: *Trichotarsus osmiae*: Oudemans, 1901: 81
Note: included in key, comparison with *Sennertia koptorthosomae*

Syn: *Trichotarsus osmiae*: Michael, 1903: 17, Fig. 22, 39.13–15

Host: *Osmia rufa*
Dist: England
Note: redescription of HDN, tritonymph, and adults. Feeding instars were reared from HDNs on old bee wax in laboratory

Syn: *Trichotarsus osmiae*: Oudemans, 1903a: 147
Note: included in key, assigned to group C in *Trichotarsus*

Syn: *Trichotarsus osmiae*: Ludwig, 1904: 216, Figs b, b'
Distr: France
Host: *Osmia cornuta*
Note: mention in review of Trouessart's (1904a, b) works

Syn: *Trichotarsus osmiae*: Trouessart, 1904a: 235, Figs b, b'
Distr: France
Host: *Osmia cornuta*
Note: description of inert HDN, erroneously stated that it has female external genital organs and is inseminated by adult males, comparison with *Chaetodactylus ludwigi*

Syn: *Trichotarsus osmiae*: Trouessart, 1904b: 365
Distr: France
Host: *Osmia cornuta*
Note: observation on development of inert HDN, erroneously stated that it has female external genital organs and is inseminated by adult males

Syn: *Trichotarsus osmiae*: Oudemans, 1905a: 22
Note: mention

Syn: *Trichotarsus osmiae*: Oudemans, 1905b: LXXX
Note: short note on morphology

Syn: *Trichotarsus osmiae*: Popovici-Baznosanu, 1913: 32, Figs. 1–12
Host: *Osmia bicornis*, *Osmia cornuta*
Distr: Romania
Note: description of postembryonic development, observation on biology in bee nests

Syn: *Trichotarsus osmiae*: Oudemans, 1911a: 165
Note: comparison with HDN of *Chaetodactylus anthidii*

Syn: *Trichotarsus osmiae*: Vitzthum, 1912d: 291
Host: *Osmia rufa* (as *Osmia bicornis*, *Osmia fronticornis*)
Distr: France

Syn: *Trichotarsus osmiae*: Vitzthum, 1919: 38
Host: Europe
Distr: *Osmia rufa*, *Andrena* spp., *Megachile* spp.
Note: comparison with HDNs and adults of *Trichotarsus ludwigi*

Syn: *Chaetodactylus osmiae*: Vitzthum, 1929: 77
Host: *Osmia rufa*, *Andrena* spp., *Megachile* spp.
Distr: Middle Europe
Note: included in key

Syn: *Chaetodactylus osmiae*: Zachvatkin, 1941: 394 (part), Figs 78, 79, 644–650, non 678.
Host: *Osmia rufa*, *Osmia tricornis*, *Osmia kohlii*.
Distr: France, Italy, England, Romania, Georgia, ?Russia: Volgogradskaya Oblast' ("Sarepta")
Note: not separated from *Ch. zachvatkini* sp. n., description, included in key

Syn: *Chaetodactylus osmiae*: Turk, 1953: 82
Distr: British Isles

Syn: *Chaetodactylus osmiae*: Türk & Türk, 1957: 207, Figs 160–161
Host: *Osmia rufa*, *Osmia "rufiventris"*
Distr: Germany, Netherlands, Italy, England, former USSR
Note: redescription of HDN, included in key

Syn: *Chaetodactylus osmiae*: Lith, 1957: 197
Host: *Osmia rufa*
Distr: Netherlands
Note: observation on biology in host nest, report of killing of bee larvae

Syn: *Trichotarsus osmiae*: Knülle, 1959: 385
Note: short note on leg morphology in inert HDN

Syn: *Chaetodactylus osmiae*: Baker, 1962a: 229
Note: mention

Syn: *Chaetodactylus osmiae*: Krombein, 1962: 238
Host: *Osmia rufa*, *Osmia cornuta*
Distr: France, Romania, Netherlands
Note: review of biology

Syn: *Chaetodactylus osmiae*: Fain, 1966: 249
Host: *Osmia rufa*, *Osmia cornuta*
Distr: Belgium
Note: historical review, discussion factors influencing formation of heteromorphic deutonymphs and possible ways of dispersal

Syn: *Chaetodactylus osmiae*: Elbadry, 1971: 88
Note: mention on possible parasitism

Orig: *Chaetodactylus mahunkai* Samšiňák, 1973: 404, Figs 3–4 (holotype and 1 paratype HDNs in "Parasitologischen Institutes in Praha" (not found in PARU, F. Dusbábek, pers. comm.), unspecified number of paratypes in HNHM, synonymized by Fain, 1981b)
Host: unknown
Distr: Hungary
Note: description of HDN

Syn: *Chaetodactylus* (*Chaetodactylus*) *osmiae*: Fain, 1981b: 4
Host: *Osmia rufa*
Note: subgenus assignment, incorrect authorship assignment (Dujardin), included in key, tentatively considered as senior synonym of *Chaetodactylus mahunkai*.

Syn: *Chaetodactylus osmiae* De Jong *et al*., 1982: 245
Host: *Apis*

Syn: *Chaetodactylus* (*Chaetodactylus*) *osmiae*: Kurosa, 1987: 373
Note: comparison with *Ch. nipponicus*; authorship attributed to Dujardin

Syn: *Chaetodactylus osmiae*: Baker, 1987: 65
Note: mention, authorship attributed to Dujardin

Syn: *Chaetodactylus osmiae*: Bosch, 1992: 77
Host: *Osmia cornuta*
Distr: Spain
Note: infestation rates in wild and managed populations of *Osmia cornuta*

Syn: *Chaetodactylus osmiae*: Chmielewski, 1993: 133
Host: *Osmia rufa*, *Anthophora* sp.
Distr: Poland
Note: culture on pollen (started from HDNs), biology of post-embryonic development in laboratory

Syn: *Chaetodactylus* (*Chaetodactylus*) *osmiae*: OConnor, 1993a: 353
Note: genus-level character acquisition, authorship attributed to Dujardin

Syn: *Chaetodactylus osmiae*: Fain & Baugnée, 1996: 23
Host: *Osmia rufa*, *Osmia cornuta*.
Distr: Belgium

Syn: *Chaetodactylus osmiae*: Van Asselt, 2000: 221, Figs 1–26
Host: *Osmia rufa*
Distr: Belgium
Note: historical review, redescription of all instars except for tritonymph, measurements, tentatively considered as senior synonym of *Chaetodactylus nipponicus*

Syn: *Chaetodactylus osmiae*: Fain & Pauly, 2001: 127
Note: mention

Syn: *Chaetodactylus osmiae*: Qu *et al*., 2003: 59
Note: mention

Syn: *Chaetodactylus osmiae*: Krunić *et al*., 2005: 143
Host: *Osmia rufa*, *Osmia cornuta*.
Distr: Serbia and Montenegro (Belgrad)
Note: observations on biology

Syn: *Chaetodactylus osmiae*: Klimov *et al*., 2007a: 1371
Host: *Osmia rufa*, *Osmia tricornis*, *Osmia cornuta*, *Osmia niveata* (as *Osmia fulviventris*)
Distr: France; Belgium; England; Germany; Hungary; Croatia; Spain
Note: HDN included in morphological phylogenetic analysis

Misidentifications: Donnadieu, 1868 (*Chaetodactylus claviger*); Banks, 1902: 176 (*Chaetodactylus krombeini* or *Ch. rozeni* sp. n.); Abou Senna, 1997 (*Chaetodactylus claviger*); Fain *et al*., 1992 (*Chaetodactylus chrysidis aurulenticola*)

29. **Chaetodactylus reaumuri** (Oudemans, 1905) (p. 110)
Orig: *Trichotarsus reaumuri* Oudemans, 1905b: LXXXI (lectotype and unknown number of paralectotype HDNs (Fain and Baugnée, 1996) in RMNH)
Host: "*Osmia rufiventris* Panz." (type host), *Osmia brevicornis* (as *Osmia panzeri*)
Distr: Czech Republic: Kolín ("Kolin, Bohemen") (type locality); "Odran, Oostenrijksch Silezië"
Note: description of HDN

Syn: *Trichotarsus reaumuri*: Oudemans, 1905a: 22
Note: mention

Syn: *Trichotarsus reaumuri*: Oudemans, 1911a: 165
Note: comparison with *Chaetodactylus anthidii* HDN

Syn: *Trichotarsus reaumuri*: Vitzthum, 1919: 31
Host: *Osmia* "*rufiventris*" Panz., *Osmia brevicornis* (as *Osmia panzeri*)
Distr: "Austrian Silesia" and Czech Republic (Österreichisch-Schlesien und Böhmen)
Note: comparison with HDN of *Chaetodactylus ludwigi*

Syn: *Chaetodactylus reaumuri*: Oudemans, 1924: 328
Note: comparison with *Chaetodactylus claviger*

Syn: *Chaetodactylus reaumuri*: Vitzthum, 1929: 77
Host: *Osmia* "*rufiventris*" Panz., *Osmia brevicornis* (as *Osmia panzeri*)
Distr: Middle Europe
Note: included in key

Syn: *Chaetodactylus reaumuri*: Zachvatkin, 1941: 396
Host: *Osmia brevicornis* (as *Osmia panzeri*), *Osmia leucogastra*
Distr: Germany; Ukraine: Crimean Peninsula; Georgia (Tbilisi)
Note: redescription of HDN, included in key

Syn: *Chaetodactylus reaumuri*: Türk & Türk, 1957: 210, Fig. 162
Host: *Osmia* "*rufiventris*" Panz., *Osmia brevicornis* (as *Osmia panzeri*), *Stelis murina*
Distr: "Ehem. Schlesien", Czech Republic, Greece: Corfu
Note: redescription, included in key

Syn: *Chaetodactylus* (*Chaetodactylus*) *reaumuri*: Fain, 1981b: 2
Note: included in key, subgeneric assignment

Syn: *Chaetodactylus* (*Chaetodactylus*) *reamuri* Kurosa, 1987: 373 (lapsus)
Note: comparison with *Ch. hirashimai*

Chaetodactylus (*Chaetodactylus*) *reaumerii* OConnor, 1993a: 362 (lapsus)
Note: genus-level character acquisition

Syn: *Chaetodactylus reaumuri*: Fain & Baugnée, 1996: 28
Host: "*Osmia rufiventris* Panzer"
Distr: Czech Republic: Kolín ("de Kolin, Silésie autrichienne")
Note: redescription, lectotype designation

30. **Chaetodactylus rozeni** sp. n. (p. 132)

31. **Chaetodactylus zachvatkini** sp. n. (p. 110)

32. **Roubikia imberba** Klimov & OConnor, 2007 (p. 103)
Orig: *Roubikia imberba* Klimov & OConnor, 2007: 819, Figs 7–8, 9D (holotype in AMNH, paratypes in AMNH, OSAL, UMMZ)
Host: *Tetrapedia* sp. (type host) and its cleptoparasites *Coelioxoides waltheriae* and *C. exulans*
Distr: Argentina: Tucumán (type locality), Salta
Note: description of HDN

33. **Roubikia latebrosa** Klimov & OConnor, 2007 (p. 103)
Orig: *Roubikia latebrosa* Klimov & OConnor in Klimov *et al*., 2007b: 118, Figs 1A, 5, 6 (holotype in USNM, paratypes in USNM, FMNH, UMMZ)
Host. *Tetrapedia* sp.
Distr: Peru: Loreto
Note: description of HDN from acarinarium on 1st metasomal tergite

Syn: *Roubikia latebrosa*: Klimov *et al*., 2007a: 1371
Host. *Tetrapedia* sp.
Distr: Peru
Note: HDN included in morphological phylogenetic analysis

34. **Roubikia officiosa** Klimov & OConnor, 2007 (p. 107)

35. **Roubikia panamensis** (Baker, Roubik & Delfinado-Baker, 1987) (p. 103)

36. **Sennertia antarctica** (Trägårdh, 1907), **comb. n.**
Orig: *Trichotarsus antarcticus* Trägårdh, 1907: 12, Fig. 4 (holotype not designated, type depository probably NHRS)
Host: marine algae
Distr: Antrarctica, Booth Is. (as Wandel Is.) (type locality)
Note: Description of HDN (number of studied specimens not specified, presumably one); speculated to be a deutonymph of supralittoral mites of the genus *Hyadesia*. This insufficiently described taxon is similar to several African species belonging to the *cerambycina*-group of the genus *Sennertia*. The geographic locality is, most likely, erroneous because carpenter bees, the only hosts of *Sennertia*, do not occur in Antarctica

Syn: *Chaetodactylus antarcticus*: Pugh, 1993: 373
Note: erroneous generic assignment, listed in catalog

