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A new subfamily of Feaellidae (Arachnida, Chelonethi, Feaelloidea) from Southeast Asia

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Abstract

The first extant representatives of the pseudoscorpion family Feaellidae from Southeast Asia are described. *Cybella* n. gen. is proposed for *Cybella deharvengi* n. sp. (type species), collected from an isolated limestone hill in Hon Chong Province, Vietnam, and *C. bedosae* n. sp., found in a limestone cave in Kampuchea, Cambodia. *Cybella* species seem to be restricted to karst formations and are probably troglophilic. The type localities of the two known species are threatened by quarrying activities, these being particularly pressing in the case of *C. deharvengi* n. sp. *Cybella* shows important differences from other Feaellidae that require a modification of the familial diagnosis and justify the erection of a new subfamily, Cybellinae. The discovery of this group provides insights into the evolution of the unusual morphology of the family, notably concerning the pleural plates of Feaellinae, which are lacking in Cybellinae. The smaller sclerites of the pleura of Pseudogarypidae and Feaellidae are shown to be muscle apodemes, which provide an additional synapomorphy for Feaelloidea. Two types of coxal spines, termed primary and secondary, are distinguished in Feaelloidea, based on the presence of a lumen within the primary spines and its absence in secondary spines. The new morphological term *atrial plate* is proposed for a sclerotized plate of the male genitalia, extending between the lateral rods and the lateral apodemes. Claims that the internal genital setae of males of non-chthonioid pseudoscorpions are secretory are reviewed and found to lack support.

Additional information concerning the fossil genus *Protofeaella* Henderickx, 2016 is provided, based on an adult male in amber from the Cretaceous (lowermost Cenomanian) of Myanmar. *Protofeaella* shares with *Cybella* the absence of pleural plates and the antiaxial position of the chemosensory setae of the movable chelal finger. However, it differs from both Cybellinae and Feaellinae in having relatively long chelal fingers that lack a tuberculate basal tooth, both of which are interpreted as symplesiomorphic states within Feaellidae. *Protofeaella* is therefore provisionally treated as a stem-group feaellid and not assigned to a subfamily.

The existence of a Cretaceous member of the Pseudogarypidae is noted in the mid-Cretaceous (late Albian–early Cenomanian) of Germany, representing the oldest record of this family.

Key words: Pseudoscorpiones, systematics, morphology, biogeography, karst, amber, palaeontology, Cretaceous, Germany, Cambodia, Myanmar, Vietnam

Introduction

The Feaellidae are morphologically unusual pseudoscorpions, with extant species being found in Brazil, sub-Saharan Africa, Madagascar, Seychelles, India and Australia (Harvey 1996a, 1996b; Harvey *et al.* 2016), and fossil species in Eocene Baltic amber (Henderickx & Boone 2014) and Cretaceous Burmese amber (Henderickx & Boone 2016). Until recently, the family contained only a single genus, *Feaella* Ellingsen, 1906, which has been divided into three subgenera (Harvey 1991). Two new genera have recently been proposed: *Protofeaella* Henderickx, 2016, for a Cretaceous species in Burmese amber (Henderickx & Boone 2016), and *Iporangella* Harvey, Andrade & Pinto-da-Rocha, 2016, for an extant species from Brazil (Harvey *et al.* 2016).

The presence of Feaellidae in Southeast Asia has previously been mentioned by Deharveng *et al.* (2009) and Harvey *et al.* (2016). The genus concerned is described here from species found in Cambodia and Vietnam. It is sufficiently different from other Feaellidae to warrant the erection of a new subfamily.

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The ecology of Feaellidae is poorly understood, but they have been found in leaf litter, under stones and under bark in forest or coastal habitats. The Cambodian and Vietnamese species were both found in limestone karsts, occupying large cavities. Although they show no signs of troglomorphy, the available records suggests that they may be restricted to karst formations. Unfortunately, the Vietnamese locality—an isolated limestone hill—has been subject to large-scale quarrying (Deharveng *et al.* 2005, 2009; Deharveng & Bedos 2012; Kiernan 2010) and the same fate probably awaits the Cambodian locality, which has been leased for quarrying.

Material and methods

The specimens from Cambodia were extracted from a soil sample using portable Berlese funnels. Most of those from Vietnam were collected by hand, at about chest height, from a small (ca 50 cm) area of a vertical wall which was humid, but not wet, and in total darkness. Examination of other parts of the cavity failed to produce any further specimens. The floor was covered with compacted clay-soil, without stones or debris, and unsuitable for pseudoscorpions. Sieving of litter at several sites outside the cavity failed to produce any further specimens, but a single tritonymph was subsequently found in a 'Berlese extraction', presumably of litter, taken nearby a few years before.

Methods for studying the extant material follow Judson (2007a), except that internal genitalia were examined in clove oil after dehydration. All material was returned to alcohol after study. The palp of the paratype protonymph of *Cybella bedosae* **n. sp.** was used for non-destructive DNA extraction by Arabi *et al.* (2012).

The complex form of the carapace in Feaellidae is rather difficult to render in a line drawing. The solution adopted here is akin to the contour lines of a topographic map. Where there is a strong declivity, the margins of the reticulation appear more prominent because the surface is observed obliquely from dorsal view. By partially drawing these apparent margins, it is possible to convey an impression of the relief, although the difference between raised and sunken parts may not be immediately evident to someone unfamiliar with the group. The form of the contour for each alveole provides an indication of the direction of inclination: each crescent is highest in its middle, hence the ends point downwards, towards the base of a declivity. Because the general form is fairly conservative, it may help to compare the figures of the carapaces given here with the scanning electron micrographs published by Henderickx (2009: 2b, 3a).

Measurements follow the reference points published by Chamberlin (1931). Because of their unusual morphology in Feaellidae, it is necessary to specify that the length of the carapace is taken from the posterior (unsclerotized) margin to the tip of the anteromedian projections; the length of the palp femur is measured from the dorsal condyle of the articulation with the trochanter and the breadth of the femur does not include the anterobasal projection. Distances between trichobothria are measured as the minimum length between the edges of the outer rims of the bothridial areoles.

Fossil material was studied using the methods given in Judson (2007b). Burmese amber is mid-Cretaceous (lowermost Cenomanian), with an age of about 99 My (Shi *et al.* 2012).

Terminology generally follows Chamberlin (1931), as modified by Harvey (1992) (for segmentation of appendages) and Judson (2007a). Concerning the latter's use of the adjectives anti- and paraxial, Harvey *et al.* (2012) wrote "The terms antaxial [sic] and paraxial have been recently proposed to describe the lateral faces of pseudoscorpion appendages (Judson 2007) to replace the inadequate and ambiguous terms anterior and posterior. This change is welcome but we here use the terms prolateral and retrolateral as used in describing spider appendages". Those comments warrant some clarification. Firstly, the terms that Judson (2007a) objected to in this context were not 'anterior' and 'posterior', but *internal* and *external*. Secondly, the terms anti- and paraxial did not originate with Judson (2007a): they were adopted for mites by Grandjean (1933) and first applied to pseudoscorpions by van der Hammen (1986); Judson (2007a) simply explained why they are more appropriate in this context than 'internal' and 'external'. Thirdly, the presentation of prolateral and retrolateral by Harvey *et al.* (2012) as alternatives to the terms antiaxial and paraxial gives the misleading impression that they are equivalent. As originally defined by Petrunkevitch (1925a, 1925b), 'prolateral' and 'retrolateral' have the same anatomical meanings as 'anterior' and 'posterior', respectively, with reference to appendages. Although they are used routinely in taxonomic descriptions of several arachnid groups, there is no compelling need for these terms. Bird *et al.* (2015) considered 'prolateral' and 'retrolateral' to be "more accurate in accounting for position and serial homology" than a variety of other terms discussed by them, but these did not include 'anterior' or 'posterior'. Evidently, authors are free to use pro- and retrolateral if they consider these terms clearer, but it is important that they be applied correctly. This has not consistently been the case so far for pseudoscorpions, with authors such as Gao & Zhang (2012), Nassirkhani & Hamidi (2015), Nassirkhani & Harvey (2013), Nassirkhani & Takalloo zade (2013) and Nassirkhani *et al.* (2016) misapplying 'prolateral' and 'retrolateral' when describing legs or coxae.

The term *apodens* is introduced here for the tooth at the apex of each chelal finger. This tooth corresponds to the *venedens* when a venom duct is present in the finger, but there is no available term when it is absent. Referring to this tooth as the apical or distal tooth would be ambiguous because the first ordinary tooth of the dental row is often referred to in these ways. The general convention in descriptions of pseudoscorpions is that tooth counts do not include the apodens, but the Feaellinae provide an exception because the apodens is difficult or impossible to distinguish from the other teeth. The other teeth of Feaellidae are here considered to form two rows: one marginal (dorsal for movable finger and ventral for fixed finger) and the other paraxial. Both rows are rather irregular, with the teeth tending to be staggered.

The new term *atrial plate* (abbreviated as *apl*) refers to a sclerotized plate extending between the lateral rods and the lateral apodemes of the male genitalia. This plate is well developed in Feaellinae and has been illustrated by Heurtault-Rossi & Jézéquel (1965), although they did not mention it in their description [it should be noted that the legends to the figures of the genitalia in Heurtault-Rossi & Jézéquel (1965) are erroneous: fig. 13 shows them in dorsal view (not posterior, as indicated in the legend) and fig. 14 shows them in anterior view (not dorsal, as indicated in legend), in an upside-down orientation (i.e. dorsal parts facing towards bottom of page)]. The atrial plate is not limited to Feaellidae, but it is particularly well developed in this family.

Two types of coxal spines are recognized here for Feaellidae. The first type is limited to coxa I and consists of long, thin, hollow spines near the posterior margin. These are considered homologous with the similar spines on coxa I of Pseudogarypidae and are here termed *primary coxal spines*. Cybellinae and most Feaellinae have only a single primary spine. Spines of the second type, here termed *secondary spines*, are more numerous and can be present, in various combinations, on coxae I, II and III. These secondary spines are variable in form and intergrade with the granulation of the coxae. A secondary spine can be distinguished from a granule in having a bladelike shape and being raised away from the cuticle distally, although the distinction is not always clear. The secondary spines of Feaellidae are arranged around a depression, which is here referred to as the *coxal pit*. This pit is always present on coxa I (as in Pseudogarypidae), but in some feaellids it extends to coxa II (e.g. Henderickx 2009: fig. 2e; Harvey *et al.* 2016: fig. 2 I). The function of this pit is presumably to accumulate washing fluid during leg cleaning (Judson 1990).

Institutional abbreviation

MNHN	Muséum national d'Histoire naturelle, Paris.

Taxonomy of extant taxa

Superfamily Feaelloidea Ellingsen, 1906

Family Feaellidae Ellingsen, 1906

Diagnosis of total-group [*Protofeaella* + Feaellinae + Cybellinae]. Feaelloidea with 2–6 projections on anterior margin of carapace. Tergite I strongly modified, distal part shelved, allowing it to pass under posterior margin of carapace. Palps 'raptorial': femur strongly expanded, chela reduced in size, palm particularly small. Movable chelal finger usually with a group or row of strongly differentiated chemosensory setae; trichobothria *t* and *sb* situated on ventral face. Chelal teeth dispersed onto paraxial face of fingers. Palp coxa strongly elongated. Coxa IV with broad, thin posterior extension.

Diagnosis of crown-group [Feaellinae + Cybellinae]. Feaellidae with a tuberculate basal tooth on each of the chelal fingers. Sternite III mostly smooth, apart from posteromedian and lateral parts, which are reticulate and bear setae; lateral ends with superficial appearance of spiracular plates, but not separate from rest of sternite. Median maxillary lyrifissure in posterior position, situated on clivus of palp coxa. Intercoxal canal well developed, covered by margins of coxae.

Remarks. Harvey (1992) diagnosed Feaellidae by the following derived states: palps with a raptorial form; median maxillary lyrifissure absent; rallum with a single blade; anterior margin of carapace with 2 or more medial lobes; carapace and tergite I with an unusual articulation joint; and spiracles fused to sternites IV and V. As discussed below, the median maxillary lyrifissure is in fact present in all Feaellidae. The number of blades in the rallum can no longer be used to separate Feaellidae from Pseudogarypidae because two blades are usually present in Cybellinae n. subfam. The spiracles of Feaellidae, like those of Pseudogarypidae, open between sternites III and IV. The impression that they have moved is due to associated anterolateral modifications on sternites IV and V, particularly the strong internal apodemes.

The diagnosis of the crown-group includes characters for which states are unknown for *Protofeaella* and hence might instead apply to the total-group.

Subfamily Feaellinae

Diagnosis. Feaellidae with two rows of well developed pleural plates that bear setae and lyrifissures. Cheliceral rallum reduced to a single blade or completely absent. Spinneret with a knife-like outline. Coxae III not reduced in size, meeting at midline. Modified chemosensory setae (when present) on ventral face of movable finger, either arranged in rows or in a compact group, but not recessed in a deep pit. Chelal fingers with compact group of apical teeth, apodens not clearly distinguishable. Trichobothrium *st* about half-way between *b* and *t* or closer to closer to *b*. Male genitalia with atrial plate well sclerotized and ornamented; median genital sac well developed; posterior plate with all internal setae simple and of the same length.