37. **Sennertia aldeodadi** Haitlinger, 2000
Orig: *Sennertia (Sennertia) aldeodadi* Haitlinger, 2000: 18, Figs 1–6 (holotype and some paratype HDNs in UWCP, some paratypes in Department of Zoology, Agricultural University, Wroclaw, and HNHM)
Host: "undetermined Anthophoridae"
Distr: Mauritius: Mahébourg (as Mohebourg)
Note: description of HDN, assignment to *cerambycina*-group

38. **Sennertia alfkeni** (Oudemans, 1900)
Orig: *Trichotarsus alfkeni* Oudemans, 1900: 115, Figs. 18–20 (lectotype and 3 paralectotype HDNs in RMNH, designated by Fain, 1974b)
Host: *Xylocopa* (*Alloxylocopa*) *circumvolans*
Distr: Japan (no specific location)
Note: description of HDN, included in key

Syn: *Trichotarsus alfkeni*: Oudemans, 1901: 82
Note: included in key

Syn: *Trichotarsus alfkeni*: Oudemans, 1903a: 147
Note: included in key, assigned to group D in *Trichotarsus*

Syn: *Sennertia alfkeni*: Oudemans, 1905a: 22
Note: assignment to *Sennertia*

Syn: *Trichotarsus Alfkeni*: Vitzthum, 1912c: 233 (part., only specimens from *X. circumvolans*)
Host: *Xylocopa circumvolans*
Distr: Japan

Syn: *Trichotarsus Alfkeni*: Vitzthum, 1912d: 290
Host: *Xylocopa circumvolans*
Distr: Japan

Syn: *Trichotarsus Alfkeni*: Vitzthum, 1912d: 289
Note: comparison with *Sennertia horrida*

Syn: *Sennertia alfkeni*: Vitzthum, 1914: 323
Note: comparison with HDN of *Sennertia morstatti*

Syn: *Sennertia alfkeni*: Vitzthum, 1919: 31
Host: *Xylocopa circumvolans*
Distr: Japan
Note: comparison of HDN with *Sennertia morstatti*, *S. horrida*

Syn: *Sennertia alfkeni*: Oudemans, 1924: 329
Note: comparison with *Sennertia sumatrensis*

Syn: *Sennertia alfkeni*: Vitzthum, 1941: 308
Note: comparison with *Sennertia frontalis*; species year description given as 1899

Syn: *Sennertia ?bifilis*: Womersley, 1941: 480, Fig. 17 (after Fain, 1982)
Host: *Xylocopa* (*Koptortosoma*) *bryorum* (as "*Mesotricha bryorum*")
Distr: Australia: Queensland

Syn: *Sennertia alfkeni*: Zachvatkin, 1941: 389, Figs 672–644 (part.)
Host: *Xylocopa circumvolans* (as "*X. kalinovskii* Rad." =*Xylocopa kalinowskii* Radoszkowski)
Distr: Japan, Korea, China
Note: redescription of HDN, included in key, *Sennertia japonica* considered as junior synonym of *S. alfkeni*; species description year given as 1901

Syn: *Sennertia alfkeni*: Fain, 1974b: 229, Figs. 11–12, 15–16
Host: *Xylocopa circumvolans*
Distr: Japan: "Kōbe"
Note: species description year given as 1901

Syn: *Sennertia alfkeni*: Delfinado & Baker, 1976: 85
Note: comparison with *Sennertia americana*

Syn: *Sennertia* (*Sennertia*) *alfkeni*: Fain, 1981a: 163
Host: *Xylocopa circumvolans*
Distr: Japan
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *japonica*-group, stated that type in RMNH, species description year given as 1901

Syn: *Sennertia* (*Sennertia*) *alfkeni*: Fain, 1982: 70
Host: *Xylocopa circumvolans* (Japan), *Xylocopa* (*Koptortosoma*) *bryorum* (Australia)
Distr: Japan, Australia: Queensland
Note: species description year given as 1901

Syn: *Sennertia* (*Sennertia*) *alfkeni*: OConnor, 1993a: 362
Note: genus-level character acquisition; year of species description was indicated as 1901

Syn: *Sennertia alfkeni*: Okabe & Makino, 2002: 73, Fig: 5, 6 (SEM pictures)
Host: *Xylocopa circumvolans* (as *Xylocopa appendiculata circumvolans*)
Distr: Japan: Ibaraki, Chiba
Note: preferred attachment site: dorsolateral hairs

Orig: *Trichotarsus japonicus* Oudemans, 1900: 117, Fig. 21 (holotype HDN in RMNH (Fain, 1974b)), synonymized by Zachvatkin (1941)
Host: *Xylocopa circumvolans*
Distr: Japan (no specific location)
Note: description of HDN, included in key

Syn: *Trichotarsus japonicus*: Oudemans, 1901: 83
Note: included in key

Syn: *Trichotarsus japonicus*: Oudemans, 1903a: 147
Note: included in key, assigned to group D in *Trichotarsus*

Syn: *Trichotarsus japonicus*: Trägårdh, 1904: 156
Note: comparison with *Sennertia simplex*

Syn: *Sennertia japonica* (as *Tr. japonicus*): Oudemans, 1905a: 22
Note: assignment to *Sennertia*

Syn: *Sennertia japonica*: Vitzthum, 1914: 323
Note: comparison with HDN of *Sennertia morstatti*

Syn: *Sennertia japonica*: Vitzthum, 1919: 43
Note: comparison with *Sennertia morstatti* and *Sennertia horrida*, species year description indicated as 1899

Syn: *Sennertia japonica*: Vitzthum, 1941: 308
Note: comparison with *Sennertia frontalis*; species year description given as 1899

Syn: *Sennertia japonicus*: Fain, 1974b: 224, Figs. 5–6
Host: *Xylocopa circumvolans*
Distr: Japan: "Kōbe"
Note: species description year given as 1901

Syn: *Sennertia* (*Sennertia*) *japonicus*: Fain, 1981a: 163
Host: *Xylocopa circumvolans*
Distr: Japan
Note: included in key, subgeneric assignment, assigned to *japonica*-group; year of species description indicated as 1901

Syn: *Sennertia japonica*: Okabe & Makino, 2002: 73, Fig: 2a, 3 (color photos in acarinaria), Fig. 4 (ESEM picture)
Host: *Xylocopa circumvolans* (as *Xylocopa appendiculata circumvolans*))
Distr: Japan: Ibaraki, Chiba
Note: preferred attachment sites: mesosomal and metasomal acarinaria

Misidentifications:
Syn: *Trichotarsus Alfkeni*: Vitzthum, 1912c: 233, Figs 19–20
Host: *Xylocopa* (*Koptortosoma*) *aestuans* (as *Koptorthosoma aestuans*) (East Sumatra), *Xylocopa* (*Koptortosoma*) *caerulea* (as *Koptorthosoma coerulea*) (Java)
Distr: Indonesia: Java, East Sumatra

39. **Sennertia americana** Delfinado & Baker, 1976 (p. 173)

40. **Sennertia argentina** Vitzthum, 1941 (p. 156)

41. **Sennertia augustii** Alzuet & Abrahamovich, 1990 (p. 192)
Orig: *Sennertia augustii* Alzuet & Abrahamovich, 1990: 628, Figs 1–20 (holotype and 12 paratype HDNs in MLPA)
Host: *Xylocopa* (*Neoxylocopa*) *augusti*
Distr: Argentina: Buenos Aires (Berazategui)
Note: description of HDNs, L, PN, TN, PN, and adults. SEM pictures of chorion microstructure

42. **Sennertia basilewskyi** Fain, 1974
Orig: *Sennertia basilewskyi* Fain, 1974a: 215 (holotype in MRAC)
Host: "Megachilidae"
Distr: Democratic Republic of the Congo: Bambesa
Note: description of HDN, host bee in MRAC (n° M 42)

Syn: *Sennertia* (*Afrosennertia*) *basilewskyi*: Fain, 1981a: 180, Figs 59–61
Host: "Megachilidae" (Bambesa) (type host), "*Chedrion nigrihirtum*" (Dingila), *Xylocopa* (*Koptortosoma*) *africana* (as *Mesotrichia africana*) (Bambesa)
Distr: Democratic Republic of the Congo: Haut-Congo Prov. ("Uélé") (Bambesa) (type locality), Dingila
Note: redescription of HDN, included in key, subgeneric assignment, unjustified paratype designation (from "*Chedrion nigrihirtum*" and *Xylocopa africana*)

Syn: *Sennertia* (*Afrosennertia*) *basilewskyi*: Fain, 1982: 67
Note: comparison with *Sennertia queenslandica*

43. **Sennertia benoiti** Fain, 1974
Orig: *Sennertia benoiti* Fain, 1974a: 218 (holotype HDN (#152422) in MRAC, paratypes not explicitly designated; Fain (1980) mentioned 12 paratype HDNs from same sample as holotype)
Host: "*Ceratina* sp. (n° 283 A)"
Distr: Côte d'Ivoir: Bafing (Touba) ("Touba, Côte-d'Ivoire")
Note: short description of HDN

Syn: *Sennertia benoiti*: Fain, 1980: 988, Figs 9–10
Host: "*Ceratina* sp. (n° 283 B)" (type host), *Ceratina* (*Pithitis*) *atopura* (Congo)
Distr: Côte d'Ivoir: Bafing, 7 km ESE Touba (type locality), Democratic Republic of the Congo
Note: redescription of HDN, emendation of type host and locality data

Syn: *Sennertia* (*Sennertia*) *benoiti*: Fain, 1981a: 157, Fig. 72
Host: "*Ceratina* sp. (n° 283 A)" (type host), *Ceratina atopura* (Congo)

Distr: Côte d'Ivoir (type locality), Democratic Republic of the Congo
Note: included in key, short redescription, subgeneric assignment, assigned to *cerambycina* group, unjustified designation of paratypes from *Ceratina atopura*

Syn: *Sennertia* (*Sennertia*) *benoiti*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo

44. **Sennertia bifida** Kurosa, 2003
Orig: *Sennertia (Eosennertia) bifida* Kurosa, 2003: 26, Figs 1–5 (holotype HDN in NSMT, 39 paratype HDNs distributed in NSMT, CNC, HNHM, IRSNB, NBGY, UMMZ, USNM)
Host: *Ceratina* (*Ceratinidia*) *japonica* (type host), *Ceratina flavipes* Smith, *Ceratina okinawana*
Distr: Japan: Hokkaido (Sapporo, Hitsujigaoka) (type locality), Honshu, Ryukyus
Note: description of HDN

45. **Sennertia bifilis** (Canestrini, 1897)
Orig: *Trichotarsus bifilis* Canestrini, 1897: 474 (holotype not designated, repository unknown)
Host: *Xylocopa* (*Koptortosoma*) *combinata*
Distr: Papua New Guinea: Madang: Astrolabe Bay (Erima)
Note: description of HDN

Syn: *Trichotarsus bifilis*: Canestrini & Kramer, 1899: 149
Distr: Papua New Guinea
Host: *Xylocopa combinata*
Note: redescription of HDN and adults; HDN and females included in key

Syn: *Trichotarsus bifilis*: Giard, 1900: 377
Note: included in key

Syn: *Trichotarsus bifilis*: Oudemans, 1901: 83
Note: included in key

Syn: *Trichotarsus bifilis*: Oudemans, 1903: 147
Note: included in key, assigned to group D in *Trichotarsus*

Syn: *Sennertia bifilis*: Oudemans, 1905a: 22
Note: transferred to *Sennertia*

Syn: *Trichotarsus bifilis*: Vitzthum, 1912d: 290
Host: *Xylocopa combinata*
Distr: Papua New Guinea

Syn: *Sennertia bifilis*: Vitzthum, 1919: 61
Note: redescription of HDN and adults

Syn: *Sennertia bifilis*: Zachvatkin, 1941: 42
Host: *Xylocopa combinata*
Note: mention

Syn: *Sennertia bifilis*: Fain, 1981a: 180
Host: *Xylocopa combinata*
Distr: Papua New Guinea: Madang (Erima)

Syn: *Sennertia bifilis* Fain, 1982: 70
Host: *Xylocopa combinata*
Distr: Papua New Guinea

Syn: *Sennertia bifilis*: Lombert *et al*., 1987: 113
Note: mention

46. **Sennertia caffra** Vitzthum, 1919
Orig: *Sennertia caffra* Vitzthum, 1919: 53, Figs 47–50 (lectotype HDN (A20031423), 2 male (A20031419, -26), 1 nymph (A20031424), 5 HDN (A20031420-22, 25) paralectotype slides labeled as "*Sennertia caffra* Vitzthum, 1920" in ZSMC) (Jürgen *et al*., 2005)
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Koptorthosoma caffra*)
Distr: South Africa: Eastern Cape (Willowmore) ("Willowmore, Kapland")
Note: description of HDN and male