Remarks. The recently described genus *Iporangella* can be placed in the Feaellinae by virtue of the well developed pleural plates and the trichobothriotaxy. However, because the morphology of the male genitalia and the basal teeth of the chelal fingers are not yet known for this genus, the diagnosis of the subfamily is provisional. Harvey *et al.* (2016) separated *Iporangella* from all other feaellids by the "lack of specialized setae on the retrolateral face of the movable chelal finger", but this is incorrectly expressed because the setae concerned (referred to here as chemosensory setae) are situated on the *ventral* face of the movable finger in *Feaella*. The statement by Heurtault (1983) that they are present on the 'internal' (paraxial) face of the finger in *F. mirabilis* Ellingsen, 1906 is incorrect. Elsewhere in their paper, Harvey *et al.* (2016) simply state that the movable chelal finger lacks specialized setae in *Iporangella*, implying that they are not present anywhere, but it would be useful to confirm this in view of their constancy in other Feaellidae.

Subfamily Cybellinae, n. subfam.

Diagnosis. Small Feaellidae lacking well developed pleural plates (segment I has a small dorsolateral plate, but this is not homologous with the plates of Feaellinae), lyrifissures in pleural membrane. Coxae III reduced in size, not meeting in midline. Cheliceral rallum usually with two blades (sometimes reduced to one). Spinneret simple, tubular. Chemosensory hairs of movable chelal finger large, bacilliform and arranged in a compact group, recessed in a deep pit on antiaxial side of finger. Apodens of both chelal fingers larger than other teeth and directed paraxially; fingers without a compact group of apical teeth. Trichobothrium *st* much closer to *t* than to *b*. Atrial plate of male genitalia weakly sclerotized and without strongly marked ornamentation, but with a distinct tubular pocket laterally; median genital sac reduced, but still with a distinct sclerotized ring at end of duct; posterior plate with two types of internal setae: posterior pair longer than others and with a spatulate shape.

Type genus. *Cybella* **n. gen.**

Remarks. The reduction in the size of coxae III and the spatulate posterior pair of internal male genital setae are unique to Cybellinae and can be regarded as autapomorphies of the group. The large pit containing the chemosensory hairs on the movable chelal finger might also be synapomorphic, but there is a doubt because the form of the pit (if present) in *Protofeaella* is uncertain. Also, Pseudogarypidae do not show clearly differentiated chemosensory setae, so they are not currently useful as an outgroup in this respect. However, when such setae have been recognized in other pseudoscorpions, they are situated antiaxially, as in certain Chthoniidae (Mahnert 2011, 2014; Judson 2016) and Olpiidae (Chamberlin 1931). Thus it can be supposed that the antiaxial position in Cybellinae is plesiomorphic, even though the pit in which they are inserted is a derived feature. Most of the other distinctive character states of Cybellinae are plesiomorphic relative to Feaellinae, based on outgroup comparison with Pseudogarypidae. *Cybella* will have an important part to play in the analysis of phylogenetic relationships within Feaellinae, since it provides a closer—and thus more pertinent—outgroup than Pseudogarypidae.

Cybella n. gen.

Diagnosis. As for the subfamily (monogeneric).

Etymology. Feminine diminutive, derived from Cybele, Greek goddess of mountains, caves and wild animals, who was often depicted with a turret-like crown on her head.

Type species. *Cybella deharvengi* **n. sp.**

Distribution. Southeast Asia: limestone hills of southern Cambodia and southern Vietnam.

Remarks. *Cybella* shows most of the derived features that characterize the family Feaellidae, including the raptorial form of the palps, the unusual trichobothriotaxy, the separation of the chelal teeth into more than one row, the presence of two anteromedian projections on the carapace, the modified form of the articulation between the carapace and tergite I, and the presence of thickened chemosensory setae on the movable chelal finger. At the same time, it shares some plesiomorphic features with Pseudogarypidae, such as the absence of well defined pleural plates, the presence of two blades in the rallum, the tubular form of the spinneret, and the apodens of each chelal finger still recognizable (as opposed to being in a terminal cluster of indistinguishable teeth). *Cybella* can therefore be considered the sister-group of all other extant Feaellidae. To emphasize the differences between the two groups, *Cybella* is here placed in its own subfamily, Cybellinae, while *Feaella* and *Iporangella* are placed in Feaellinae. Monophyly of Feaellinae is supported by the synapomorphic reduction of the rallum to one blade or none, a blade-shaped spinneret, the presence of well-defined plural plates bearing lyrifissures and the clustering of teeth at the end of the movable finger, amongst which the apodens can no longer be easily recognized.

The poor development of the pleural plates in Cybellinae is of particular interest. In Feaellinae, there are two rows of plates—one dorsal and one ventral—running along the pleural membranes on each side of the opisthosoma. These plates are fully sclerotized, with a reticulate sculpturing, and bear setae, gland pores and lyrifissures. They therefore resemble miniature versions of the tergites and sternites. Although setae, gland pores and lyrifissures are all present on the dorsal and ventral folds of the pleurum of Cybellinae, they are not grouped together in the same way. As discussed below, the absence of pleural plates in Cybellinae is considered to be plesiomorphic.

Cybella deharvengi n. sp.

Figs 2–47

Diagnosis. See under *Cybella bedosae* **n. sp.**

Etymology. This species is named after Louis Deharveng (MNHN), who discovered the cavity in which the types were found and who has made many important contributions to our knowledge of soil and cave faunas in Southeast Asia.

Type material. Holotype ♂, Vietnam, Kien Giang, Kien Luong, Hon Chong, Nui Bai Voi (Mo So Lon), ‘grotte des Feaellidae’, 1013′25.81″N 10436′57.35″E, 32 m a.s.l., on wall of limestone cavity in near-total obscurity, 2 June 2008, leg. M. Judson (MNHN Ps-704.43). Paratypes: 3 ♂, 1 tritonymph, same details as holotype (2 ♂, MNHN Ps-704.44–45, and tritonymph, MNHN Ps-704.46; 1 ♂ deposited in Institute of Tropical Biology, Hanoi, Vietnam).

Non-type material. 1 tritonymph, Vietnam: Kien Giang, Kien Luong, Hon Chong, Nui Bai Voi, near Grotte-hôpital de Mo So [=Hang Moi Chau or Hang Mo So], 1013′31.6″N 10436′59.2″E, 29 m a.s.l., 16 January 2003, litter, Berlese extraction, leg. Le Cong Man, collector’s code VIET-ManKG23 (MNHN Ps-704.47). Tarsus of left leg I missing.

Description of male. Sclerotized parts amber-brown (Fig. 2); body and appendages covered with finely granular cerotegument, apart from non-reticulate areas, such as the fingers of chelicerae and chelae. Vestitural setae very small and simple, only chelal fingers, chelicera and manducatory process with larger setae. Carapace (Fig. 4) longer than broad, distinctly broadened proximally. Anterolateral corners truncate, not projecting anteriorly, median projections small, directed slightly towards midline, two raised mounds between eyes and an unpaired mound in middle of mesozone, behind which is a moderate ridge that is only weakly produced laterally. Two pairs of large eyes, with reflective tapeta. One pair of lyrifissures near eyes, one lateral pair behind posterior eyes, and 2–5 posteriorly; one specimen with a single lyrifissure on mesozone (total number of lyrifissures 6–9). Carapace with about 37 setae (N = 1), of which 6 on posterior margin and 4 laterally on each side, below level of eyes (Fig. 5).

FIGURES 1–2. *Cybella deharvengi* **n. sp.** 1, area of cavity wall on which the types were found (photograph L. Deharveng); 2, habitus of male, dorsal view.

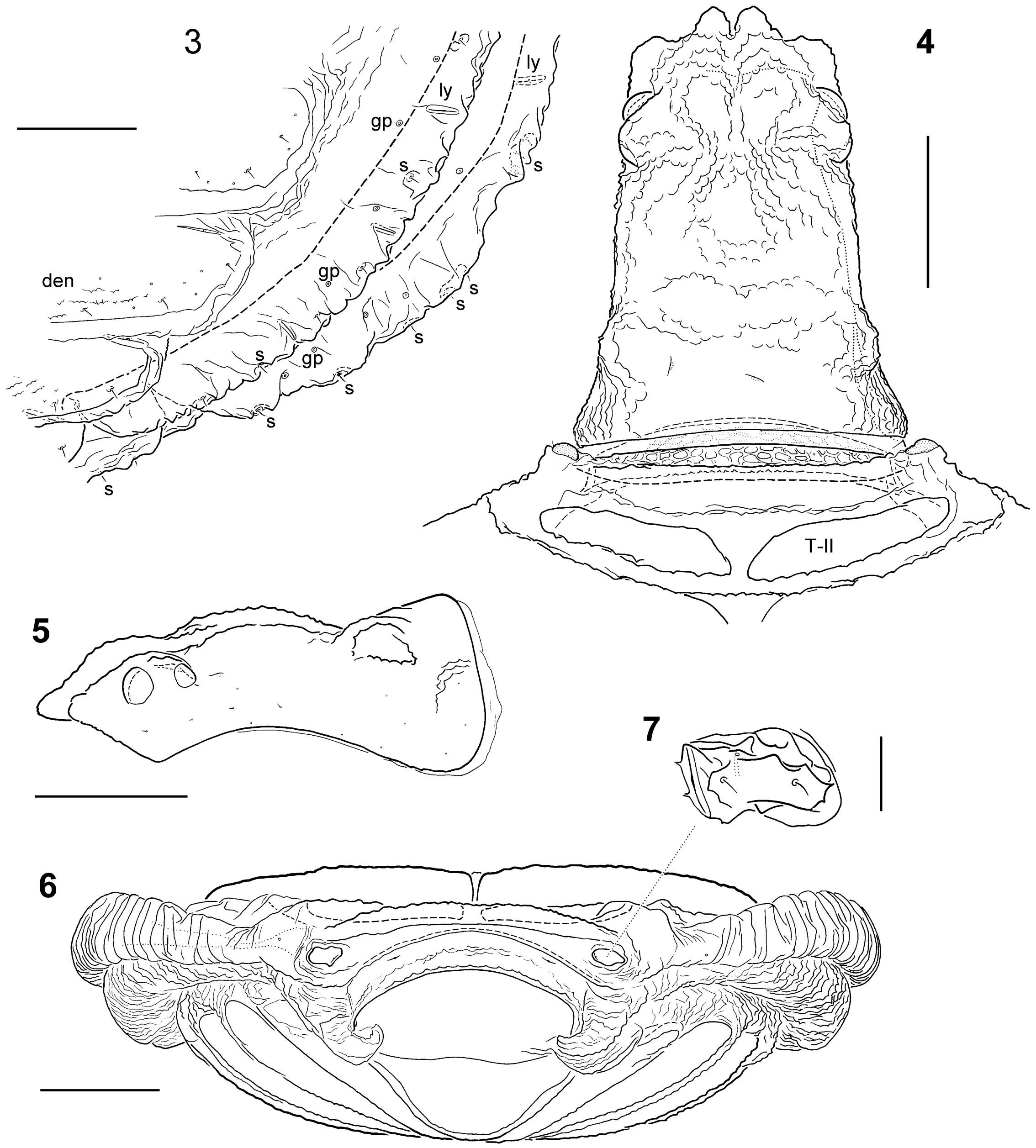
Tergite I (Fig. 4) distinctly shelved to allow posterior margin of carapace to pass over distal portion; posterior margin desclerotized; undivided medially, but flanked on each side by a small, sclerotized plate, each bearing 1 or 2 setae (no seta on main part of tergite I); lyrifissures absent. Membrane between tergites I and II extensive and rounded over posterior part of I. Tergites II–IX divided medially; setae per half-tergite 8 : 10–11 : 13–15 : 13–15 : 14–15 : 14–16 : 13–16 : 12–14; tergite X undivided, with 21 setae. Segment XI with 10–11 posterior setae plus 3 around anal mound (total 13–14). Tergite XII with 2 setae. Tergite I without lyrifissures; half-tergite II with 1 anterolateral and 1 submedian lyrifissure; half-tergites III–IX with 1 anterolateral and 3–4 posterior lyrifissures; tergite X with a total of 5 lyrifissures.

Pleural membranes very broad, with two longitudinal folds (Figs 3, 6) on each side; dorsal fold with setae on segments III–XI and lyrifissures on V–VII; ventral fold with setae on segments VI–XI and lyrifissures on VIII–X; lyrifissures set in slight depressions in folds; simple gland pores opening ventrally on folds (Fig. 3); pleural plates absent (only tiny areas of sclerotization around pores and areoles of setae).