Syn: *Sennertia caffra*: Vitzthum, 1941: 310
Note: comparison with *Sennertia argentina*, year of species description indicated as 1920

Syn: *Sennertia caffra*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Koptorthosoma caffra*)
Note: mention

Syn: *Sennertia* (*Sennertia*) *caffra*: Lombert *et al*., 1987: 113
Host: *Xylocopa* (*Koptortosoma*) *caffra*
Note: mention

Syn: *Sennertia* (*Sennertia*) *caffra*: Fain, 1981a: 159, Figs. 15–17, 69 (lectotype designation: HDN V3094 (A20031423))
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Xylocopa* (*Koptorthosoma*) *caffra*)
Distr: South Africa: Eastern Cape, Willowmore
Note. Redescription, included in key, mention of 11 paralectotype slides with males and HDNs, subgeneric assignment, included in the *cerambycina*-group

Syn: *Sennertia* (*Sennertia*) *caffra*: Haitlinger, 2000: 17
Distr: South Africa

47. **Sennertia cantabrica** Zachvatkin, 1941
Orig: *Sennertia cantabrica* Zachvatkin, 1941: 385, Figs 23, 662–664 (holotype not designated, syntypes not found in ZIN)
Host: *Xylocopa* (*Xylocopa*) *cantabrita* (as *Xylocopa cantabrica*)
Distr: Algeria
Note: description of HDN, TN

Syn: *Sennertia* (*Sennertia*) *cantabrica*: Fain, 1981a: 163
Host: *Xylocopa* (*Xylocopa*) *cantabrita* (as *Xylocopa cantabrica*)
Distr: Algeria
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *japonica*-group, stated that "type" in ZIN

Syn: *Sennertia cantabrica*: Lombert *et al*., 1987: 113
Host: *Xylocopa* (*Xylocopa*) *cantabrita* (as *Xylocopa cantabrica*)
Distr: Algeria

Syn: *Sennertia* (*Sennertia*) *cantabrica*: Haitlinger, 2000: 17

48. **Sennertia capensis** Fain, 1971
Orig: *Sennertia capensis* Fain, 1971: 266 (holotype (152424) and 15 paratype HDNs in MRAC)
Host: *Xylocopa* (*Gnathoxylocopa*) *sicheli*
Distr: South Africa: Eastern Cape (Willowmore)

Syn: *Sennertia* (*Sennertia*) *capensis*: Fain, 1981a: 157, Figs. 7, 10, 11, 64
Host: *Xylocopa* (*Gnathoxylocopa*) *sicheli*
Distr: South Africa: Eastern Cape (Willowmore)
Note: included in key, redescription of HDN, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *capensis*: Haitlinger, 2000: 17
Distr: South Africa

49. **Sennertia cerambycina** (Scopoli, 1763)
Orig: *Pediculus Cerambycinus* Scopoli, 1763: 386 (holotype not designated, syntypes presumed lost)
Host: *Xylocopa violacea* (as *Apis Violaceae*)
Distr: "Carniola" (in modern Slovenia)
Note: description of HDN

Orig: *Trichodactyle Xylocopae* Donnadieu, 1868: 84, Figs 1, 3, 4, 7, 9.
Host: *Xylocopa violacea*
Distr: France
Note: description of HDN

Syn: *Trichodactylus osmiae*: Gervais, 1844: 266 (part.)
Host: *Xylocopa violacea*
Distr: France (Paris)
Note: short description, not distinguished from *Chaetodactylus osmiae*

Syn: *Trichodactylus xylocopae*: Murray, 1877: 252 (part.), Fig.
Host: *Xylocopa violaceae*
Note: mention, character discussion

Syn: *Trichodactylus Xylocopae*: Canestrini & Fanzago, 1878: 205, Fig. 7.*3*
Host: *Xylocopa violacea* (as *Xylocopa violaceum*)
Distr: Italy

Syn: *Trichodactylus Xylocopae*: Mégnin, 1880: 147
Note: mention; evidence presented that *Trichodactylus* may be a developmental stage of other free-living Astigmata

Syn: *Trichodactylus Xylocopae*: Berlese, 1884b: 12
Note: comparison of adults with *Homopus*, *Dermacarus*, and *Trichodactylus anonymus*

Syn: *Trichodactylus Xylocopae*: Berlese, 1885: XVIII, n. 1, Fig. 1.
Host: *Xylocopa violacea*
Distr: Italy
Note: description of HDN and adults; authorship inconsistently attributed to Donnadieu or Dugès.

Syn: *Trichodactylus Xylocopae*: Canestrini & Berlese, 1885: 206, Figs 6.*1–5*.
Host: *Xylocopa violacea*
Note: authorship attributed to Dugès; description of HDN and adults

Syn: *Trichotarsus Xylocopae*: Canestrini, 1888a: 394, Fig. 36.*1–6*
Note: description of male, female, and HDN, authorship attributed to Donnadieu

Syn: *Trichotarsus Xylocopae*: Canestrini, 1888b: 23, Figs 2.*7–9*
Host: *Xylocopa violacea* (as *Xylocopa violaceae*)
Distr: Italy
Note: short description of adults and HDNs.

Syn: *Trichotarsus xylocopae*: Berlese, 1892: fasc. LXV, n 1
Host: *Xylocopa violacea*
Distr: Italy
Note: hyperphoresy of HDNs on both males and females of mite *Aeroglyphus peregrinans* (as *Glycyphagus peregrinans*) (Aeroglyphidae); name given in plural form, *Trichodacyli xylocopae*

Syn: *Trichotarsus Xylocopae*: Berlese, 1897: 105, Figs 4.*4–5*.
Host: *Xylocopa violacea* (as *Xylocopa violaceae*)
Distr: "All Europe"
Note: authorship cited as "(Dugès) Canestrini"; HDN included in key; *Eutarsus cancriformis* Hessling, 1852 (=*Cheyletus eruditus* (Schrank, 1781)) considered as junior synonym of *Trichotarsus Xylocopae* "Dugès, 1834" (p. 110)

Syn: *Trichotarsus xylocopae*: Canestrini, 1897: 474
Note: comparison with *Sennertia bifilis* HDN

Syn: *Trichotarsus xylocopae*: Canestrini & Kramer, 1899: 149
Host: *Xylocopa violacea*
Distr: Europe
Note: redescription of HDN and adults; HDN and females included in key

Syn: *Trichotarsus xylocopae*: Tietze in Canestrini, 1899: 938
Host: *Xylocopa violacea*
Distr: Italy
Note: authorship attributed to Dugès

Syn: *Trichotarsus xylocopae*: Giard, 1900: 377
Host: *Xylocopa violacea*
Distr: France
Note: included in key

Syn: *Trichotarsus xylocopae*: Oudemans, 1900: 116
Note: comparison with HDNs of *Trichotarsus japonicus* and *Trichotarsus alfkeni*

Syn: *Trichotarsus xylocopae*: Oudemans, 1901: 81
Note: included in key, comparison with *Sennertia koptorthosomae*

Syn: *Trichotarsus xylocopae*: Oudemans, 1902: 44
Note: comparison with *Trichotarsus hipposideros*

Syn: *Trichotarsus xylocopae*: Oudemans, 1903a: 147
Note: included in key, assigned to group D in *Trichotarsus*

Syn: *Trichotarsus Xylocopae*: Berlese, 1903a: 322
Host: *Xylocopa violacea*
Note: short note on damage to host nest

Syn: *Sennertia cerambycina*: Oudemans, 1905a: 22
Note: designated as type species of *Sennertia*

Syn: *Trichotarsus cerambycinus*: Oudemans, 1905b: LXXX
Note: redescription of HDN; considered as senior synonym of *Trichotarsus xylocopae*

Syn: *Trichotarsus xylocopae*: Trägårdh, 1907: 12
Note: comparison with *Trichotarsus antarcticus*

Syn: *Trichotarsus xylocopae*: Popovici-Baznosanu, 1913: 32
Note: mention

Syn: *Trichotarsus xylocopae*: Vitzthum, 1912c: 232, Fig 17, 18
Host: *Xylocopa violacea* (Germany, Mediterranean), *Xylocopa* (*Xylocopa*) *valga* (as *Xylocopa vulga*) (Italy)
Distr: "Mediterranean countries", Italy, southern Germany

Syn: *Trichotarsus xylocopae*: Vitzthum, 1912d: 292
Host: *Xylocopa violacea*, *Xylocopa valga* (as *Xylocopa vulga*)
Distr: Europe, including Germany

Syn: *Sennertia cerambycina*: Vitzthum, 1919: 42
Note: comparison with *Sennertia morstatti*, *S. perturbans, S. caffra*, *S. horrida*, and *S. bifilis*

Syn: *Sennertia cerambycina*: Vitzthum, 1929: 77
Host: *Xylocopa violacea*
Distr: Middle Europe
Note: included in key, Fig. 120 ("*Sennertia cerambycina*") is actually *Sennertia horrida*

Syn: *Sennertia cerambycina*: Vitzthum, 1933: 152
Host: *Xylocopa violacea*

Syn: *Sennertia cerambycina*: Eyndhoven, 1941: 325, Fig. 1
Distr: Netherlands
Host: *Xylocopa violacea*

Syn: *Sennertia cerambycina*: Vitzthum, 1941: 307
Host: *Xylocopa violacea*
Distr: South Europe

Syn: *Sennertia cerambycina*: Zachvatkin, 1941: 382, Figs 638–643, 653–655
Host: *Xylocopa* (*Xylocopa*) *violacea*, *Xylocopa* (*Xylocopa*) *valga* (as *X. valga* and X. *valga* "*pyrrhopyga*." (=*pyropyga* Friese)), *Xylocopa* (*Xylocopa*) *varentzowi* (as *X. varentzovi*), *Xylocopa* (*Proxylocopa*) *nitidiventris*, *Xylocopa (Proxylocopa) przewalskyi* (as *X. przewalskii*), *Xylocopa* (*Copoxyla*) *turanica*. Also phoretic on *Polochrum repandum* Spinola, 1806 (Hymenoptera, Sapygidae) (cleptoparasite of *Xylocopa*), occasionally found on *Hoplitis princeps* (as *Osmia princeps*), *Osmia (Monosmia) apicata* (as *Osmia macroglossa*), *Megachile* (*Eutricharaea*) *leachella* (as *Megachile argentata*, and *Anthophora* (*Paramegilla*) *balassogloi* (as *Anthidium christofi* F. Mor.)
Distr: "All southern, central, and eastern Europe, up to 55°N; West and Central Asia up to Tibet and Gashun Gobi Desert (China) on the east and up to northern Iran to the south".

Syn: *Sennertia cerambycina*: Eyndhoven, 1952: XXXIV
Host: *Xylocopa violacea*
Distr: Netherlands

Syn: *Sennertia cerambycina*: Skaife, 1952: 76
Host: *Xylocopa violacea*
Distr: Europe

Syn: *Sennertia xylocopae*: Türk & Türk, 1957: 210, Fig. 163
Host: *Xylocopa violacea*
Distr: Germany, France, Netherlands
Note: redescription, included in key

Syn: *Sennertia cerambycina*: Elbadry, 1971: 87
Note: comparison with HDN of *Sennertia egyptiaca*

Syn: *Sennertia cerambycina*: Fain, 1971: 265
Note: comparison with HDN *Sennertia mesotrichia*

Syn: *Sennertia* (*Sennertia*) *cerambycina*: Lombert *et al*., 1987: 113
Note: mention

Syn: *Sennertia* (*Sennertia*) *cerambycina*: Fain, 1981a: 152, Figs 1, 4, 65
Host: *Xylocopa violacea*, *Xylocopa violacea* group
Distr: Italy, Spain, Netherlands, Europe, Central Asia
Note: redescription of HDN, included in key, subgenus and *cerambycina* species-group assignment

Syn: *Sennertia* (*Sennertia*) *cerambycina*: OConnor, 1993a: 362
Note: genus-level character acquisition

Syn: *Sennertia* (*Sennertia*) *cerambycina*: Vicidomini, 1996: 71
Host: *Xylocopa violacea*
Distr: Italy
Note: note on host associations

Syn: *Sennertia cerambycina*: Vicidomini & Meloni, 1999: 138
Host: *Xylocopa violacea*
Distr: Greece

Misidentifications: Banks, 1902: 176 (*Sennertia lucrosa* sp. n.)