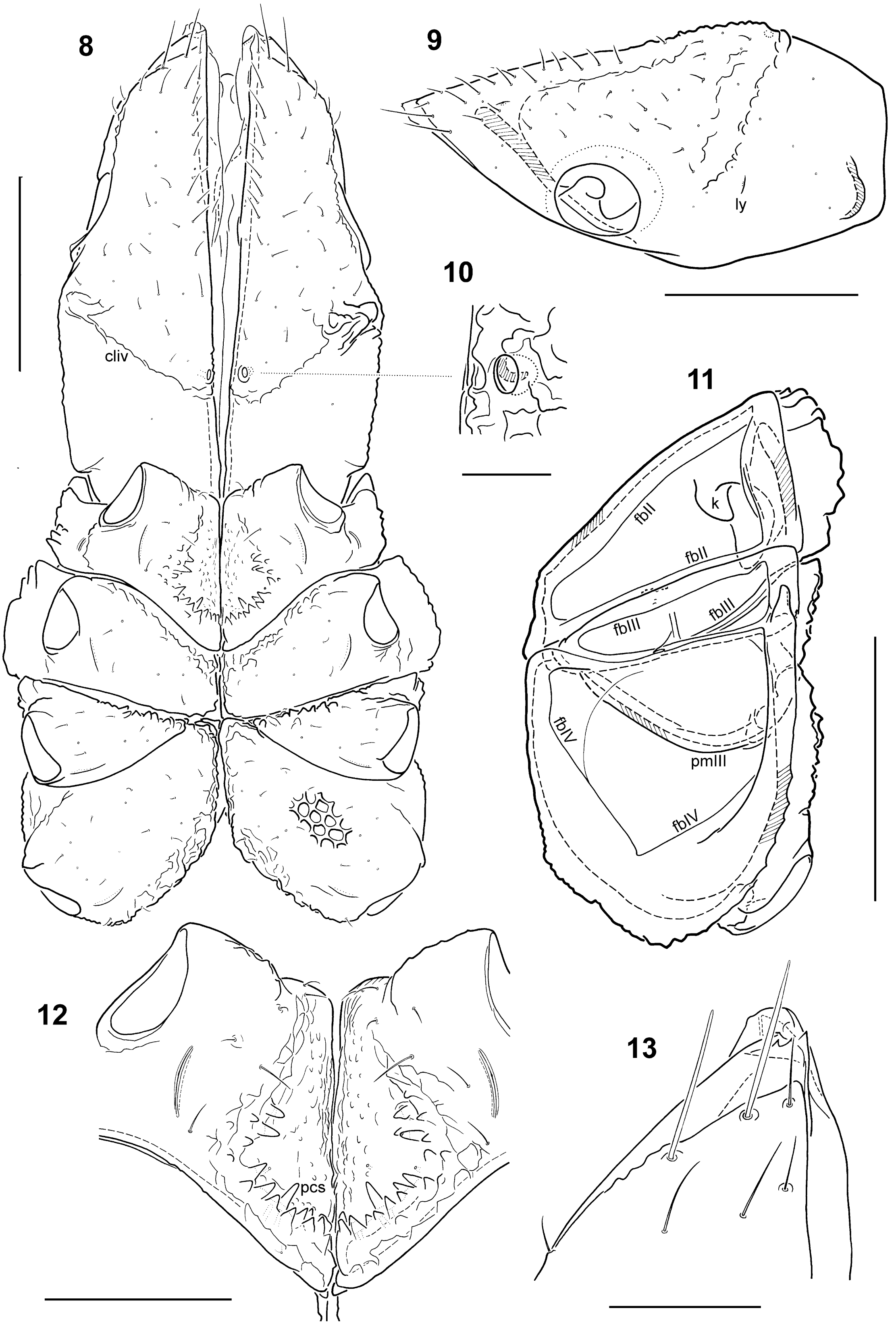
Palp coxa elongate, almost as long as combined length of leg coxae I–IV (Fig. 8). Manducatory process (Fig. 13) with 1 small apical seta and a large subapical seta, both simple; another large seta is present at base of manducatory process. Clivus (Figs 8–9) well marked, but not projecting laterally. A single, normal lyrifissure behind foramen of palp coxa (Fig. 9) (similar to position of posterior maxillary lyrifissure in Iocheirata). Median maxillary lyrifissure (Fig. 10) circular, central disk porous; internal apodeme present and attached to muscle. Coxa I (Fig. 12) with 1 primary and 8–15 secondary spines arranged around rim of pit. Coxa III with enlarged, irregular granules anteromedially (Fig. 8). Setae of coxae: P ca 30, I 6–7, II 7–10, III 6–8, IV 9–14.

Anterior genital sternite (Fig. 16) with 8 median setae and a pair of lyrifissures; posterior genital sternite with a median pair of lyrifissures, 9–11 median setae and a single pair of lateral setae (total 11–13). Sternites IV–X divided medially. Darkened bars weakly developed on sternites VI–VIII, stronger on IX. Denticulation on sternites VIII–XI (weak on VIII and XI). Setae of half-sternites (IV–X) 8–10 : 8–10 : 9 : 9–11 : 7–10 : 6–9 : 7; all setae posterior. Segment XI undivided, with 11 setae anteriad of anal opening. Sternite XII with 2 setae, closer together than those of tergite XII. Each half-sternite usually with 1 paraxial and 1 antiaxial lyrifissure, but occasionally with up to 4; segment XI with only antiaxial lyrifissures and a pair in front of anal opening.

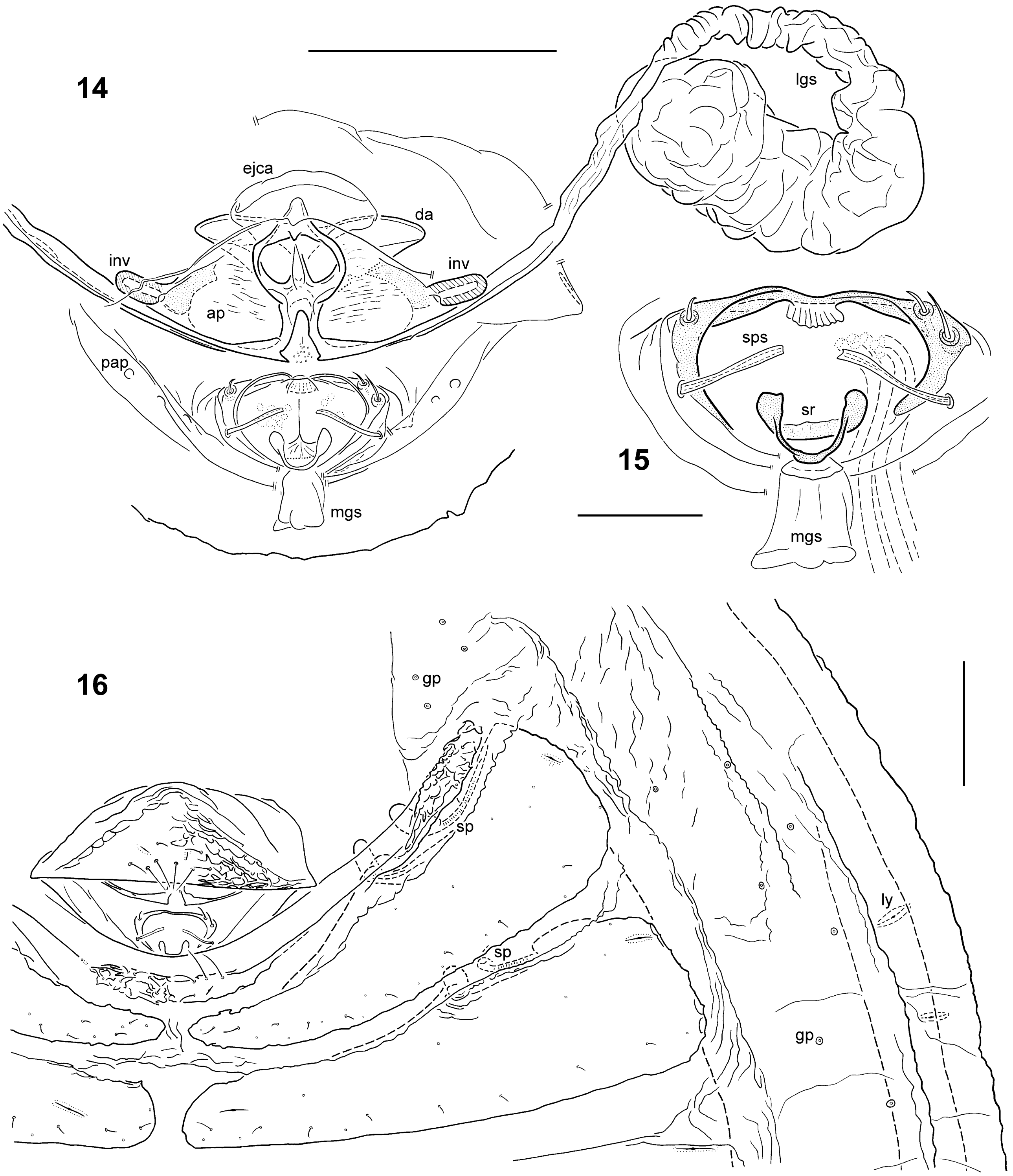
Male genitalia (Figs 14–15) relatively simple; atrial plate weakly sclerotized and without strongly marked ornamentation, but with a distinct tubular pocket laterally (Fig. 14: *inv*); lateral sacs of moderate size, without an apical constriction; median sac reduced, but with a distinct sclerotized ring at end of duct (Fig. 15: *sr*); posterior wall of atrium with a small number of papillae (Fig. 14: *pap*) that are not associated with glands; posterior plate with 3–4 internal setae on each side, of which the posterior pair is enlarged and slightly spatulate. Mature, encysted spermatozoa (observed in *vas deferens*) with a maximum diameter of 4 µm.



FIGURES 3–7. *Cybella deharvengi* **n. sp.**, male. 3, pleurum at level of segments VIII–X, ventral view; 4, carapace and anterior tergites, dorsal view; 5, carapace, lateral view; 6, opisthosoma, anterior view, prosoma removed; 7, lateral tergal plate of segment I, seen in same orientation as Fig. 6. Abbreviations: *den*, denticulate ornamentation; *gp*, gland pore; *ly*, lyrifissure; *s*, setae; *T–II*, tergite II. Scale lines 0.2 mm (Figs 1–6), 0.05 mm (Fig. 7).

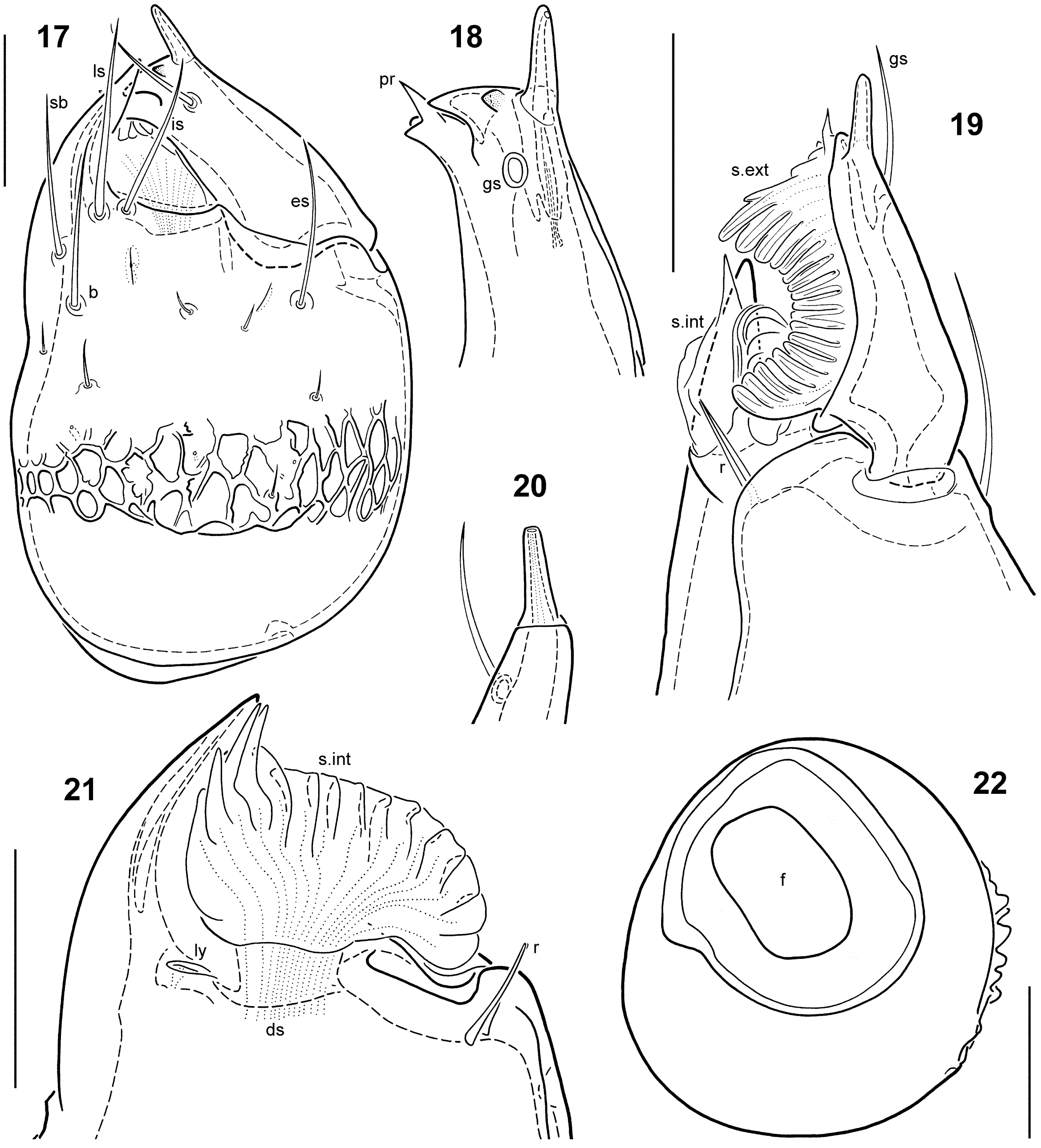


FIGURES 8–13. *Cybella deharvengi* **n. sp.**, male. 8, coxae, ventral view; 9, left palp coxa, lateral view; 10, median maxillary lyrifissure; 11, right coxae II–IV, dorsal (internal) view; 12, median part of coxae I, showing pit and coxal spines; 13, manducatory process of right palp coxa, ventral view. Abbreviations: *cliv*, clivus; *fbII*, border of internal foramen of coxa II, *fbIII*, border of internal foramen of coxa III, *fbIV*, border of internal foramen of coxa IV, *k*, condyle; *pcs*, primary coxal spine; *pmIII*, posterior margin of coxa III. Scale lines: 0.2 mm (Fig. 9) 0.1 mm (Figs 11–12), 0.05 mm (Figs 10, 13), 0.03 mm (Fig. 10).

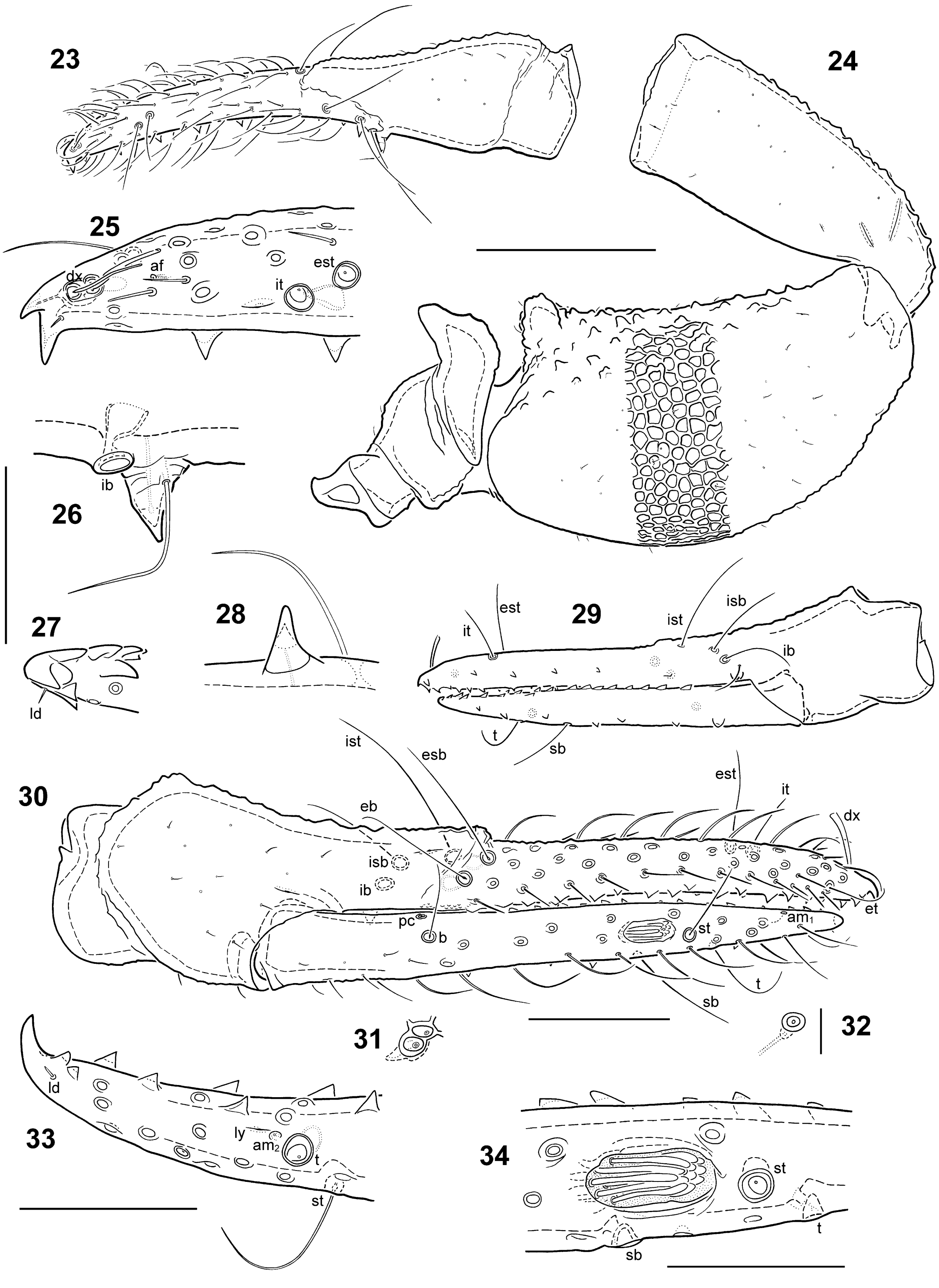


FIGURES 14–16. *Cybella deharvengi* **n. sp.**, male. 14, genitalia, ventral view; 15, posterior genital plate, ventral view 16 right side of opisthosomal segments II–V, ventral view. Abbreviations: *apl*, atrial plate; *da*, dorsal apodeme; *dpdg*, ducts of posterior dorsal gland; *ejca*, ejaculatory canal atrium; *gp*, gland pore; *inv*, invagination at side of atrial plate; *lgs*, lateral genital sac; *ly*, lyrifissure; *mgs*, median genital sac; *pap*, papilla on atrial wall; *sp*, spiracle; *sps*, spatulate seta; *sr*, sclerotized ring. Scale lines: 0.1 mm (Figs 14, 16), 0.05 mm (Fig. 15).

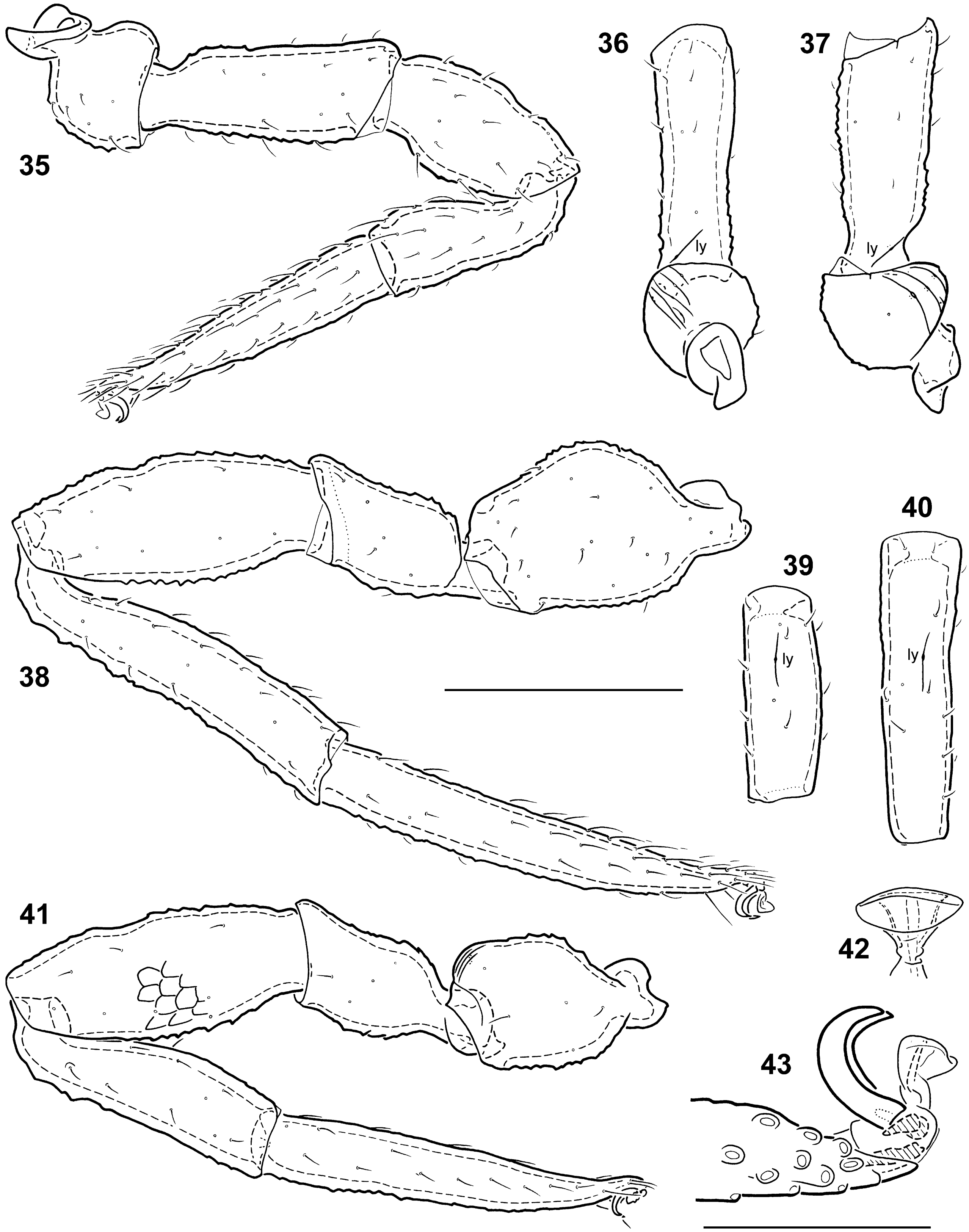
Chelicera with reticulation ending fairly abruptly in a raised crest; palm with 5 large and 6–7 small setae; 2 lyrifissures on antiaxial face (Fig. 17), 1 on paraxial face at base of fixed finger (Fig. 21). Base of fixed finger concave on paraxial side. Movable finger with a single, large tooth subdistally (Fig. 18). Spinneret short (18–23 µm) simple, tubular (not flattened), but flared at base (Figs 18–20); 3 internal silk ducts, these lying side by side and thus only evident in ventral view. Serrula exterior (Fig. 19) with 18–21 blades, arranged in an arc, plus a small, distally-directed apical process (Fig. 18) (total 20–22). Serrula interior (Fig. 21) with about 13–15 blades, basal blades enlarged and difficult to distinguish individually (counts based on internal canals). Rallum (Figs 19, 21) with two long (anterior 26 µm, posterior 25 µm), simple blades, closely appressed and thus difficult to distinguish, tips blunt, but this is only evident when they are observed at high magnification; in close proximity to basal blade of serrula exterior. Galeal seta (*gs*) barely extending beyond tip of spinneret.



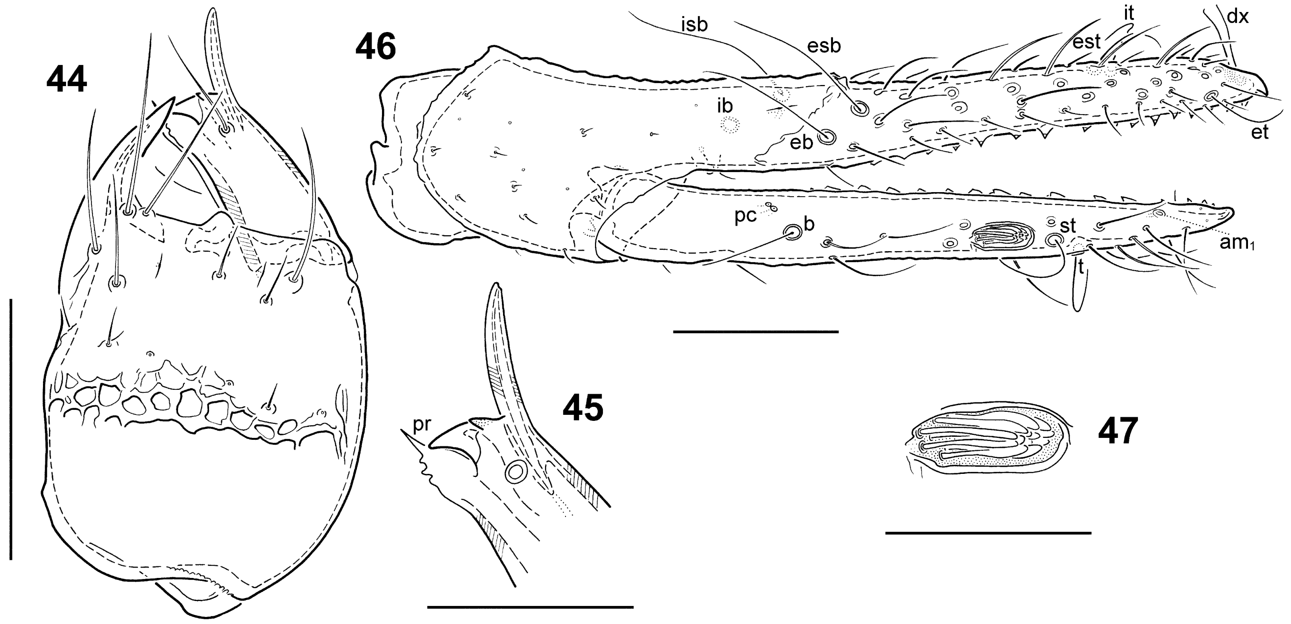
FIGURES 17–22. *Cybella deharvengi* **n. sp.**, male, left chelicera. 17, whole chelicera, antiaxial view; 18, tip of movable finger, antiaxial view; 19, distal part of chelicera, ventral view; 20, spinneret, ventral view; 21, distal part of chelicera (movable finger omitted), paraxial view; 22, chelicera in posterior view (dorsal at top, paraxial side to left). Abbreviations: *ds*, ducts of serrula interior; *f*, foramen; *gs*, galeal seta; *ly*, lyrifissure; *pr*, distal process of serrula exterior; *r*, rallum; *s.ext*, serrula exterior; *s.int.*, serrula interior. Other abbreviations (*b*, *es*, *gs*, *is*, *ls*, *sb*) are designations of setae. Scale lines 0.05 mm (Figs 18–20 share same scale line).