50. **Sennertia ceratinarum** Fain, 1974
Orig: *Sennertia ceratinarum* Fain, 1974a: 216 (holotype and paratype HDNs in MRAC)
Host: *Ceratina* (*Pithitis*) *turneri*
Distr: South Africa: KwaZulu-Natal (Salt Rock)
Note: short description of HDN

Syn: *Sennertia ceratinarum*: Fain, 1980: 983, Figs 1–2
Host: "*Ceratina* nr. *turneri*" (type host) (South Africa, HDNs attached behind wings), *Ceratina acutipyga* (South Africa), *Ceratina atopura* (Congo), *Ceratina* (*Pithitis*) *nilotica* (Congo), *Ceratina* (*Pithitis*) *viridis* (as *Ceratina congoensis* and *Pithitis viridis*) (Cameroon, Congo)

Distr: South Africa: KwaZulu-Natal (Salt Rock) (type locality); Democratic Republic of the Congo; Cameroon
Note: redescription of HDN, unjustified paratype designation (from all hosts not included in original description)

Syn: *Sennertia* (*Sennertia*) *ceratinarum*: Fain, 1981a: 156, Fig. 76
Host: *Ceratina* sp. (type host), *Ceratina acutipyga* (South Africa), *Ceratina atopura*, *Ceratina nilotica* (as *Ceratina nilicota*), *Ceratina* (*Pithitis*) *viridis* (as *Ceratina congoensis* and *Pithitis viridis*) (Congo, Cameroon)
Distr: South Africa: KwaZulu-Natal (type locality); Democratic Republic of the Congo; Cameroon
Note: included in key, short redescription, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *ceratinarum*: Haitlinger, 2000: 17
Note: mention

51. **Sennertia congoicola** Fain, 1971
Orig: *Sennertia congoicola* Fain, 1971: 265 (holotype and 3 paratype HDNs in MRAC)
Host: "*Mesotrichia striata*" (type host), *Xylocopa* (*Koptortosoma*) *imitator* (as *Mesotrichia imitator*)
Distr: Democratic Republic of the Congo
Note: description of HDN, collected from 1st metasomal segment

Syn: *Sennertia* (*Sennertia*) *congoicola*: Fain, 1981a: 161, Figs. 18, 19, 22, 67
Host: "*Mesotrichia striata*" (type host), *Xylocopa imitator* (as *Mesotrichia imitator*), *Xylocopa* (*Mesotrichia*) *torrida* (as *Mesotrichia torrida*) (Moanda)
Distr: Democratic Republic of the Congo (type locality) including "Moanda"
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *congoicola*: Haitlinger, 1999: 59
Distr: Democratic Republic of the Congo
Note: comparison with *Sennertia herminae*

Syn: *Sennertia* (*Sennertia*) *congoicola*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo

52. **Sennertia dalyi** Fain, 1980
Orig: *Sennertia dalyi* Fain, 1980: 990, Figs 11, 12 (holotype (#152446) and 32 paratype HDNs in MRAC)
Host: *Ceratina* (*Euceratina*) *dallatorreana* (type host), *Ceratina* (*Euceratina*) *chalybea* (Maktar), *Ceratina* (*Euceratina*) *mocsaryi* (Ain Draham), *Ceratina* (*Euceratina*) *callosa* (Grombalia)
Distr: Tunisia: Jundūbah, 3.5 S Tabarka (type locality), 'Ayn ad Darāhim; Silyānah (Maktar); Nābul (Grombalia)
Note: description of HDN, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *dalyi*: Fain, 1981a: 163
Host: *Ceratina dallatorreana* (as *Ceratina dellatorreana*) (type host), *Ceratina chalybea*, *Ceratina mocsaryi*, *Ceratina callosa*
Distr: Tunisia
Note: included in key, subgeneric assignment

Syn: *Sennertia* (*Sennertia*) *dalyi*: Haitlinger, 2000: 17
Distr: Tunisia

53. **Sennertia dalyi nilotica** Fain, 1980
Orig: *Sennertia dalyi nilotica* Fain, 1980: 990 (holotype (#152450) and 26 paratype HDNs in MRAC)
Host: "*Pithitis* sp. n. A", *Ceratina* (*Pithitis*) *tarsata* (as *Pithitis tarsata*), "*Ceratina* sp. n."
Distr: Egypt: Al Qalyūbīyah, Banhā ("Benha, Delta du Nil")
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *dalyi nilotica*: Fain, 1981a: 163
Host: "*Pithitis* n. sp. A.", *Ceratina tarsata* (as *Pithitis tarsata*), "*Ceratina* n. sp."
Distr: Egypt: Al Qalyūbīyah, Banhā ("Benha, Nile Delta")

54. **Sennertia delfinadoae** Fain, 1981
Orig: *Sennertia* (*Asiosennertia*) *delfinadoae* Fain, 1981a: 172, Figs 44–46, 63 (holotype HDN in IRSNB)
Host: "rat"
Distr: India
Note: description of HDN, included in key, host acknowledged as accidental

Orig: *Sennertia bakeri* Ramaraju & Mohanasundaram, 2001: 109, Figs 4–6 (holotype (78/2b) and 3 paratype HDNs in TNAU), **syn. n.**
Host: *Xylocopa* (*Nodula*) *amethystina*
Distr: India: Tamil Nādu (Coimbatore)
Note: description of HDN

55. **Sennertia devincta** Klimov & OConnor, 2007 (p. 148)
Orig: *Sennertia devincta* Klimov & OConnor in Klimov *et al.*, 2007b: 121, Figs 1*B*, 7, 8 (holotype in CAS, 2 paratypes in CAS and UMMZ)
Host: *Ceratina* sp.
Distr: Peru: Huanuco
Note: description of HDN from acarinarium on 1st metasomal tergite

56. **Sennertia dissimilis** Zachvatkin, 1941
Orig: *Sennertia dissimilis* Zachvatkin, 1941: 385, Figs 658–660, 665 (holotype not designated, syntypes not found in ZIN)
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa dissimilis*)
Distr: Japan
Note: description of HDN, included in key, found with *S. horrida* and *S. oudemansi*

Syn: *Sennertia dissimilis* Fain, 1981a: 182
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa dissimilis*)
Distr: Japan
Note: redescription of HDN, stated that holotype in ZIN

57. **Sennertia donaldi** Turk, 1948 (p. 148)
Orig: *Sennertia donaldi* Turk, 1948: 84, Figs 1–4 (4 syntype HDNs in BMNH (A. Baker (BMNH), pers. comm.))
Host: *Xylocopa* (*Neoxylocopa*) *frontalis*
Distr: Trinidad and Tobago: Saint George (Piarco)
Note: description of HDN

Syn: *Sennertia* (*Spinosennertia*) *argentina*: Fain, 1981a: 176 (part.)

Syn: *Sennertia* (*Spinosennertia*) *argentina*: Alzuet & Abrahamovich, 1987: 350 (part.)

Syn: *Sennertia* (*Spinosennertia*) *argentina*: Haitlinger, 1999: 59 (part.)

Syn: *Sennertia* (*Spinosennertia*) *donaldi*: Klimov *et al*., 2007b: 130
Host: *Xylocopa* (*Neoxylocopa*) *frontalis* (type host), *Xylocopa* (*Neoxylocopa*) *fimbriata*.
Distr: Trinidad and Tobago (type locality); Brazil; Venezuela
Note: included in key, removed from synonymy of *Sennertia argentina*

58. **Sennertia duweinii** Sherbef & Duweini, 1980
Orig: *Sennertia duweinii* Sherbef & Duweini, 1980: 245 (holotype and 10 paratypes, repository not indicated)
Host: *Xylocopa* (*Koptortosoma*) *aestuans*
Distr: not indicated, ?Egypt
Note: description of HDN, found inside acarinarium

59. **Sennertia egyptiaca** Elbadry, 1971: 87
Orig: *Sennertia egyptiaca* Elbadry, 1971: 87, Figs 1–2 (holotype and some paratype HDNs in ESEC; remaining paratype HDNs in ASUA).
Host: *Xylocopa* (*Koptortosoma*) *aestuans*
Distr: Egypt: Al Qāhirah, Shubrā al Khaymah ("Shoubra Elkheima, Cairo") (type locality); Sudan
Note: description of HDNs from "abdominal acarinarium" of host

Syn: *Sennertia egyptiaca*: Sherbef & Duweini, 1980: 246
Note: comparison with *Sennertia duweinii*

Syn: *Sennertia egyptiaca* Fain, 1981a: 182
Host: *Xylocopa* (*Koptortosoma*) *aestuans*
Distr: Egypt
Note: considered as inadequately described, closely related to *S. cerambycina*

60. **Sennertia elseni** Fain, 1971
Orig: *Sennertia elseni* Fain, 1971: 266 (holotype and 8 paratype HDNs in MRAC)
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Mesotrichia olivacea*)
Distr: Democratic Republic of the Congo: Bas-Congo (Muanda) ("Moanda")
Note: description of HDN, collected from 1st metasomal segment

Syn: *Sennertia* (*Sennertia*) *elseni*: Fain, 1981a: 161, Figs 20, 21, 23, 71
Host: *Xylocopa caffra* (as *Mesotrichia olivacea*)
Distr: Democratic Republic of the Congo: Bas-Congo, Muanda ("Moanda")
Note: included in key, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *elseni*: OConnor, 1993a: 362
Note: generic character acquisition

Syn: *Sennertia* (*Sennertia*) *elseni*: Haitlinger, 1999: 59
Distr: Democratic Republic of the Congo

Syn: *Sennertia* (*Sennertia*) *elseni*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo

Syn: *Sennertia* (*Sennertia*) *elseni*: Fain & Pauly, 2001: 132
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Xylocopa olivacea*) (Congo), *Xylocopa* (*Koptortosoma*) *calens* (Madagascar, except Ranomafana), *Melanempis* sp. (Madagascar, Ranomafana) (cleptoparasitic bee of the family Nomadinae)
Distr: Democratic Republic of the Congo: Bas-Congo, Muanda ("Moanda"); Madagascar: Toamasina, Toliara, "Ranomafana"

61. **Sennertia faini** Baker & Delfinado-Baker, 1983 (p. 170)

62. **Sennertia flabellifera** Oudemans, 1924
Orig: *Sennertia flabellifera* Oudemans, 1924: 331 (holotype originally not designated, syntypes in RMNH (Buitendijk, 1945))
Host: *Xylocopa* (*Koptortosoma*) sp. (as *Koptorthosoma* sp.)
Distr: Indonesia: Java (Bogor) (as "Buitenzorg")
Note: description of larva and protonymph

Syn: *Sennertia flabellifera*: Lombert *et al*., 1987: 113
Host: Xylocopa sp. nest
Distr: Indonesia: Java

63. **Sennertia frontalis** Vitzthum, 1941 (see p. 179)

64. **Sennertia gargantua** Zachvatkin, 1941
Orig: *Sennertia gargantua* Zachvatkin, 1941: 385, Figs 656, 657 (holotype originally not designated; syntypes not found in ZIN)
Host: *Xylocopa* (*Nodula*) *punctilabris*, *Xylocopa* (*Xylocopa*) *valga* (as "*X. valga* F.")
Distr: Uzbekistan, Tajikistan
Note: description of HDN, included in key

Syn: *Sennertia* (*Sennertia*) *gargantua*: Fain, 1981a: 155
Host: *Xylocopa punctilabris*, *Xylocopa valga*
Distr: Turkey (probably error)
Note: redescription of HDN, included in key, stated that type in ZIN, subgeneric assignment, assigned to *cerambycina*-group

65. **Sennertia greeni** (Oudemans, 1917)
Orig: *Hericia greeni* Oudemans, 1917: 345 (holotype not designated, syntypes in RMNH (Buitendijk, 1945))

Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Sri Lanka: Central (Eton estate) ("Eton Estate, Punduloga, Ceylon")
Note: short description of feeding instars, including male and female; no HDNs found

Syn: "tiny mite" Green, 1902: 233
Host: *Xylocopa tenuiscapa* [nest]
Distr. Sri Lanka ("Ceylon")
Note: originally proposed to be possibly a developmental stage of *Dinogamasus* (=*Greenia*) (Laelapidae)

Syn: *Sennertia greeni*: Oudemans, 1924: 330
Note: assignment to *Sennertia*

Syn: *Sennertia greeni*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Platynopoda tenuiscapa*)
Note: mention

Syn: *Sennertia greeni*: Lombert *et al*., 1987: 113
Host: *Xylocopa tenuiscapa*
Distr: Sri Lanka

66. **Sennertia haustrifera** sp. n. (p. 151)

67. **Sennertia herminae** Haitlinger, 1999
Orig: *Sennertia (Sennertia) herminae* Haitlinger, 1999: 57, Figs 1–6 (holotype HDN in UWCP at least one of 2 paratype HDNs in HNHM)
Host: *Xylocopa* sp.
Distr: Madagascar: Antananarivo (Antananarivo)
Note: description of HDN