FIGURES 23–34. *Cybella deharvengi* **n. sp.**, male right palp. 23, chela, dorsal view; 24, palp minus chela, dorsal view (reticulate ornamentation drawn in part on femur); 25, tip of fixed chelal finger, dorsal view; 26, basal tuberculate tooth of fixed finger, dorsal view (relative to chela); 27, tip of movable chelal finger, paraxial view; 28, basal tuberculate tooth of movable chelal finger, ventral view (relative to chela), distal end to left; 29, chela, paraxial view (setae omitted); 30, chela, antiaxial view; 31, coupled sensilla; 32, distal sensillum; 33, distal end of movable finger, ventral view; 34, grouped chemosensory setae, antiaxial view. Abbreviations: *af*, apical sensillum of fixed finger; *am*$_1$, apical sensilla of movable finger; *dx*, duplex trichobothria; *ld*, probable lamina defensor; *ly*, lyrifissure; *pc*, coupled sensilla. Other abbreviations (*eb*, *esb*, *est*, *et*, *ib*, *isb*, *ist*, *it*, *b*, *sb*, *st*, *t*) are standard designations of trichobothria. Scale lines: 0.2 mm (Figs 23–24, 29), 0.1 mm (Fig. 30), 0.05 mm (Figs 25–28, 33–34), 0.01 mm (Figs 31–32).



FIGURES 35–43. *Cybella deharvengi* **n. sp.**, male right legs. 35, leg I, antiaxial view; 36, trochanter and femur of leg I, dorsal view; 37, trochanter and femur of leg I, paraxial view; 38, leg IV, antiaxial view; 39, patella of leg I, dorsal view; 40, patella of leg IV, dorsal view; 41, leg III, antiaxial view; 42, arolium of leg III, ventral; 43 apotele of leg I, antiaxial view. Abbreviations: *ly*, lyrifissure;. Scale lines 0.2 mm (Figs 35–41), 0.05 (Figs 42–43).



FIGURES 44–47. *Cybella deharvengi* **n. sp.**, paratype tritonymph. 44, chelicera, antiaxial view; 45, tip of movable cheliceral finger, antiaxial view; 46, right chela, antiaxial view; 47 grouped chemosensory setae, antiaxial view. Abbreviations: am_1, apical sensillum of movable finger; *pr*, distal process of serrula exterior; *pc*, coupled sensilla. Scale lines 0.1 mm (Figs 44, 46), 0.05 mm (Fig. 45), 0.02 mm (Fig. 47).

Palps of typical feaellid facies, femur very robust, patella and chela small (Figs 23–24). Trochanter with a strong, thick, dorso-ventrally flattened, anterodistal projection. Femur with a moderate anterobasal projection and a dorsobasal mound; reticulation becoming strongly raised anteriorly, producing a tooth-like appearance in dorsal view. Patella with 1 large and 1 small lyrifissure dorsally near base, and 1 small dorsal lyrifissure apically. Chela with reticulate cuticle extending onto base of fixed finger, but not raised distally. Fixed finger with 4 lyrifissures: 1 antiaxial and 1 paraxial at base; 1 antiaxial behind trichobothria *eb* and *esb*; 1 dorsal, just in front of trichobothrium *it*. Movable finger with 2 ventral lyrifissures, one near middle and the other just in front of trichobothrium *t*. Fixed finger with apodens plus 15–16 marginal, 7–9 paraxioventral, 5 paraxial and 1 tuberculate basal-paraxial tooth (total 29–31). Tuberculate tooth of fixed finger with an ordinary seta at base (Fig. 26), that of movable finger with a seta nearby, but not on tubercle (Fig. 28). Tuberculate tooth of movable finger in a more distal position relative to that of fixed finger (Fig. 29). Fixed finger with a minute dorsal seta near apex (Fig. 25), movable finger with a similar seta ventrally near apex (Figs 27, 33), these perhaps representing the *lamina defensor* of other pseudoscorpions. Movable finger weakly S-shaped in ventral view; with 1 apical, 18–20 marginal (almost aligned), 5–8 paraxial and 1 basal tuberculate tooth (total 27–28). Sensillum af_1 in dorsal position, slightly closer to *dx* than to *it*. Movable finger with coupled sensilla (*pc*) above trichobothrium *b* (Figs 30–31); sensillum am_1 slightly behind tip, in dorso-antiaxial position; a small pore or sensillum is also present ventrally, immediately in front of trichobothrium *t* (Fig. 33). Fixed chelal finger with 13 chemosensory setae in antiaxial row. Movable finger with 13–14 bacilliform setae (20–24 µm long) in pit (Figs 30, 34); walls of pit finely granular (probably due to a thin lining of exocuticle). Trichobothria typical; *sb* and *t* of movable finger situated on ventral face, *sb* level with posterior rim of pit containing chemosensory setae. Hair of trichobothrium x_2 thicker than that of x_1 and abruptly curved at tip; tip of x_1 blunt (very slightly bulbous).

Legs with reticulate-scaly ornamentation; very few gland pores present. Setae generally short and strongly curved, but those of ventral faces longer. Femur of leg I with a large, oblique, paraxio-basal lyrifissure. Patella of legs I–IV with a dorsal lyrifissure orientated parallel to long axis and set in a depression. Trochanters of legs III and IV with a small posterodorsal spur just beyond pedicel; trochanters inflated, with maximum diameter oblique to dorso-ventral axis. Tarsus of leg I (but not other legs) with slight torsion distally, dorsal face orientated slightly anteriorly. Subterminal setae not obviously differentiated from other setae. Arolia simple, broad, distinctly shorter than claws; claws simple, not broadened distally (Figs 42–43).

Measurements (in mm, standard ratios in parentheses). Body 1.8×1.2–1.3. Carapace 0.546–0.619×0.433–0.447

(1.3–1.4). Chelicera 0.202–0.247×0.128–0.154 (1.6), palm 0.132–0.175 (1.1), movable finger 0.095–0.114 (0.65×palm), spinneret 0.018–0.023. Palp femur 0.493–0.522×0.264–0.281 (1.8–2.1), patella 0.396–0.414×0.155–0.172 (2.4–2.6), chela 0.555–0.571×0.126–0.132 (4.3–4.5), palm 0.142–0.148 (1.1–1.2), movable finger 0.401–0.413 (2.5–2.9). Chelicera 0.247×0.154 (1.6), palm 0.175 (1.1), movable finger 0.114 (0.65). Leg I (N=3) trochanter 0.150×0.110 (1.4), femur 0.211–0.223×0.075–0.81 (2.7–2.8), patella 0.178–0.194×0.088–0.092 (2.0–2.1), tibia 0.165–0.190×0.063–0.068 (2.6–3.0), tarsus 0.256–0.263×0.053–0.054 (4.8–4.9). Leg III (N=1) trochanter 0.196×0.112 (1.7), femur 0.212×0.088 (2.4), patella 0.247×0.103 (2.4), tibia 0.220×0.070 (3.2), tarsus 0.326×0.056 (5.9). Leg IV (N=3) trochanter 0.251–0.264×0.126–0.135 (1.9–2.0), femur 0.161–0.188×0.075–0.088 (2.0–2.2), patella 0.256–0.275×0.094–0.108 (2.4–2.7), tibia 0.337–0.361×0.059–0.066 (5.1–6.0), tarsus 0.325–0.386×0.048–0.055 (6.8–7.2).

Description of tritonymph. Generally similar to adult and almost of same size, but less sclerotized and thus lighter in colour. Carapace with untanned dorsolateral lines running along its length, giving the impression that the carapace is divided into three plates (one dorsal and two lateral); posterior depression less marked than in adult. Anterolateral plates less sclerotized than in adult and hence less evident. Chelicera (Fig. 44) with 5 large and 5 small setae on palm; galeal seta 0.78 from base; spinneret (Fig. 45) distinctly longer than in male, tubular and gently curved ventrally, base flared in dorsoventral view, but not in lateral view; rallum with two blades (anterior 23 µm, posterior 22 µm long), as in adult; serrula exterior with 19 blades plus anteriorly-directed process, distal 3 blades; serrula interior obscured. Fixed finger of chela with apodens plus 18 marginal teeth, 6 paraxial teeth and a basal tuberculate tooth (total 26), movable finger with apodens plus 17 teeth in slightly irregular marginal row, 7 paraxial teeth and basal tuberculate tooth (total 26). Movable finger with 13 bacilliform chemosensory setae in pit (Fig. 47), surface of pit granular on left chela, but not on right chela. Trichobothria as in adult, except *isb* and *sb* absent (Fig. 46).

Measurements of paratype tritonymph (in mm, standard ratios in parentheses). Body 1.80×1.1 (1.5). Carapace 0.533×0.416 (1.3). Chelicera 0.182×0.119 (1.5), palm 0.136 (1.15), movable finger 0.087 (0.64). Palp femur 0.459×0.241 (1.9), patella 0.355×0.149 (2.4), chela 0.539×0.126 (4.3), palm 0.138 (1.1), movable finger 0.378 (2.8). Leg I femur 0.192×0.070 (2.8), patella 0.167×0.081 (2.1), tibia 0.159×0.059 (2.7), tarsus 0.234×0.051 (4.6). Leg IV trochanter 0.232×0.121 (1.9), femur 0.161×0.075 (2.1), patella 0.242×0.095 (2.5), tibia 0.304×0.095 (3.2), tarsus 0.344×0.055 (6.3).

Measurements of smaller (non-type) tritonymph (in mm, standard ratios in parentheses). Body 1.48×0.96 (1.5). Carapace 0.463×0.370 (1.3). Palp femur 0.394×0.203 (1.9), patella 0.310×0.136 (2.3), chela 0.501×0.110 (4.6), palm 0.122 (1.1), movable finger 0.0.34 (2.8).

Remarks. The cavity in which the types were found was accessible by a vertical opening that was just sufficient for a person to slide through. The feaellids were found on a small, exposed surface (no more than 1 m^2) on a wall facing away from the entrance. This surface differed from the rest of the wall in having a pocked appearance and a dark, rust-like colour (Fig. 1), presumably due to a metal oxide. It was humid, but not wet. The rest of the walls of the cavity, most of which were wet, were not found to have feaellids on them. The pseudoscorpions were near the entrance and would have been in permanent obscurity, but not total darkness. The floor of the cavity consisted of compact clay-soil, unsuitable for pseudoscorpions. The collecting details accompanying the non-type tritonymph from leaf litter do not specify whether it came from a cavity or a truly epigean habitat. However, given the large number of litter samples made by Le Cong Man, L. Deharveng and A. Bedos at Nui Bai Voi, it seems likely that this species has a preference for cavities or caves.

The identification of the non-type tritonymph is discussed below. The collection details for this specimen suggest that it was found in an epigean habitat, although the possibility that it came from one of the many cavities around the Grotte-hôpital cannot be excluded. Sifting of litter (by the author) and Berlese extractions of litter outside the cavity (by Louis Deharveng and Anne Bedos) did not produced any other feaellids.

***Cybella bedosae* n. sp.**

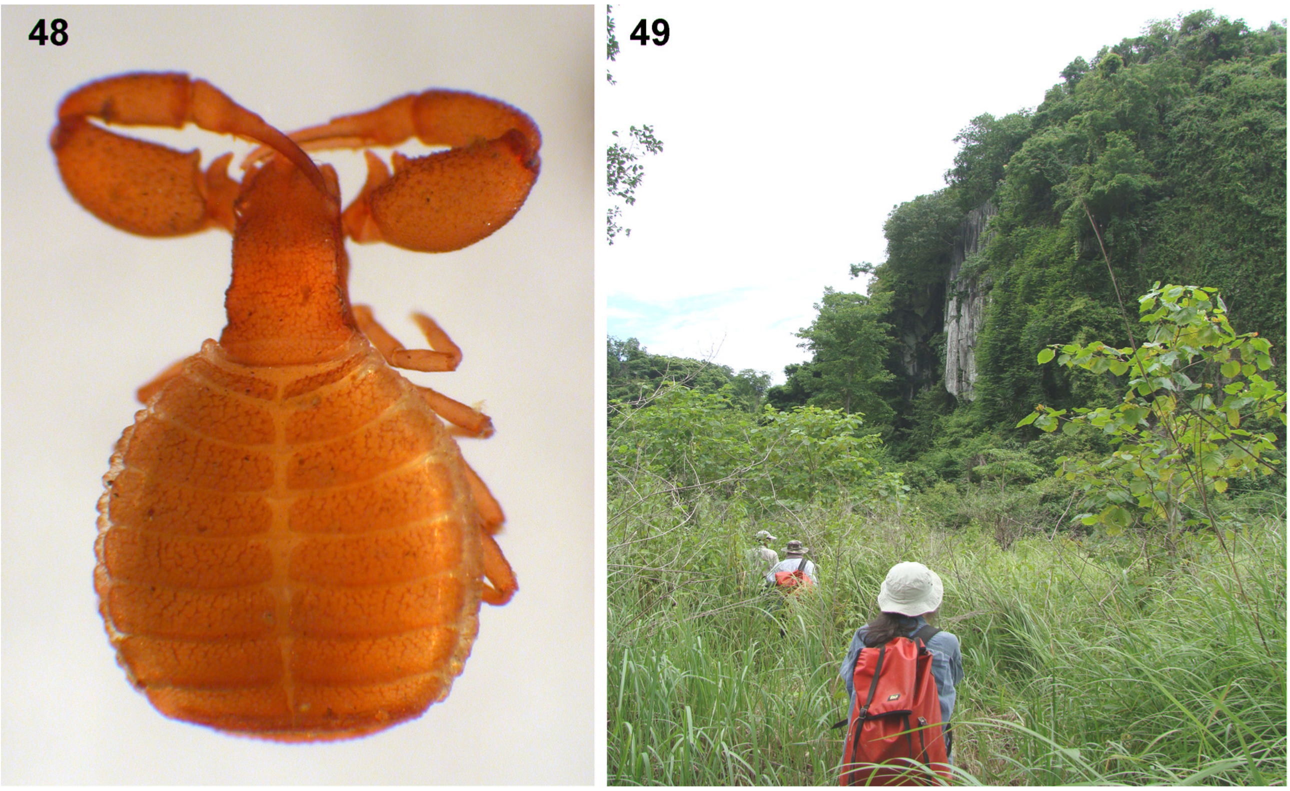
Figs 48, 50–87

Diagnosis. Very similar to *C. deharvengi* **n. sp.**, but larger (e.g. male palp femur length 0.573 versus 0.493–0.522 mm), with chela less robust (4.8 times longer than broad, versus 4.3–4.5), most segments of legs more attenuate (e.g. femur of leg IV 2.8 times longer than broad, versus 2.0–2.1), trichobothrium *sb* slightly proximad of pit (versus below pit), trichobothria *eb* and *esb* separated by more than one bothridial diameter (versus half a diameter), anterior genital sternite with 12 setae (versus 8), and lateral diverticulum of male atrial plate of longer.

Etymology. This species is named after Anne Bedos (MNHN), who helped collect the types and who has contributed much to our knowledge of the soil and cave faunas of SE Asia.

Type material. Holotype: ♂, Cambodia, Kampuchea, Kampot, Phnom Laang, Kien Krol, 1042′14.4″N 10420′41.1″E, 45 m a.s.l., Berlese extraction of soil from low passage (“boyau”) on left side of cave, 20 November 2005, leg. L. Deharveng & A. Bedos (MNHN Ps116-01; collectors’ number KAM05-21). Paratype protonymph (MNHN Ps116-02), collected with holotype.

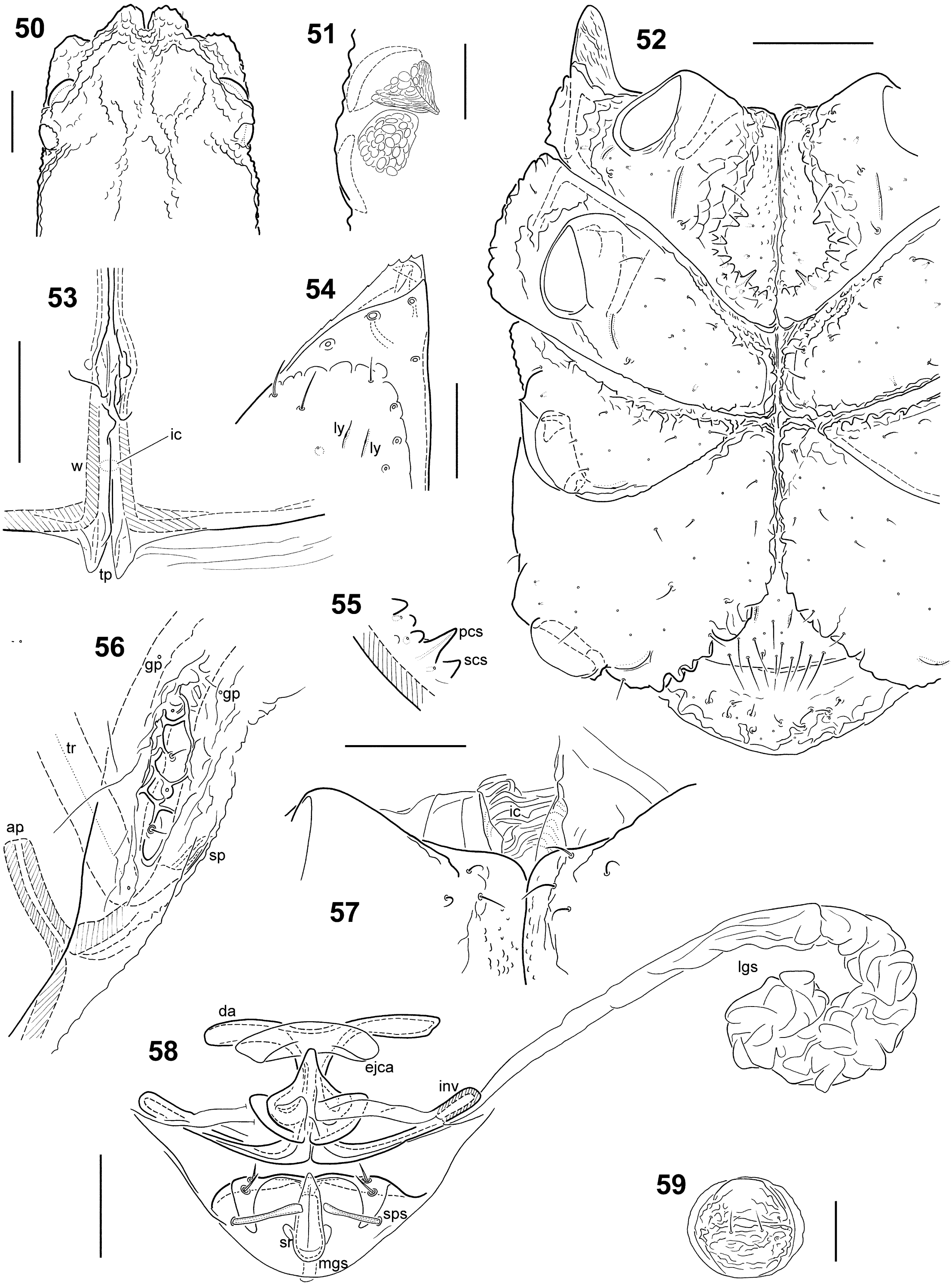
DNA sequences. Partial sequences, obtained by non-destructive extraction from the palp of the paratype protonymph (voucher no. MNHN-JAD72), were deposited in GenBank for 18S RNA (accession no. JN018313.1) and 28S RNA (accession no. JN018410.1) by Arabi *et al.* (2012).



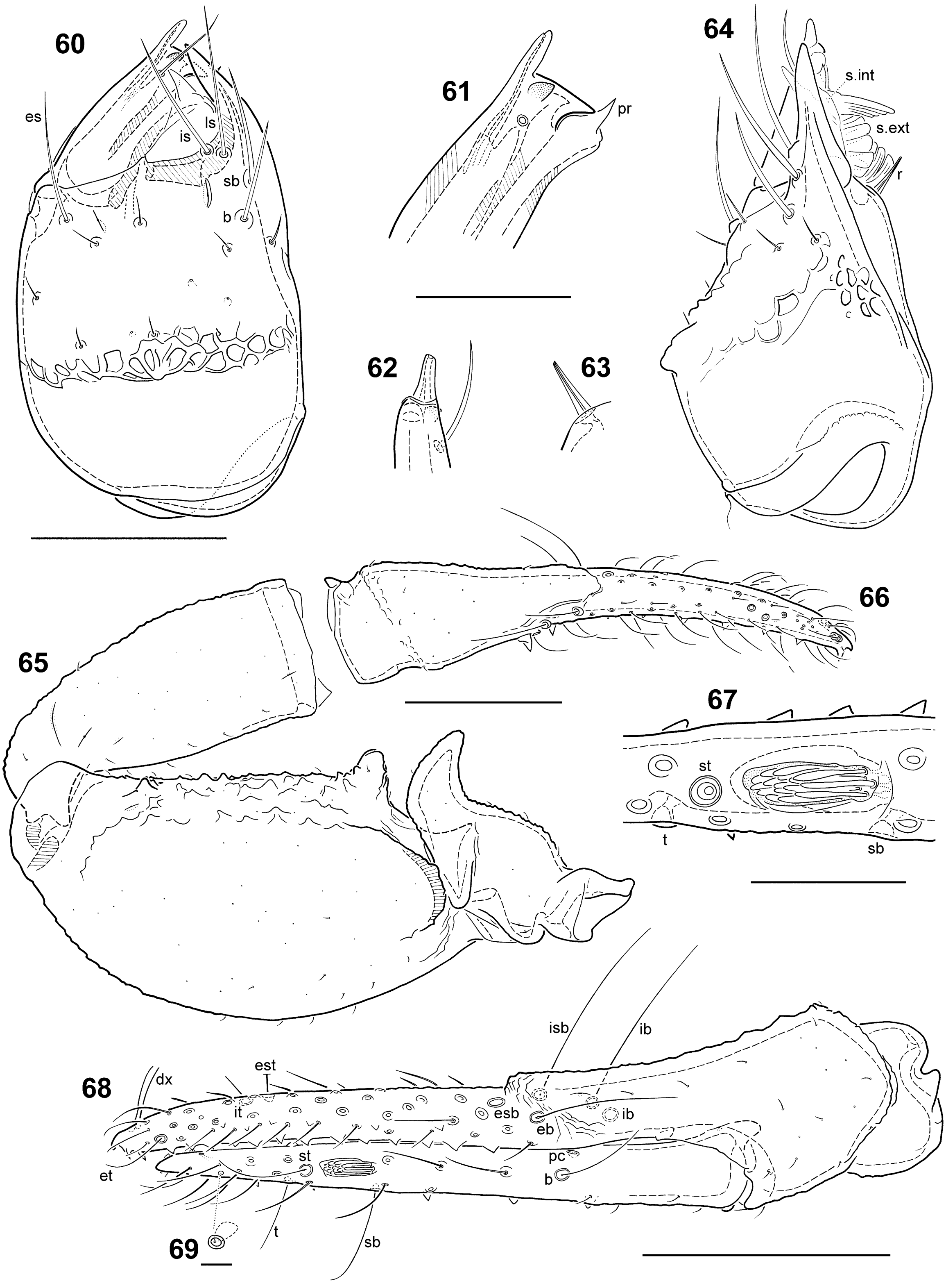
FIGURES 48–49. *Cybella bedosae* **n. sp.** 48, habitus of male, dorsal view; 49, type locality, Kien Krol, Cambodia (photograph taken 23 June 2008); cave (not visible) is at base of hill.

Description of male (limited to characters showing differences from *C. deharvengi* **n. sp.**). Tergal and sternal chaetotaxy not determined due to accumulation of exocuticle and debris, but where visible numbers of setae similar to those seen in *C. deharvengi* **n. sp.** Coxa I with 1 primary and 10–12 secondary spines around pit (Figs 52, 55). Coxal setae (Fig. 52): P 3 on manducatory process + 32 (total 35), I 8, II 9 (1 lateral), III 7 (1 lateral), 10 (1 lateral). Anterior genital sternite (Fig. 52) with 12 setae, posterior genital sternite (Fig. 52) with 14 setae (2+10+2). Male genitalia (Fig. 58) very similar to those of *C. deharvengi* **n. sp.**, but comparison of dorsal apodeme, lateral rods and atrial plate hampered by differences in orientation in the specimens examined (this depending on the degree to which the genital plates are open or closed); lateral sacs longer and thinner than those of *C. deharvengi* **n. sp.**; lateral pockets of atrial plate slightly longer than those of *C. deharvengi* **n. sp.**; posterior plate with 1 pair of modified basal setae, which seems to be more rounded at the tip than those of *C. deharvengi* **n. sp.**, and 2 small, simple setae on each side.