Syn: *Sennertia (Sennertia) herminae*: Haitlinger, 2000: 17
Distr: Madagascar

68. **Sennertia hipposideros** (Oudemans, 1902)
Orig: *Trichotarsus hipposideros* Oudemans, 1902: 44 (holotype HDN in RMNH)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma temciscapa* Westw.)
Distr: India
Note: description of HDN

Syn: *Sennertia hipposideros*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Platynopoda tenuiscapa*)
Note: mention

Syn: *Trichotarsus hipposiderus* Oudemans, 1903a: 145, Figs 46–47 (unjust. emend.)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa* Westw.)
Distr: India
Note: redescription of HDN, from "first abdominal ring", marked as "nov. sp.", included in key

Syn: *Trichotarsus hipposiderus*: Trägårdh, 1904: 156
Note: comparison with *Sennertia simplex*

Syn: *Sennertia hipposiderus* Oudemans, 1905a: 22
Note: assignment to *Sennertia*

Syn: *Trichotarsus hipposiderus*: Trägårdh, 1907: 12
Note: comparison with *Trichotarsus antarcticus*

Syn: *Trichotarsus hipposiderus*: Vitzthum, 1912d: 290
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: India

Syn: *Sennertia hipposidera* Vitzthum, 1919: 43 (unjust. emend.)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: India
Note: year of species description indicated as 1901; comparison with *Sennertia morstatti*

Syn: *Sennertia hipposideruns* Vitzthum, 1941: 310 (lapsus)
Note: comparison with *Sennertia argentina*; year of species description indicated as 1903

Syn: *Sennertia hipposiderus*: Fain, 1974b: 226, Figs 7–8
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: India
Note: redescription of holotype HDN

Syn: *Sennertia* (*Sennertia*) *hipposiderus* Fain, 1981a: 156
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (India), *Xylocopa* (*Mesotrichia*) *latipes* (Malaysia)
Distr: India, Malaysia
Note: included in key, subgeneric assignment, assigned to group *cerambycina*

Syn: *Sennertia hipposiderus*: OConnor, 1993b: 161
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (India), *Xylocopa* (*Mesotrichia*) *latipes* (Malaysia)
Distr: India, Malaysia
Note: found in metasomal acarinarium, nidicolous feeding instars either of this species or *Sennertia koptorthosomae*

Syn: *Sennertia hipposiderus*: Krantz, 1998: 298
Host: *Xylocopa* (*Mesotrichia*) *latipes* (as *Xylocopa* (*Mesotrichia*) *latipes*)
Distr: Malaysia

69. **Sennertia horrida** (Vitzthum, 1912)
Orig: *Trichotarsus horridus* Vitzthum, 1912d: 290, Figs 21, 22 (lectotype (A20031430) and 2 paralectotype HDNs (A20031428-29) labeled as *Sennertia horrida* in ZSMC (Jürgen *et al*., 2005); designated by Fain, 1981a)
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa* (*Koptorthosoma?*) *dissimilis*)
Distr: Indonesia: Jakarta ("Batavia")
Note: description of HDN

Syn: *Sennertia horrida*: Vitzthum, 1919: 57, Figs 51–52
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa* (*Koptorthosoma?*) *dissimilis*)

Distr: Indonesia: Jakarta (as "Java, Batavia")
Note: redescription of HDN, emendation of host name

Orig: *Sennertia sumatrensis* Oudemans, 1924: 329 (lectotype and 15 paralectotype HDNs on slide No. 3055 (designated by Fain, 1974b) in RMNH) (synonymized by Fain, 1981a)
Host: *Xylocopa* sp.
Distr: Indonesia: Sumatra ("Medan, Deli")
Note: description of HDN

Syn: *Sennertia cerambycina*: Vitzthum, 1929: 92, Fig. 120

Syn: *Sennertia horrida*: Vitzthum, 1941: 308
Note: comparison with *Sennertia frontalis*

Syn: *Sennertia horrida*: Zachvatkin, 1941: 387, Figs 62–64
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa dissimilis*)
Distr: Japan, India: Assam
Note: redescription of HDN, included in key

Syn: *Sennertia horrida*: Turk, 1948: 85
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa dissimilis*)
Note: comparison with *Sennertia donaldi*

Syn: *Sennertia sumatrensis*: Fain, 1974b: 228, Figs 9–10, 13–14
Host: *Xylocopa* sp.
Distr: Indonesia: Sumatra ("Medan, Deli")
Note: redescription of HDN, lectotype designation

Syn: *Sennertia* (*Sennertia*) *horrida*: Fain, 1981a: 170
Host: *Xylocopa* sp.
Distr: Indonesia: Jakarta ("Batavia"), Sumatra ("Medan, Deli")
Note: included in key, subgeneric assignment, assigned to *horrida* group, considered as senior synonym of *Sennertia sumatrensis*, lectotype designation

Syn: *Trichotarsus horrida* Fain, 1981a: 170 (as basionym attributed to Vitzthum, 1912d)

Syn: *Sennertia horrida*: Klimov *et al*., 2007b: 124
Host: *Xylocopa* (*Biluna*): *X. nasalis*, *X. auripennis*, *X. fallax*, *X. iridipennis*, *X. mcgregori*, *X. mimetica*
Distr: Indonesia: Java (type locality), Sumatra; India
Note: included in key, synonymized with *Sennertia leucothorae* Ramaraju & Mohanasundaram, 2001

Orig: *Sennertia leucothorae* Ramaraju & Mohanasundaram, 2001: 107, Figs 1–3 (holotype (78/2a) and 24 paratype HDNs in TNAU. Paratypes in the BMNH and USNM) synonymized by Klimov *et al*., 2007b
Host: *Xylocopa* (*Koptortosoma*) *aestuans* (as *Xylocopa leucothorae*)
Distr: India: Tamil Nādu (Coimbatore)

70. **Sennertia hurdi** sp. n. (p. 164)

71. **Sennertia ignota** Delfinado & Baker, 1976
Orig: *Sennertia ignota* Delfinado & Baker, 1976: 85, Figs 33, 34 (holotype and 11 paratype HDNs in USNM; original repositories NYSM (holotype, paratypes), NYSM and USNM (paratypes))
Host: *Xylocopa* sp.
Distr: Peru: Piura, Talara
Note: description of HDN, 10 paratype HDNs mentioned originally

Syn: *Sennertia* (*Amsennertia*) *ignota*: Fain, 1981a: 178
Host: *Xylocopa* sp.
Distr: Peru: Piura, Talara
Note: included in key, subgeneric assignment

Syn: *Sennertia ignota*: Baker & Delfinado-Baker, 1983: 119
Host: *Xylocopa* sp.
Distr: Peru: Piura (Talara)
Note: comparison with *Sennertia faini*

Syn: *Sennertia* (*Amsennertia*) *ignota*: Alzuet & Abrahamovich, 1987: 346
Host: *Xylocopa* sp.
Distr: Peru: Piura (Talara)
Note: comparison with *Sennertia longipilis*

Syn: *Senertia ignota* [sic!]: Ramaraju & Mohanasundaram, 2001: 107
Host: *Xylocopa* sp.
Distr: Peru
Note: comparison with *Sennertia leucothorae*, *Sennertia bakeri*, and *Sennertia carpenteri*

72. **Sennertia indica** Delfinado & Baker, 1976
Orig: *Sonnertia indica* [sic!] Delfinado & Baker, 1976: 87, Figs 35, 36 (holotype HDN in USNM (no. 3687), 2 paratype HDNs in NYSM)
Host: *Ceratina binghami* (as *Tithitis binghami*)
Distr: India: Haryāna (Hisār) (as Hissar)
Note: description of HDN

Syn: *Sennertia indica*: Fain, 1981a: 182
Host: *Ceratina binghami* (as *Pithitis binghami*)
Distr: India
Note: redescription, assigned to subgenus *Sennertia* and *cerambycina* group

Syn: *Seneria* [sic!] *indica*: Ramaraju & Mohanasundaram, 2001: 107
Host: *Ceratina binghami* (as *Pithitis binghami*)

73. **Sennertia jeanalexi** Fain, 1971
Orig: *Sennertia jeanalexi* Fain, 1971: 269 (holotype and 15 paratypes in MRAC)
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Mesotrichia* (*Koptorthosoma*) *nigrita*) (Bubulu) (type host); *Xylocopa* (*Koptortosoma*) *lepeletieri* (as *Mesotrichia lepeletieri*) (Bambesa)
Distr: Democratic Republic of the Congo: "Bubulu river, near Mvungu, Mayumbe" (type locality), Bambesa
Note: short description of HDN

Syn: *Sennertia jeanalexi*: Fain, 1974a: 216
Note: comparison with *Sennertia basilewskyi*

Syn: *Sennertia* (*Afrosennertia*) *jeanalexi*: Fain, 1981a: 178, Figs 54, 57, 58
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Mesotrichia* (*Koptorthosoma*) *nigrita*); *Xylocopa* (*Koptortosoma*) *lepeletieri* (as *Mesotrichia lepeletieri*)
Distr: Democratic Republic of the Congo
Note: redescription, included in key, subgeneric assignment

Syn: *Sennertia* (*Afrosennertia*) *jeanalexi*: Fain, 1982: 67
Note: comparison with *Sennertia queenslandica*

Syn: *Sennertia (Afrosennertia) jeanalexi*: OConnor, 1993a: 362
Note: genus-level character acquisition

74. **Sennertia koptorthosomae** (Oudemans, 1901)
Orig: *Trichotarsus koptorthosomae* Oudemans, 1901: 82, Fig. 3.*53–54* (part.) (lectotype and paralectotype HDN in RMNH, designated by Fain, 1974b)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (original host subgenus *Koptorthosoma*)
Distr: India, Indonesia: Java
Note: description of HDN from "acarid chamber", included in key

Syn: *Trichotarsus koptorthosomae*: Oudemans, 1903a: 147
Note: included in key, assigned to group D in *Trichotarsus*

Syn: *Trichotarsus coptorthosomae* Trägårdh, 1904: 156 (unjust. emend.)
Note: comparison with *Sennertia simplex*

Syn: *Sennertia coptorthosomae*: Oudemans, 1905a: 22 (unjust. emend.)
Note: assignment to *Sennertia*

Syn: *Trichotarsus koptorthosomae*: Vitzthum, 1912d: 290 (part.)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: India, Indonesia: Java

Syn: *Sennertia koptorthosomae*: Vitzthum, 1919: 3
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: India, Indonesia: Java

Syn: *Sennertia koptorthosomae*: Oudemans, 1924: 329
Host: *Xylocopa* (*Koptortosoma*) sp. (as *Koptorthosoma* sp.)
Distr: Indonesia: Java (Bogor) (as "Java, Buitenzorg")

Syn: *Sennertia koptorthosomae*: Vitzthum, 1941: 310
Note: comparison with *Sennertia argentina*

Syn: *Sennertia koptorthosomae*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Platynopoda tenuiscapa*)
Note: mention

Orig: *Sennertia koporthosomae* Buitendijk, 1945: 358 (lapsus)
Distr: Ceylon; Indonesia: Java
Note: mention

Syn: *Sennertia koptorthosomae*: Fain, 1974b: 219, Figs 1–2
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Indonesia: Java, Sumatra ("Medan, Deli")
Note: redescription, lectotype designation"

Syn: *Sennertia* (*Sennertia*) *koptorthosomae*: Fain, 1981a: 156
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Indonesia: Java
Note: included in key, subgeneric assignment, assigned to group *cerambycina*

Syn: *Sennertia koptorthosomae*: OConnor 1993b: 161
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (Indonesia), *Xylocopa* (*Mesotrichia*) *latipes* (Malaysia)
Distr: Indonesia: Java, Sumatra; Malaysia
Note: found in metasomal acarinarium, nidicolous feeding instars either of this species or *Sennertia hipposideros*

Syn: *Sennertia koptorthosomae*: Krantz, 1998: 298
Host: *Xylocopa* (*Mesotrichia*) *latipes*
Distr: Malaysia

75. **Sennertia latipilis** Fain, 1974
Orig: *Sennertia latipilis* Fain, 1974a: 217 (holotype (#152458) and 47 paratype HDNs in MRAC)
Host: "Apidae (n° 139A)" (type host), *Ceratina* (*Ctenoceratina*) *penicilligera*
Distr: Kenya: "Malindi"
Note: short description of HDN

Syn: *Sennertia latipilis*: Fain, 1980: 986, Figs 5–6
Host: Apidae (type host), *Ceratina penicilligera*
Distr: Kenya: "Malindi"
Note: redescription of HDN, number of paratypes from type host indicated as 6