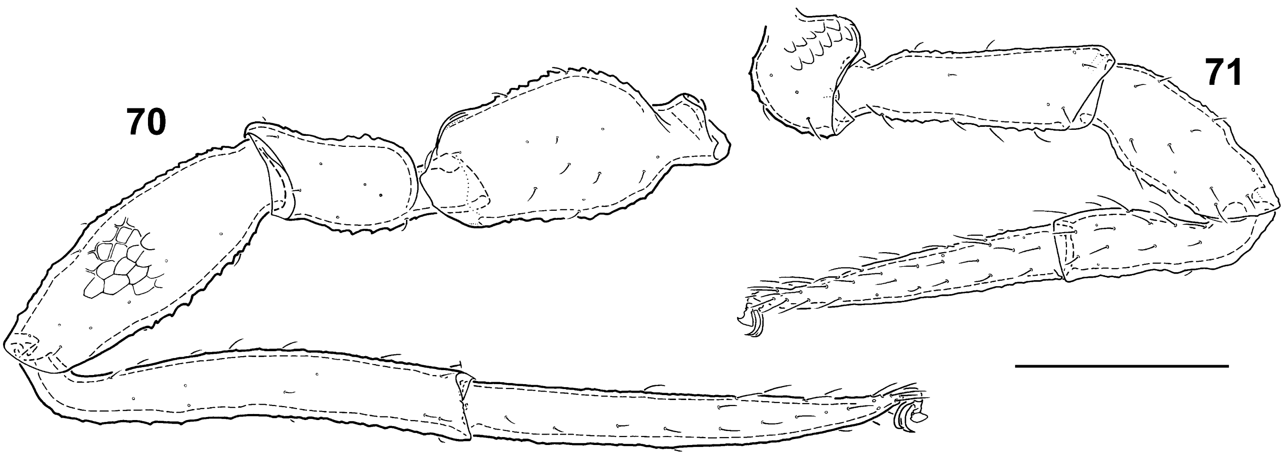
Chelicera (Figs 60–64) with 6–7 small setae on palm, in addition to the 5 large setae. Galeal seta (*gs*) 0.85 from base, extending well beyond tip of spinneret (by nearly half length of hair). Spinneret (Figs 61–62) slightly thicker



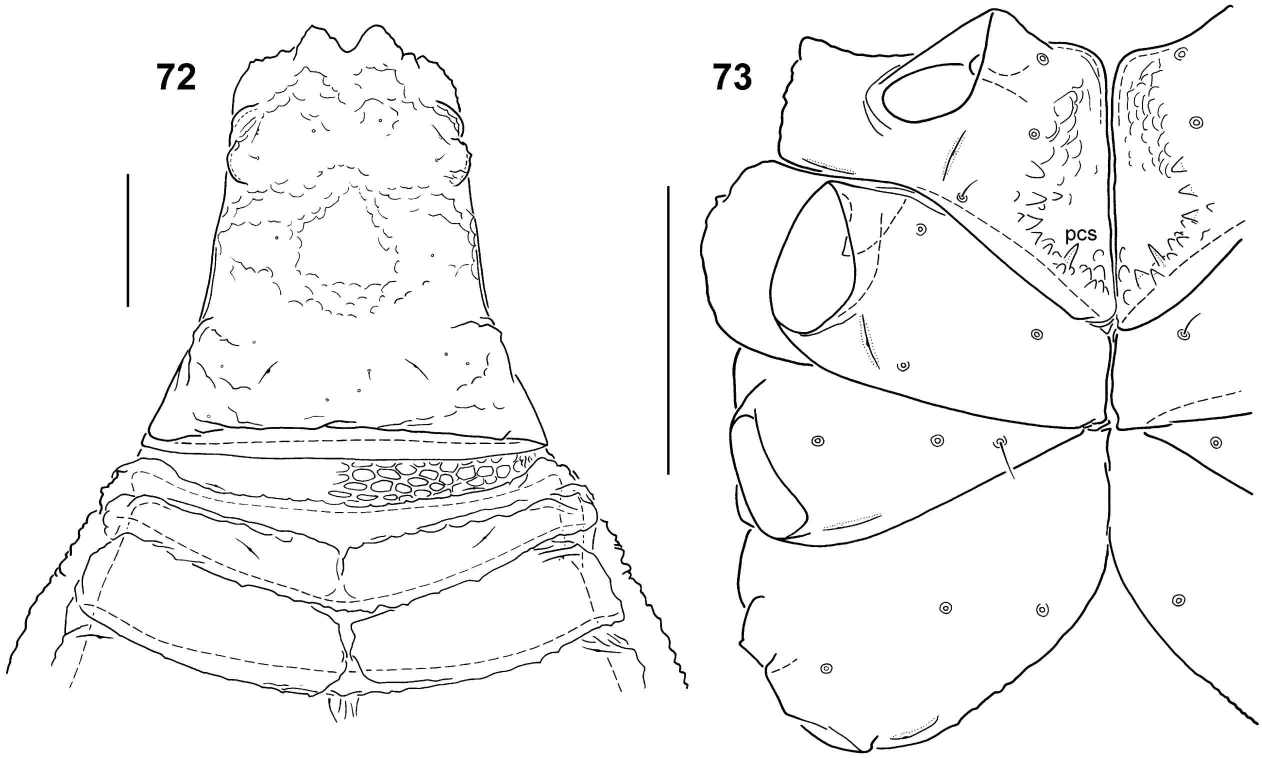
FIGURES 50–59. *Cybella bedosae* **n. sp.**, male. 50, anterior part of carapace, dorsal view (setae omitted); 51, tapeta of right eyes, ventral (internal) view; 52, leg coxae and median parts of sternites II–III, ventral view; 53, intercoxal canal between posterior parts of palp coxae (membrane torn distally); 54, manducatory process of right palp coxa, ventral view (lyrifissure abnormally doubled); 55, primary spine and adjacent secondary spines of right coxa I; 56, left spiracle and adjacent apodeme of segment III, ventral view; 57, membranous part of intercoxal canal between coxa I and palp coxae (latter removed), ventral view; 58, genitalia, ventral view (right *lgs* omitted; part of anterior wall of genital atrium removed on left of drawing); 59, tergite (upper) and sternite (lower) of segment XII, ventral view. Abbreviations: *ap*, apodeme; *da*, dorsal apodeme; *ejca*, ejaculatory canal atrium; *gp*, gland pore; *ic*, intercoxal canal; *inv*, invagination at side of atrial plate; *lgs*, lateral genital sac; *ly*, lyrifissure; *mgs*, median genital sac; *pcs*, primary coxal spine; *scs*, secondary coxal spine; *sp*, spiracle; *sps*, spatulate seta; *sr*, sclerotized ring; *tp*, posteromedian tecta of palp coxae; *tr*, trachea; *w*, wall of coxa in cross-section. Scale lines 0.1 mm (Figs 50, 52), 0.05 (Figs 51, 53–59).



FIGURES 60–69. *Cybella bedosae* **n. sp.**, male. 60, left chelicera, antiaxial view; 61, distal end of movable finger of left chelicera, antiaxial view; 62, spinneret of left chelicera, ventral view; 63, rallum of left chelicera, antiaxial view; 64, left chelicera, dorsal view; 65, left palp, minus chela, dorsal view; 66, left chela, dorsal view; 67, chemosensory setae of movable finger of left chela, antiaxial view; 68, left chela, antiaxial view; 69, distal sensillum of movable finger Abbreviations: *dx*, duplex trichobothria, *pc*, coupled sensilla; *pr*, distal process of serrula exterior; *s.ext*, serrula exterior; *s.int*, serrula interior; *r*, rallum. Other abbreviations (*eb*, *esb*, *est*, *et*, *ib*, *isb*, *ist*, *it*, *b*, *sb*, *st*, *t*) are standard designations of trichobothria. Scale lines 0.2 mm (Figs 65–66), 0.1 mm (Figs 60, 64, 68), 0.05 mm (Figs 61–63, 67), 0.01 (Fig. 69) (figures 61–63 share same scale line).



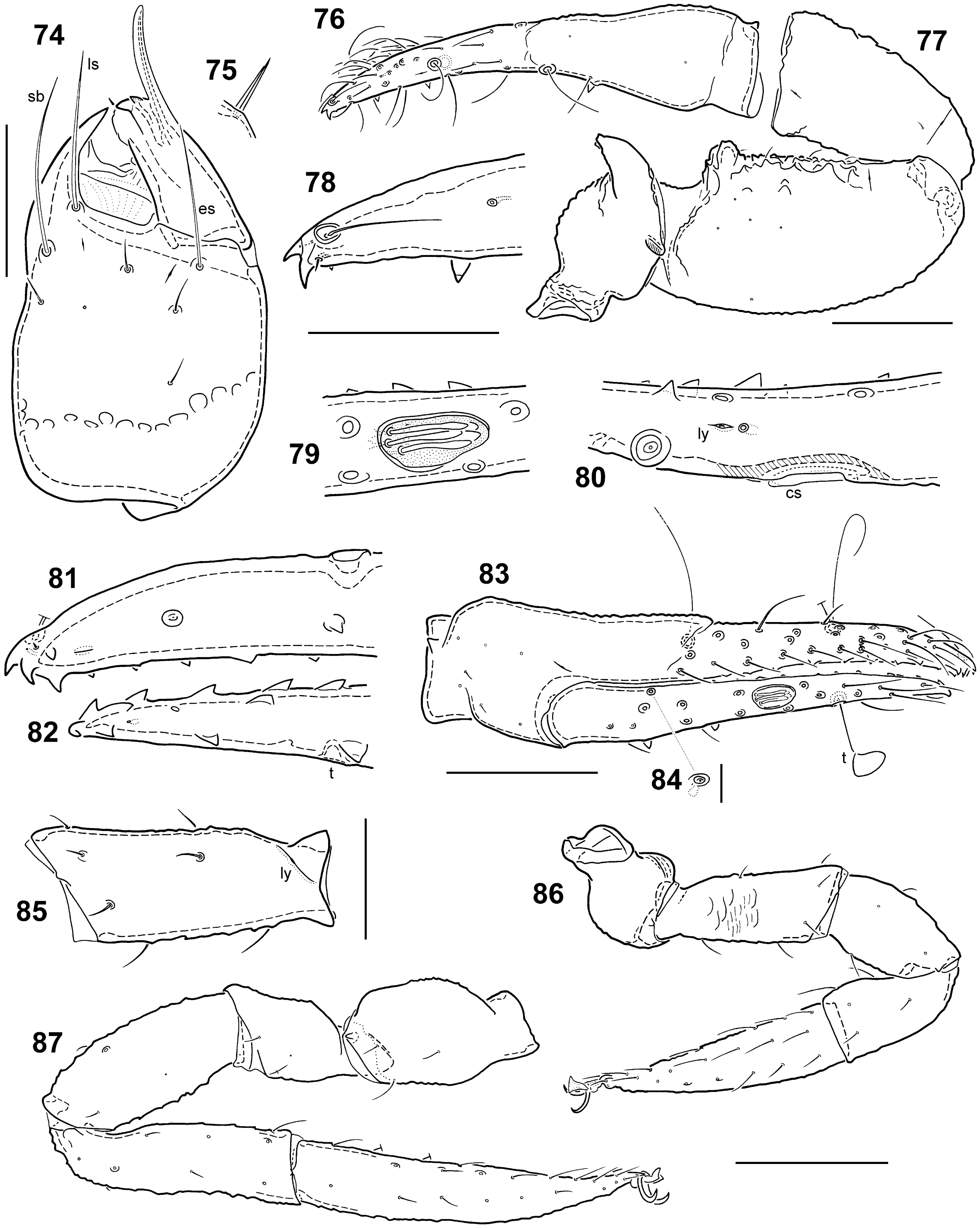
FIGURES 70–71. *Cybella bedosae* **n. sp.**, male, legs. 70, right leg IV, antiaxial view; 71, right leg I, antiaxial view. Scale line 0.2 mm.



FIGURES 72–73. *Cybella bedosae* **n. sp.**, protonymph. 72, carapace and anterior segments (I–III) of opisthosoma, dorsal view, reticulation of tergite I only partially drawn; 73, leg coxae, ventral view. Abbreviation: *pcs*, primary coxal spine. Scale lines 0.1 mm.

than in *C. deharvengi* **n. sp.**, but still tubular (i.e. not blade-shaped), length 16 µm. Serrula exterior with 19–20 blades, plus small distally-directed apical process. Serrula interior with 17 internal ducts; apically with a distally-directed process, followed by two rows of three, low, rounded mounds; basal blades forming a velum. Rallum with 1 (right chelicera) or 2 (left chelicera; Fig. 63) blades, length 23 µm.

Palp as illustrated (Figs 65–69). Fixed chelal finger with 12 chemosensory setae in antiaxial row. Movable finger with 14–16 long (22–24 µm), spatulate, chemosensory setae in pit (Fig. 67). Trichobothria (Figs 66, 68) *eb* and *esb* separated by 1.2–1.8 bothridial diameters (absolute distance 17–22 µm); *sb* slightly proximad of posterior edge of pit. Fixed finger with 30 teeth: apodens plus 22 marginal, 6 paraxial and basal tuberculate tooth. Movable finger with 28 teeth: apodens plus 21 marginal, 7 paraxial and basal tuberculate tooth.