Syn: *Sennertia* (*Sennertia*) *latipilis*: Fain, 1981a: 156, Fig. 70
Apidae (type host), *Ceratina penicilligera*
Distr: Kenya: "Malindi"
Note: included in key, short redescription, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *latipilis*: Haitlinger, 2000: 17
Distr: Kenya

76. **Sennertia lauta** Klimov & OConnor, 2007
Orig: *Sennertia lauta* Klimov & OConnor in Klimov *et al*., 2007b: 125, Figs 2, 11, 12 (holotype in AMNH, 74 paratypes in AMNH, CUIC, HNHM, OSU, UMMZ)
Host: *Xylocopa* (*Zonohirsuta*) *fuliginata* (type host, Philippines), *X*. (*Z*.) *dejeanii* (Malaysia, Philippines), *X*. sp. (Malaysia)
Distr: Philippines: Davao (type locality), Dapitan, Palawan, Zamboanga; Malaysia: Sarawak
Note: description of HDN from groove between scutellum and metanotum (host female) and anterior scutum and adjacent pronotum (host male), included in key

77. **Sennertia leclercqi** Fain, 1971
Orig: *Sennertia leclercqi* Fain, 1971: 268 (holotype and 16 paratype HDNs in MRAC)
Host: *Xylocopa* (*Xenoxylocopa*) *inconstans* (as *Mesotrichia inconstans*)
Distr: Democratic Republic of the Congo: Sud-Kivu, Uvira (type locality) and Lake Albert
Note: short description of HDN

Sennertia (*Sennertia*) *leclercqi*: Fain, 1981a: 157, Figs 6–9
Host: *Xylocopa* (*Xenoxylocopa*) *inconstans* (as *Mesotrichia inconstans*)
Distr: Democratic Republic of the Congo
Note: included in key, redescription of HDN, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *leclercqi*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo

78. **Sennertia leei** Fain, 1982 (p. 150)
Orig: *Sennertia* (*Sennertia*) *leei* Fain, 1982: 67, Figs 3–4 (holotype (N 19811) and 12 paratype (N19812-N198111) HDNs in SAM; 1 paratype HDN in author's collection)
Host: *Xylocopa* (*Lestis*) *bombylans* (as *Lestis bombylans*)
Distr: Australia: New South Wales (Kuring-gai) ("Ku-rin-gai")
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *leei*: OConnor, 1993a: 362
Note: genus-level character acquisition for male, female, and deutonymph

79. **Sennertia longipilis** Alzuet & Abrahamovich, 1987 (p. 148)
Orig: *Sennertia* (*Amsennertia*) *longipilis* Alzuet & Abrahamovich, 1987: 346, Figs 8–9 (holotype and 7 paratype HDNs in MLPA)
Host: *Xylocopa* (*Schonnherria*) *splendidula splendidula*
Distr: Argentina: Misiones Prov.
Note: description of HDN

Syn: *Sennertia longipilis*: Abrahamovich & Alzuet, 1989: 115
Host: Host: *Xylocopa* (*Schonnherria*) *splendidula splendidula*
Distr: Argentina: Misiones Prov.
Note: study of spatial distribution on host; year of species description indicated as 1988

Syn: *Sennertia* (*Amsennertia*) *longipilis*: Alzuet, Abrahamovich, 1989: 236

80. **Sennertia loricata** sp. n. (p. 181)

81. **Sennertia lucrosa** sp. n. (p. 164)

82. **Sennertia madagascarensis** Fain, 1971
Orig: *Sennertia madagascarensis* Fain, 1971: 270 (holotype and 17 paratype HDNs in MRAC)
Host: *Xylocopa* (*Prosopoxylocopa*) *mirabilis*
Distr: Madagascar: Antananarivo (Antananarivo) ("Tananarive")
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *madagascarensis*: Fain, 1981a: 170, Figs 35, 39, 40
Host: *Xylocopa* (*Prosopoxylocopa*) *mirabilis*
Distr: Madagascar: Antananarivo (Antananarivo) ("Tananarive")
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *horrida*-group, emendation of number of paratypes (12)

Syn: *Sennertia* (*Sennertia*) *madagascarensis*: OConnor, 1993a: 362
Note: generic character acquisition

Syn: *Sennertia madagascarensis*: Fain & Pauly, 2001: 125
Host: *Xylocopa* (*Prosopoxylocopa*) *mirabilis*
Distr: Madagascar

Syn: *Sennertia madagascarensis*: Klimov *et al*., 2007b
Host: *Xylocopa* (*Prosopoxylocopa*) *mirabilis*, *Xylocopa* (*Koptortosoma*) *calens*
Distr: Madagascar
Note: included in key

83. **Sennertia mesotrichia** Fain, 1971
Orig: *Sennertia mesotrichia* Fain, 1971: 265 (holotype and paratype HDNs in MRAC)
Host: *Xylocopa* (*Koptortosoma*) *africana* (type host) (as *Mesotrichia africana*) (Bambesa, "several other localities"); *Xylocopa* (*Koptortosoma*) *lepeletieri* (as *Mesotrichia lepeletieri*) (Katompi)
Distr: Democratic Republic of the Congo: Bambesa (type locality) and other localities including Katompi
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *mesotrichia*: Fain, 1981a: Figs 2, 3, 5, 66
Host: *Xylocopa* (*Koptortosoma*) *africana* (as *Mesotrichia africana*) (Bambesa, "other localities in Zaïre"); *Xylocopa* (*Koptortosoma*) *lepeletieri* (as *Mesotrichia lepeletieri*) (Katompi); *Xylocopa* (*Xylomelissa*) *tarsata* (Ituri)
Distr: Democratic Republic of the Congo: Bambesa (type locality) and other localities including Katompi and Ituri
Note: redescription of HDN, included in key, subgeneric assignment, assigned to group *cerambycina*

Syn: *Sennertia* (*Sennertia*) *mesotrichia*: Haitlinger, 2000: 17
Note: mention

84. **Sennertia micheli** Fain, 1971
Orig: *Sennertia micheli* Fain, 1971: 268 (holotype HDN in IRSNB)
Host: *Bembix borrei* Handlirsch, 1893 (Hymenoptera: Sphecidae)
Distr: Indonesia: Java
Note: short description of HDN

Syn: *Sennertia* (*Sennertia*) *micheli*: Fain, 1981a: 164, Figs. 24, 26–28
Host: *Bembix borrei*

Distr: Indonesia: Java
Note: redescription of holotype HDN, subgeneric assignment, assigned to *japonica*-group

85. **Sennertia monicae** Fain, 1971
Orig: *Sennertia monicae* Fain, 1971: 269 (holotype and 18 paratype HDNs in MRAC)
Host: *Xylocopa* (*Xenoxylocopa*) *inconstans* (as *Mesotrichia inconstans*)
Distr: Democratic Republic of the Congo: Sud-Kivu (Uvira) (type locality)
Note: short description of HDN

Syn: *Sennertia monicae*: Fain, 1974a: 215
Note: comparison with *Sennertia basilewskyi*

Syn: *Sennertia* (*Afrosennertia*) *monicae*: Fain, 1981a: 178, Figs 53, 55, 56
Host: *Xylocopa* (*Xenoxylocopa*) *inconstans* (as *Mesotrichia inconstans*)
Distr: Democratic Republic of the Congo
Note: redescription, included in key, subgeneric assignment, emendation of number of paratypes (12)

Syn: *Sennertia* (*Afrosennertia*) *monicae*: Fain, 1982: 67
Note: comparison with *Sennertia queenslandica*

86. **Sennertia morstatti** Vitzthum 1914
Orig: *Sennertia morstatti* Vitzthum, 1914: 323, Figs. 16–17 (syntypes: male, 2HDN slides ZSMC A20031431-3 (Jürgen *et al*., 2005))
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)
Distr: Tanzania: Amani (“Amani, Deutsch-Ostafrica”)
Note: description of HDN (male not mentioned)

Syn: *Sennertia morstatti*: Vitzthum, 1919: 42, Figs 35–41
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)
Distr: Tanzania: Amani (as “Amani, Ostafrica”)
Note: redescription of HDN, description of male and female

Syn: *Sennertia morstatti*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)

Syn: *Sennertia morstatti*: Skaife, 1952: 76
Distr: Tanzania (“Tanganyika”)
Note: mention

Orig: *Sennertia moandensis* Fain, 1971: 267 (holotype and 1 paratype HDN in MRAC) (synonymized by Fain, 1981a)
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Mesotrichia nigrita*)
Distr: Democratic Republic of the Congo, Moanda (as “Moanda, Congo ex belge”)

Syn: *Sennertia tanythrix* Fain, 1971: 267 (part., specimens from *X. nigrita*)
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Mesotrichia nigrita*)
Distr: Democratic Republic of the Congo: Haut-Congo Prov. “Uélé”

Sennertia (*Sennertia*) *morstatti*: Fain, 1981a: 164, Figs 25, 29, 20
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*) (Congo), *Xylocopa* (*Koptortosoma*) sp. (as *Xylocopa* (*Koptorthosoma*) sp.) (Sudan), Megachilidae (Congo)
Distr: Tanzania: Amani (as “Amani, E. Africa”), Democratic Republic of the Congo, Sudan
Note: included in key, redescription, assigned to *japonica* group, considered as senior synonym of *Sennertia moandensis* Fain, 1971

Sennertia (*Sennertia*) *morstatti*: Lombert *et al*., 1987: 113
Host: *Xylocopa* (*Koptortosoma*) *nigrita*
Note: mention

Syn: *Sennertia* (*Sennertia*) *morstatti*: Sherbef & Duweini, 1980: 245
Distr: Tanzania (“Tanganyika”)

87. **Sennertia oudemansi** Zachvatkin, 1941
Orig: *Sennertia oudemansi* Zachvatkin, 1941: 390, Figs 675–677 (holotype originally not designated, not found in ZIN)
Host: *Xylocopa* (*Biluna*) *nasalis* (as *Xylocopa dissimilis*)
Distr: Japan (no specific location)
Note: description of HDN, included in key, occurrence with *Sennertia horrida* and *S. dissimilis*

Syn: *Sennertia oudemansi*: Turk, 1948: 84
Note: comparison with *Sennertia donaldi*

Syn: *Sennertia* (*Asiosennertia*) *oudemansi*: Fain, 1981a: 176
Note: short redescription, included in key, subgeneric assignment

88. **Sennertia perturbans** Vitzthum, 1919
Orig: *Sennertia perturbans* Vitzthum, 1919: 48, Figs 42–46 (syntypes in ZSMC: female and male (A20031434), female (A20031436), and TN (A20031435)) (Jürgen *et al*., 2005)
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)
Distr: Tanzania: Amani (“Amani, Ostafrica”)
Note: description of TN, male, and female

Syn: *Sennertia perturbans*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)

Syn: *Sennertia perturbans*: Fain, 1981a: 145
Note: mention

Syn: *Sennertia perturbans*: Lombert *et al*., 1987: 113
Host: *Xylocopa* (*Koptortosoma*) *nigrita*

89. **Sennertia pirata** sp. n. (p. 144)

90. **Sennertia potanini** Zachvatkin, 1941
Orig: *Sennertia potanini* Zachvatkin, 1941: 390, Figs 669–671 (Lectotype and 6 paralectotype HDNs in ZIN, designated here)

Host: *Xylocopa* (*Biluna*) *tranquebarorum* or *Xylocopa* (*Bomboixylocopa*) *rufipes* (as *Xylocopa pictifrons*)
Distr: China: Sichuan (Yazhou)
Note: description of HDN, included in key

Syn: *Sennertia* (*Sennertia*) *potanini*: Fain, 1981a: 170
Host: *Xylocopa (Biluna) tranquebarorum* or *Xylocopa (Bomboixylocopa) rufipes* (as *Xylocopa pictifrons*)
Distr: Western China
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *horrida*-group

Syn: *Sennertia* (*Sennertia*) *potanini*: Klimov *et al*., 2007b: 125
Host: *Xylocopa* (*Biluna*) *tranquebarorum* or *Xylocopa* (*Bomboixylocopa*) *rufipes* (as *Xylocopa pictifrons*)
Distr: China
Note: included in key

91. **Sennertia queenslandica** Womersley, 1941
Orig: *Sennertia queenslandica* Womersley, 1941: 479, Fig. 16 (lectotype (N 198112) and 12 paralectotype (N198113-N198124) HDNs in SAM, designated by Fain, 1982)
Host: *Xylocopa* (*Koptortosoma*) *bryorum* (as *Mesotricha bryorum*)
Distr: Australia: Queensland (Moa Island) ("Moa Id., Torres Straits")

Syn: *Sennertia (Asiosennertia) queenslandica*: Fain, 1981a: 176
Host: *Xylocopa* (*Koptortosoma*) *bryorum* (as *Mesotrichia bryorum*)
Distr: Australia: Queensland
Note: provisional assignment to subgenus *Asiosennertia*

Syn: *Sennertia* (*Afrosennertia*) *queenslandica*: Fain, 1982: 68, Figs 1–2
Host: *Xylocopa* (*Koptortosoma*) *bryorum* (as *Mesotrichia bryorum*)
Distr: Australia: Queensland
Note: redescription, lectotype designation, assignment to subgenus *Afrosennertia*

92. **Sennertia ratiocinator** Klimov & OConnor, 2007
Orig: *Sennertia ratiocinator* Klimov & OConnor in Klimov *et al*., 2007b: 128 (holotype in AMNH, 31 paratype HDNs in AMNH, HNHM, OSU, UMMZ)
Host: *Xylocopa* (*Zonohirsuta*) *bhowara* (type host), *X*. (*Zonohirsuta*) *dejeanii*, *Xylocopa* (*Nodula*) *amethystina*
Distr: Sri Lanka: North Western (type locality), Southern, North Eastern
Note: description of HDN from groove between scutellum and metanotum (host female) and anterior scutum and adjacent pronotum (host male), included in key

93. **Sennertia recondita** sp. n. (p. 151)

94. **Sennertia robusta** Delfinado & Baker, 1976
Orig: *Sennertia robusta* Delfinado & Baker, 1976: 87, Figs 37–38 (holotype (no. 3688) and 2 paratype HDNs in USNM)
Host: "megachilid bee (PL-480; India: Hissar; probably in BLCU) (type host), *Xylocopa* sp. ("India", probably in USNM)
Distr: India, Haryāna (Hisār) ("Hissar") (type locality)
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *robusta*: Fain, 1981a: 157
Host: *Xylocopa* sp.
Distr: India
Note: included in key, subgeneric assignment, assigned to group *cerambycina*

Syn: *Sennertia* (*Sennertia*) *robusta*: Haitlinger, 2000: 18
Distr: India

Syn: *Senertia* [sic!] *robusta*: Ramaraju & Mohanasundaram, 2001: 107
Host: "megachilid bee and *Xylocopa* sp."
Note: mention

Orig: *Sennertia carpenteri* Ramaraju & Mohanasundaram, 2001: 109, Figs 7–9 (holotype (No. 55/1) and 3 paratype HDNs in TNAU), **syn. n.**
Host: *Xylocopa* (*Nodula*) *amethystina*
Distr: India: Tamil Nādu, Coimbatore
Note: description of HDN

95. **Sennertia roepkei** Oudemans, 1924
Orig: *Sennertia roepkei* Oudemans, 1924: 330 (holotype not designated, syntypes in RMNH (Buitendijk, 1945))
Host: On eggs of *Horia* (as "*Cissites* (= *Horia*)") (Coleoptera: Meloidae) in nest of *Xylocopa* sp.
Distr: Indonesia: Java (Bogor) (as "Buitenzorg")
Note: description of larva, protonymph, female, and male

Syn: *Sennertia roepkei*: Lombert *et al*., 1987: 113
Host: *Xylocopa* sp. nest
Distr: Indonesia: Java

96. **Sennertia sayutara** Klimov & OConnor, 2007 (p. 161)

97. **Sennertia scutata** Fain, 1974
Orig: *Sennertia scutata* Fain, 1974a: 217 (holotype and 28 paratype HDNs in MRAC)
Host: *Ceratina truncata* ("Cape"), *Ceratina* (*Pithitis*) *nasalis* (as *Ceratina viridior*) (Cape Town)
Distr: South Africa: former Cape Prov. (type locality) and Western Cape: Cape Town
Note: short description of HDN

Syn: *Sennertia scutata*: Fain, 1980: 986, Figs 7–8
Host: *Ceratina truncata*
Distr: South Africa: former Cape Prov.
Note: redescription of HDN , mention that paratype specimens from *Ceratina nasalis* (as *C. viridior*) have shorter setae c_3 and may represent a new taxon

Syn: *Sennertia* (*Sennertia*) *scutata*: Fain, 1981a: 159, Fig. 68
Host: *Ceratina truncata*
Distr: South Africa
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *scutata*: Haitlinger, 2000: 17
Distr: South Africa

98. **Sennertia segnis** sp. n. (p. 170)

99. **Sennertia shimanukii** Baker & Delfinado-Baker, 1983 (see p. 176)

100. **Sennertia simplex** (Trägårdh, 1904)
Orig: *Trichotarsus simplex* Trägårdh, 1904: 156, Figs 17–18 (holotype HDN in NHRS (Fain, 1981a))
Host: *Xylocopa* (*Koptortosoma*) *nigrita*
Distr: Cameroon
Note: description of HDN

Syn: *Sennertia simplex*: Vitzthum, 1919: 32
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)
Distr: Cameroon
Note: comparison with *Sennertia morstatti*

Syn: *Sennertia simplex*: Vitzthum, 1941: 308
Note: comparison with *Sennertia frontalis* and *Sennertia argentina*

Syn: *Sennertia simplex*: Zachvatkin, 1941: 42
Host: *Xylocopa* (*Koptortosoma*) *nigrita* (as *Koptorthosoma nigrita*)

Syn: *Sennertia* (*Sennertia*) *simplex*: Fain, 1981a: 159, Figs 12–14, 74
Host: *Xylocopa* (*Koptortosoma*) *nigrita*
Distr: Cameroon
Note: redescription of HDN, included in key, subgeneric assignment, assigned to group *cerambycina*

Syn: *Sennertia* (*Sennertia*) *simplex*: Haitlinger, 2000: 17
Distr: Cameroon

101. **Sennertia sodalis** sp. n. (p. 156)

102. **Sennertia spinifera** Fain, 1974
Orig: *Sennertia ceratinarum spinifera* Fain, 1974a: 217 (holotype and 75 paratype HDNs in MRAC)
Host: *Ceratina* (*Propithitis*) *aereola*
Distr: Democratic Republic of the Congo ("N.E. Lusambo, Zaïre")
Note: short description of HDN

Syn: *Sennertia spinifera*: Fain, 1980: 984, Figs 1–2, Fig. 3–4
Host: *Ceratina aereola*
Distr: Democratic Republic of the Congo ("N.E. Lusambo, Zaïre")
Note: redescription of HDN

Syn: *Sennertia* (*Sennertia*) *spinifera*: Fain, 1981a: 156, Fig. 75
Host: *Ceratina aereola*
Distr: Democratic Republic of the Congo ("N.E. Lusambo, Zaïre")
Note: included in key, short redescription, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *spinifera*: Haitlinger, 2000: 17
Note: mention

103. **Sennertia splendidulae** Alzuet & Abrahamovich, 1989 (p. 148)
Orig: *Sennertia* (*Amsennertia*) *brevipilis* Alzuet & Abrahamovich 1987, Figs 1–7 (holotype and 15 paratype HDNs in MLPA; preocc. *Sennertia vanderhammeni brevipilis* Fain, 1974)
Host: *Xylocopa* (*Schonnherria*) *splendidula splendidula*
Distr: Argentina: Buenos Aires Prov. (La Plata)
Note: description of HDN

Syn: *Sennertia splendidulae*: Abrahamovich & Alzuet, 1989: 115
Host: *Xylocopa splendidula splendidula*
Distr: Argentina: Buenos Aires, Catamarca, Corrientes, Entre Ríos, Jujuy, La Pampa, Mendoza, Misiones, Río Negro, San Luis
Note: year of species description indicated as 1989, *Sennertia brevipilis* also used inconsistently as valid name

Orig: *Sennertia* (*Amsennertia*) *splendidulae* Alzuet & Abrahamovich, 1989: 236 (nom. n. pro *Sennertia* (*Amsennertia*) *brevipilis* Alzuet, Abrahamovich, "1988")

Syn: *Sennertia* (*Amsennertia*) *splendidulae*: Abrahamovich & Alzuet, 1990: 319
Host: *Xylocopa splendidula splendidula*
Distr: Argentina: Buenos Aires Prov.
Note: observations on interaction of mites and bees in nest; year of species description indicated as 1988

Syn: *Sennertia* (*Amsennertia*) *splendidulae*: Alzuet & Abrahamovich, 1991: 1, Figs 1–24
Host: *Xylocopa splendidula splendidula*
Distr: Argentina: Buenos Aires Prov.
Note: description of egg, larva, protonymph, tritonymph, male and female, SEM pictures. Host nest from *Eucalyptus*. Year of species description inconsistently indicated as 1988 and 1989.

Syn: *Sennertia splendidulae*: Abrahamovich & Alzuet, 1990: 630
Host: *Xylocopa splendidula splendidula*
Note: comparison with *Sennertia augustii*; year of species description indicated as 1988

Syn: *Sennertia* (*Amsennertia*) *splendidulae*: OConnor, 1993a: 362

Syn: *Sennertia splendidulae*: OConnor, 1993b: 164

104. **Sennertia surinamensis** Fain & Lukoschus, 1971 (p. 148)
Orig: *Sennertia surinamensis* Fain & Lukoschus in Fain, 1971: 270 (holotype and 5 paratypes in RMNH)
Host: *Ceratina* (*Calloceratina*) *chloris*
Distr: Suriname: Paramaribo (Paramaribo)
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *surinamensis*: Fain, 1981a: 170, Figs 38, 41–43
Host: *Ceratina* (*Calloceratina*) *chloris*
Distr: Suriname
Note: redescription of HDN, subgeneric assignment, assigned to *horrida*-group, emendation of repository of holotype (IRSNB))

Syn: *Sennertia* (*Sennertia*) *surinamensis*: Alzuet & Abrahamovich, 1987: 348
Host: *Ceratina* (*Calloceratina*) *chloris*
Distr: Suriname

Syn: *Sennertia surinamensis*: Klimov *et al*., 2007a: 1371
Host: *Ceratina* (*Calloceratina*) *chloris* (also as *Ceratina laeta*)
Distr: Suriname; French Guiana, Panama
Note: HDN included in morphological phylogenetic analysis

105. **Sennertia tanythrix** Fain, 1971
Orig: *Sennertia tanythrix* Fain, 1971: 267 (holotype and 15 paratype HDNs in MRAC) (part., excluding specimens from *X. nigrita*)
Host: *Xylocopa* (*Mesotrichia*) *torrida* (as *Mesotrichia torrida*) (type host); *Xylocopa* (*Koptortosoma*) *imitator* (as *Mesotrichia imitator*); *Xylocopa* (*Koptortosoma*) *nigrita* (as "*Mesotrichia nigrita*)"
Distr: Democratic Republic of the Congo: Haut-Congo Prov. "Uélé" (type locality)
Note: description of HDN, in several specimens of *Xylocopa torrida* collected from 1st metasomal segment

Syn: *Sennertia* (*Sennertia*) *tanythrix*: Fain, 1981a: 167, Figs 33, 34, 36
Host: *Xylocopa* (*Mesotrichia*) *torrida* (as *Mesotrichia torrida*) (type host); *Xylocopa* (*Koptortosoma*) *imitator* (as *Mesotrichia imitator*)
Distr: Democratic Republic of the Congo: Haut-Congo Prov. "Uélé" (type locality)
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *japonica* group, paratype specimens from *X. nigrita* identified as *Sennertia morstatti*

Syn: *Sennertia* (*Sennertia*) *tanythrix*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo

106. **Sennertia tunisiana** Fain, 1980
Orig: *Sennertia tunisiana* Fain, 1980: 991 (holotype and 36 paratype HDNs in MRAC)
Host: *Ceratina* (*Ceratina*) *cucurbitina* (Maktar, Grombalia, "Ain Sebaa") (type host), *Ceratina* (*Euceratina*) *albosticta* ("Ain Sebaa"), *Ceratina* (*Euceratina*) *mocsaryi* ('Ayn ad Darāhim), *Ceratina dallatorreana* (Tabarka), *Ceratina chalybea* ("Maletar")
Distr: Tunisia: Silyānah (Maktar) (type locality), Nābul (Grombalia), Jundūbah ('Ayn ad Darāhim, Tabarka), "Maletar", "Ain Sebaa" (probably in Morocco)
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *tunisiana*: Fain, 1981a: 163
Host: *Ceratina cucurbitina*, *Ceratina* (*Euceratina*) *albosticta*, *Ceratina mocsaryi*, *Ceratina dallatorreana* (as *Ceratina dellatorreana*), *Ceratina* (*Euceratina*) *chalybea*
Distr: Tunisia
Note: included in key, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *tunisiana*: Haitlinger, 2000: 17
Distr: Tunisia

107. **Sennertia vaga** sp. n. (p. 150)

108. **Sennertia vanderhammeni brevipilis** Fain, 1974
Orig: *Sennertia vanderhammeni brevipilis* Fain, 1974b: 224 (holotype and several paratype HDNs in RMNH, 2 paratype HDNs in IRSNB)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Indonesia: Java

Syn: *Trichotarsus koptorthosomae* Oudemans, 1901: 82 (part.)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (original host subgenus *Koptorthosoma*)
Distr: India, Indonesia: Java
Note: description of HDN, from "acarid chamber", included in key

Syn: *Sennertia* (*Sennertia*) *vanderhammeni brevipilis*: Fain, 1981a: 156
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Indonesia: Java
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *cerambycina* group

Syn: *Sennertia* (*Sennertia*) *vanderhammeni brevipilis*: Alzuet & Abrahamovich, 1989: 236
Note: mention of homonymy with *Sennertia brevipilis* Alzuet and Abrahamovich

Syn: *Sennertia* (*Sennertia*) *vanderhammeni brevipilis*: Abrahamovich & Alzuet, 1990: 319
Note: indication on homonymy with *Sennertia brevipilis* Alzuet and Abrahamovich

109. **Sennertia vanderhammeni** Fain, 1974
Orig: *Sennertia vanderhammeni* Fain, 1974b: 222, Figs 3–4 (holotype and 15 paratype HDNs in RMNH, 2 paratype HDNs in IRSNB)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Sri Lanka: Central (Peradeniya) ("Peradeniya. Ceylon")
Note: description of HDN

Syn: *Trichotarsus koptorthosomae* Oudemans, 1901: 82 (part.)
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (original host subgenus *Koptorthosoma*)
Distr: India; Indonesia: Java

Note: description of HDN, from "acarid chamber", included in key

Syn: *Sennertia* (*Sennertia*) *vanderhammeni*: Fain, 1981: 156
Host: *Xylocopa* (*Mesotrichia*) *tenuiscapa* (as *Koptorthosoma tenuiscapa*)
Distr: Indonesia: Java
Note: redescription of HDN, included in key, subgeneric assignment, assigned to *cerambycina* group

110. **Sennertia varicosa** Fain, 1971
Orig: *Sennertia varicosa* Fain, 1971: 268 (holotype and 6 paratype HDNs in MRAC)
Host: *Xylocopa* (*Mesotrichia*) sp. (as *Mesotrichia* sp.) (type host) (Kundelungu), *Xylocopa* (*Xenoxylocopa*) *inconstans* (as *Mesotrichia inconstans*) (Uvira and Minta-Luemba)
Distr: Democratic Republic of the Congo: Katanga ([Monts] Kundelungu) (type locality), Sud-Kivu (Uvira); Angola "Minta-Luemba"
Note: description of HDN

Syn: *Sennertia* (*Sennertia*) *varicosa*: Fain, 1981a: 167, Figs 31, 32, 37
Host: *Xylocopa* (*Mesotrichia*) sp. (as *Mesotrichia* sp.) (type host) (Kundelungu), *X.* (*Xenoxylocopa*) *flavescens* (as *Mesotrichia flavescens inconstans*) (Uvira and Angola)
Distr: Democratic Republic of the Congo, : Katanga (=Shaba): ([Monts] Kundelungu) (type locality), Sud-Kivu (Uvira); Angola
Note: included in key, redescription, subgeneric assignment, emendation of number of paratypes from Angola and host subspecies, assigned to *japonica* group

Syn: *Sennertia* (*Sennertia*) *varicosa*: Haitlinger, 2000: 17
Distr: Democratic Republic of the Congo, Angola

111. **Sennertia vitzthumi** Fain, 1981
Orig: *Sennertia* (*Asiosennertia*) *vitzthumi* Fain, 1981a: 172, Figs 47, 48, 62 (holotype HDN in ZSMC A20031437)
Host: Unknown
Distr: Unknown (probably Oriental)
Note: description of HDN, included in key. Original label information: "No. V 3068. *Sennertia alfkeni* Ouds. 2-Ny, Exuvie,14.9.1928".

112. **Sennertia zhelochovtsevi** Zachvatkin, 1941
Orig: *Sennertia zhelochovtsevi* Zachvatkin, 1941: 388, Figs 661, 666–668 [Lectotype (designated here) and 2 paralectotype HDNs in ZIN].
Host: *Xylocopa olivieri* (type host), *Xylocopa rufa*
Distr: Greece (type locality), Turkey, Armenia, "Middle Asian republics" of the former USSR (including Uzbekistan)
Note: description of HDN, included in key, mention of differences between specimens distributed in Greece and "Transcaucasus" (Georgia, Armenia and Azerbaijan) from those in Uzbekistan (Buhara). There is only one slide in ZIN with 3 HDNs with the following label (translated from Russian): "Fam. Glycyphagidae: *Sennertia zhelochovtsevi* A. Z., hypopi, Zachvatkin det. 1944, on *Xylocopa olivieri*, Greece". We designate one of the HDNs as the lectotype.

Syn: *Sennertia zhelochovtsevi*: Turk, 1948: 84
Note: comparison with *Sennertia donaldi*

Syn: *Sennertia* (*Sennertia*) *zhelochovtsevi*: Fain, 1981a: 148
Host: *Xylocopa olivieri*, *Xylocopa* sp.
Distr: Greece, Turkey, "Central Asia"
Note: included in key, short redescription of HDN, subgeneric assignment, assigned to *horrida*-group

Syn: *Sennertia zhelochovtsevi*: Klimov *et al*., 2007a: 1371
Host: *Xylocopa olivieri*
Distr: Greece
Note: HDN included in morphological phylogenetic analysis

Species Inquirendae

1. **Chaetodactylus** sp.
Orig: *Trichotarsus osmiae*: Banks, 1902: 176
Host: *Osmia*
Distr: New York, Nassau Co., Sea Cliff
Note: misidentification, *Chaetodactylus krombeini* or *Chaetodactylus rozeni*

2. **Sennertia** sp.
Orig: sine nomine ("parasiten" [of *Dinogamasus*], "acaridensoört", "acariden"): Zollinger, 1846: 297
Host: *Xylocopa violacea* (misidentification)
Distr: Indonesia (Java)
Note: Found in acarinarium (erroneously attributed to male host) and also recorded from flowers of *Alstonia sericea*; considered as parasite of *Dinogamasus*

Syn: *sine nomine* ("Die kleinen anderweitigen Läuse"="small other lice"): Frantzius, 1851: 240
Host: *Xylocopa amethystina*
Distr: Indonesia (Java)
Note: Review of Zollinger's account (1846) and discussion on relationships with bee host and *Dinogamasus*, amended host name

Orig: *Trichotarsus* sp. Oudemans, 1903: 138 [*Sennertia*]
Host: *Xylocopa aestuans* (as *Coptorthosoma aestuans*)
Distr: Indonesia (Java)
Note: Review of Zollinger's (1846) and Frantzius' (1851) accounts, amended host name

3. **Sennertia** sp.
Orig: *Sennertia* sp. Skaife, 1952: 75, Fig. 7 (HDN), 8 (male)
Host: *Xylocopa* (*Koptortosoma*) *caffra* (as *Mesotrichia caffra*)
Note: observation on biology in nest

Taxa Incorrectly Attributed to Chaetodactylidae

Dermacarus Haller, 1880 (Glycyphagidae) considered as subgenus of *Trichodactylus* by Berlese (1884b)

Eutarsus cancriformis Hessling, 1852 (=*Cheyletus eruditus* (Schrank, 1781) after Oudemans, 1938) incorrectly synonymized with *Trichotarsus xylocopae* by Berlese (1897)

Glyciphagus anonymus Haller, 1882 [sic!] (=*Carpoglyphus lactis* (Linnaeus, 1758)) (transferred to *Trichodactylus* by Berlese, 1884a, b)

Homopus Koch, 1843 [part.] (=*Myacarus* Zachvatkin, 1941 (subgenus of *Glycyphagus*); Glycyphagidae) placed in synonymy with *Trichodactylus* by Berlese (1884b)

Scutacarus femoris Gros, 1845 (transferred to *Trichodactylus* by Murray, 1877) (=*Scutcarus acarorum* Goeze, 1780, family Scutacaridae)

Trichotarsus affinis Trägårdh, 1905 (Winterschnidtiiae: Ensliniellinae)

Trichotarsus bomborum Berlese, 1897 (Winterschmidtiidae)

Trichotarsus clypeatus Tietze in Canestrini, 1899 (synonymized with *Disparipes bombi* Michael by Vitzthum, 1912a= *Scutcarus acarorum* Goeze, 1780, family Scutacaridae)

Trichotarsus helenae Oudemans, 1902 (transferred to *Horstia* by Oudemans, 1905a)

Trichotarsus intermedius Oudemans, 1902 (transferred to *Tortonia* by Oudemans, 1911a)

Trichotarsus manicati Giard, 1900 (transferred to *Sennertionyx* by Zachvatkin, 1941)

Trichotarsus ornatus Oudemans, 1900 (transferred to *Horstia* by Oudemans, 1905a)

Trichotarsus pulcherrimus Vitzthum, 1912 (transferred to *Horstia* by Vitzthum, 1919)

Trichotarsus trifilis Canestrini, 1897 (transferred to *Horstia* by Oudemans, 1905a)

APPENDIX 8. MUSEUM ABBREVIATIONS

AMNH USA, New York, New York, American Museum of Natural History.

ASUA Egypt, Cairo, Ain Shams University.

BLCU USA, Utah, Logan, Utah State University, Bee Biology and Systematics Laboratory

BMNH United Kingdom, London, The Natural History Museum (=British Museum (Natural History).

CAS USA, California, San Francisco, California Academy of Sciences.

CNC Canada, Ontario, Ottawa, Canadian National Collection of Insects.

CUIC USA, New York, Ithaca, Cornell University.

EMEC USA, California, Berkeley, University of California, Essig Museum of Entomology.

ESALQ Brazil, Piracicaba, Escola Superior de Agricultura “Luiz de Queiroz”.

ESEC Egypt, Cairo, Entomological Society of Egypt.

FMNH USA, Illinois, Chicago, Field Museum of Natural History.

FSCA USA, Gainesville, Florida State Collection of Arthropods.

GRSM (GSNP) USA, Tennessee, Gatlinburg, Great Smoky Mountains National Park.

HNHM Hungary, Budapest, Hungarian Natural History Museum.

INHS USA, Illinois, Champaign, Illinois Natural History Survey.

IRSNB Belgium, Brussels, Institut Royal des Sciences Naturelles de Belgique.

KU (KSBS) USA, Kansas, Lawrence, University of Kansas, State Biological Survey of Kansas.

LACM USA, California, Los Angeles, Los Angeles County Museum of Natural History.

MLPA Argentina, La Plata, Universidad Nacional de La Plata, Museo de la Plata.

MNHN France, Paris, Muséum National d’Histoire Naturelle.

MRAC Belgium, Tervuren, Musée Royal de l’Afrique Centrale.

MSU (MEMU). USA, Mississippi, Mississippi State, Mississippi State University.

MUSM Peru, Lima, Universidad Nacional Mayor de San Marcos, Museo de Historia Natural.

NBGY Ukraine, Yalta, Nikita (Nikitskiy) Botanical Gardens.

NHRS Sweden, Stockholm, Naturhistoriska Riksmuseet.

NSMT Japan, Tokyo, National Science Museum (Natural History).

NYSM USA, New York, Albany, New York State Museum.

OSAL USA, Ohio, Columbus, Ohio State University, The Acarology Laboratory.

OSU USA, Ohio, Columbus, Ohio State University (Insect collection).

PARU Czech Republic, České Budějovice, Institute of Parasitology of the Academy of Sciences of the Czech Republic (formerly in Prague).

RMNH Netherlands, Leiden, Nationaal Natuurhistorische Museum (formerly Rijksmuseum van Natuurlijke Historie).

SAM Australia, South Australia, Adelaide, South Australian Museum.

TNAU India, Tamil Nadu, Coimbatore, Tamil Nadu Agricultural University.

UCD (UCDC) USA, California, Davis, University of California, R.M. Bohart Museum of Entomology.

UMMZ USA, Michigan, Ann Arbor, University of Michigan, Museum of Zoology.

UNAM Mexico, Mexico City, Universidad Nacional Autónoma de México.

USNM USA, Washington D.C., National Museum of Natural History

UWCP Poland, Wroclaw, University of Wroclaw

WAMP Australia, Western Australia, Perth, Western Australian Museum

ZIN Russia, St. Petersburg, Russian Academy of Sciences, Zoological Institute

ZSMC Germany, München, Zoologische Staatssammlung.

APPENDIX 9. HOST INDEX

Valid names are in normal font; nonvalid names and combinations are in italics.