FIGURES 74–87. *Cybella bedosae* **n. sp.**, protonymph, appendages. 74, right chelicera, antiaxial view; 75, rallum of right chelicera, paraxial view; 76, chela of right palp, dorsal view; 77, right palp, minus chela, dorsal view; 78, tip of fixed finger, dorsal view, setae omitted; 79, chemosensory setae of movable finger of right chela, ventral view; 80, chemosensory setae of movable finger of right chela, antiaxial view; 81, tip of fixed finger of right chela, paraxial view, setae omitted; 82, tip of movable finger of right chela, paraxial view, setae omitted; 83, right chela, antiaxial view; 84, proximal sensillum (p_1) of movable chelal finger, antiaxial view; 85, femur of right leg I, paraxial view, showing paraxial lyrifissure; 86, right leg I, antiaxial view (scaly ornamentation only partly indicated on femur, omitted on other segments); 87, right leg IV, antiaxial view. Abbreviations: *cs*, chemosensory seta; *ly*, lyrifissure. Other abbreviations are notations of cheliceral setae and chelal trichobothria. Scale lines 0.1 mm (Figs 76–77, 83, 86–87), 0.05 mm (Figs 74–75, 78–82, 85; Figs 75 and 78–82 share same scale line), 0.01 mm (Fig. 84).

Legs as illustrated (Figs 70–71).

Measurements (in mm, standard ratios in parentheses). Body (contracted) 1.82×1.25 (1.5). Carapace 0.659×0.47 (1.4). Chelicera 0.234×0.141 (1.7), palm 0.159 (1.1), movable finger 0.094. Palp femur 0.573×0.298 (1.8), patella 0.453×0.178 (2.5), chela 0.665×0.138 (4.8), palm 0.162 (1.2), movable finger 0.474 (2.9). Leg I femur 0.256×0.079 (3.3), patella 0.214×0.090 (2.4), tibia 0.212×0.062 (3.4), tarsus 0.304×0.051 (5.9). Leg IV trochanter 0.289×0.140 (2.1), femur 0.246×0.087 (2.8), patella 0.298×0.110 (2.7), tibia 0.426×0.063 (6.8), tarsus 0.418×0.052 (8.1).

Description of protonymph. Sclerotized parts pale straw-yellow, except tips of cheliceral fingers and teeth of chela, which are reddish-brown. Carapace (Fig. 72) distinctly broadened posteriorly; less elongate than in adult; anteromedian projections small, anterolateral corners of carapace more rounded than in adult; two pairs of lyrifissures; two pairs of eyes with reflective tapeta, anterior pair sessile, posterior pair weakly raised, both pairs less prominent than in adult. Tergite I (Fig. 72) with same general form as in adult, but presence or absence of separate lateral plate could not be determined due to weak sclerotization; tergites II–VIII divided (II and VIII weakly so); setae difficult to count, but most half-tergites with about 6 setae; denticulation present on tergites VIII–IX. Pleural membranes with two folds, as in adult, lyrifissures (orientated dorsoventrally) on dorsal fold; only 1 gland pore seen (anteriorly on dorsal fold), but others might be present; no setae observed; plates absent.

Palp coxa not as elongate as in adult, median maxillary lyrifissure present, with same form and position as that of adult; no lyrifissure distad of foramen. Coxa I with 1 primary and 9–10 secondary spines flanking pit (Fig. 73); no pores in pit. Coxae III reduced in size, reaching closer to midline than in adult, overlapped by coxae II. Palp coxa with 12 setae (including 3 on manducatory process), leg coxae each with 3 setae. Sternites IV–X divided, setae 0 : 2 : 2+2 : 3+3 : 3+3 : 4+4 : 4+4 : 4+4 : 4+4 : 4 (2 flanking anal tubercle) : 2 (slightly closer together than those of tergite XI); denticulate granulation on IX–XI.

Chelicera (Figs 74–75) with distinction between smooth basal part and distal reticulate part of palm less well marked than in adult; three large (probably *ls*, *sb* and *es*) and four small setae on palm; movable finger without seta; rallum of 2 blades (Fig. 75), as in adult; spinneret (Fig. 74) simple, much longer (30 µm) than in adult, recurved apically. Serrula exterior with 10 blades plus apical process. Serrula interior with 10 ducts.

Palp (Figs 76–84) similar to that of adult, trochanter with well developed horn, femur with moderate anterobasal projection. Chela with three trichobothria on fixed finger and one on movable finger. Trichobothrium x_1 inserted dorsally in shallow depression, hair straight and directed backwards, length 44 µm; trichobothrium *t* distinctly crooked (Fig. 83); hairs of other trichobothria (*ist* and *it*) lost or broken. Fixed finger with 21 teeth: apodens plus 14 marginal (irregular distally), 5 paraxial and basal tuberculate tooth. Movable finger with 21 teeth: apodens plus 15 marginal, 4 paraxial and basal tuberculate tooth. Tuberculate tooth of fixed finger bearing seta at base. Fixed finger with 3 lyrifissures: one on each side at base and 1 dorsal, just in front of trichobothrium *it*. Movable finger with 1 ventral lyrifissure, situated between *t* and pit; a single spot sensillum situated immediately behind lyrifissure (Fig. 80). Movable finger with 5 clavate chemosensory setae in a pit that is shallower than that of adult (Figs 79–80). Proximal sensillum p_1 (Fig. 84) situated about a third from base of movable finger (Fig. 83); p_2 absent.

Legs (Figs 85–87) similar to those of adult (apart from usual differences), except that the trochanter of leg IV is relatively smaller and all femora lack the dorsal lyrifissure and its depression; femur of leg IV with large dorso-paraxial lyrifissure at base (Fig. 85) (as in adult).

Measurements (in mm, standard ratios in parentheses). Body 0.85×0.54 (1.6). Carapace 0.309×0.315 (0.98). Chelicera 0.129×0.082 (1.6), palm 0.092 (1.1), movable finger 0.062 (0.7×palm), spinneret 0.030 (0.5×movable finger). Palp femur 0.249×0.168 (1.5), patella 0.197×0.101 (1.9), chela 0.364×0.088 (4.1), palm 0.090 (1.0), movable finger 0.278 (3.1). Leg I trochanter 0.095×0.064 (1.5), femur 0.118×0.045 (2.6), patella 0.093×0.052 (1.8), tibia 0.093×0.048 (2.0), tarsus 0.173×0.041 (4.2). Leg IV trochanter 0.128×0.069 (1.8), femur 0.095×0.051 (1.9), patella 0.136×0.057 (2.4), tibia 0.166×0.045 (3.7), tarsus 0.230×0.042 (4.5).

Remarks. An attempt by Anne Bedos and the author to collect more material of *C. bedosae* **n. sp.** at the type locality in June 2008 was thwarted by dense brush outside the cave, which had grown since the previous visit in 2005, due to the cessation of grazing activity at the site. Berlese extractions of litter and soil samples taken just outside the cave in 2005 and nearby in 2008 did not produce any feaellids.

Although *C. bedosae* **n. sp.** and *C. deharvengi* **n. sp.** are very similar and known from only a few specimens, they appear to be isolated geographically, occurring in disjunct limestone hills about 60 km apart. Feaellidae appear to have very poor powers of dispersal and show high levels of endemism, so it seems reasonable to infer that two closely related species are involved, rather than a single variable or clinal species.

Notes on the morphology and phylogenetic position of the Cretaceous genus *Protofeaella*

Given its geographical proximity and the fact that it was considered an "archetype" of Feaellidae by Henderickx & Boone (2016), it is of interest to compare the Cretaceous genus *Protofeaella* with *Cybella* **n. gen.** Because the original description of *P. peetersae* Henderickx, 2016 is rather incomplete, it is supplemented here by the examination of a further specimen in Burmese amber, received from J. Wunderlich. Although this specimen is in rather mediocre condition, it does allow some additional information to be given, notably concerning the arrangement of the trichobothria and the position of the chemosensory setae of the movable chelal finger.

Protofeaella Henderickx, 2016

Protofeaella Henderickx *in* Henderickx & Boone 2016: 8.

Revised diagnosis. Extinct, Cretaceous genus of Feaellidae Pleural plates absent. Carapace with 4 anterior lobes, only median lobes projecting forwards, lateral lobes extending laterally. Coxae III meeting in mid-line. Trochanteral horn well developed, with broad base. Palp femur with moderate anterobasal projection. Chelal palm very short. Chelal fingers long and curved in dorsal view, with paraxial teeth, but without tuberculate basal tooth. Trichobothria of movable chelal finger with *sb*, *st* and *t* distad of middle, *sb* and *st* situated ventrally, *t* and *st* at same level (*t* below *st*). Chemosensory setae of movable finger situated on antiaxial face, apparently grouped in a depression, just behind trichobothrium *st*.

Type species. *Protofeaella peetersae* Henderickx, 2016, by monotypy. Henderickx (*in* Henderickx & Boone 2016) designated "*Protofeaella*" as the "type species" and "*Protofeaella peetersae*" as the "type specimen" of the genus. Because neither of these incorrect designations is in accordance with the *International Code of Zoological Nomenclature* (Articles 67.5, 68.2), I consider *P. peetersae* to have been fixed as the type species by monotypy, rather than by original designation.

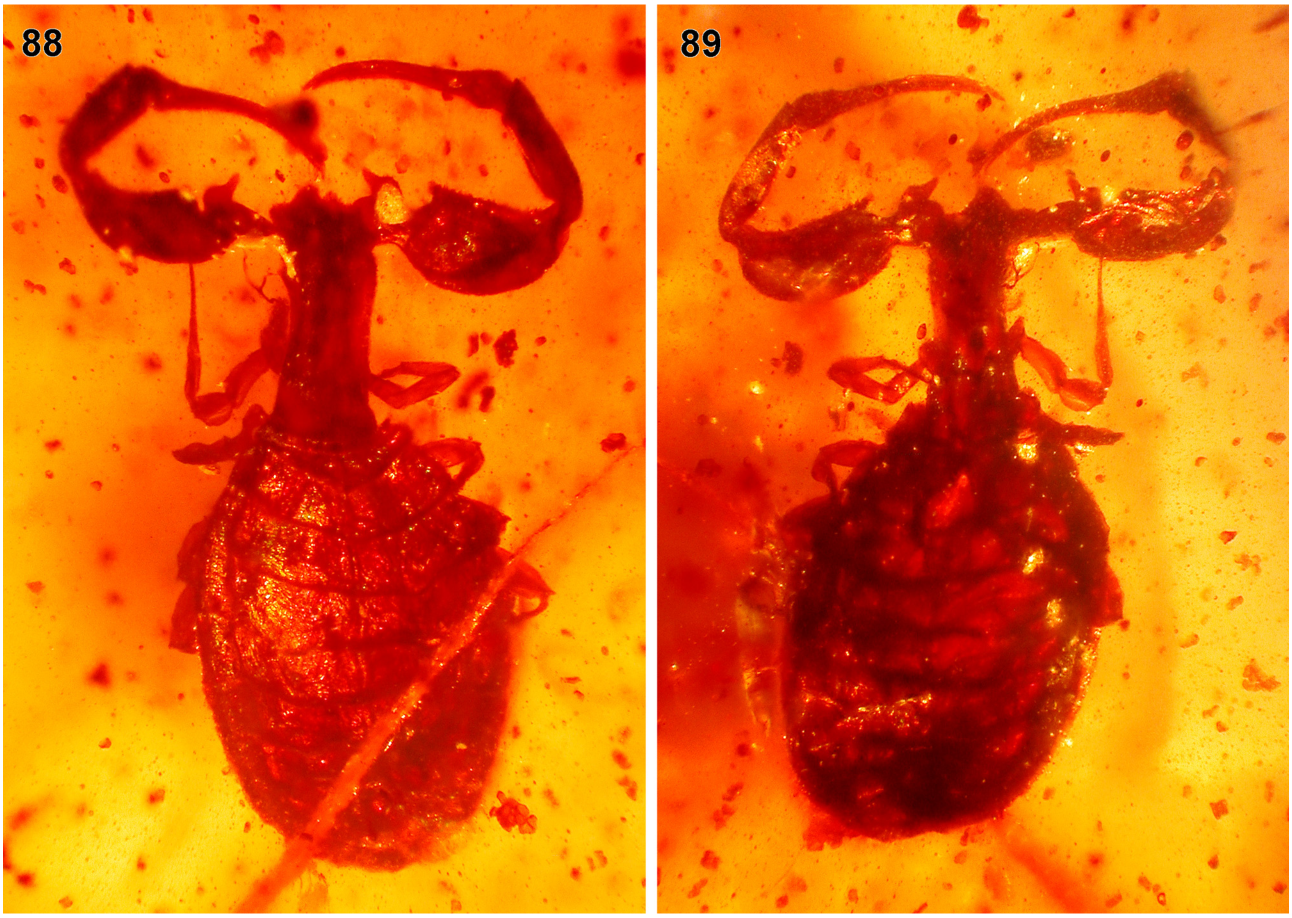
Distribution. Cretaceous of Myanmar.

Remarks. *Protofeaella* resembles *Cybella* in lacking pleural plates, in having the chemosensory setae of the movable chelal finger in an antiaxial position and in having trichobothrium *st* much closer to *t* than to *b*. As discussed below, the lack of pleural plates is symplesiomorphic within Feaellidae. The position of the chemosensory setae is unknown for Pseudogarypidae (they are not clearly differentiated from other setae), but in other pseudoscorpions they are usually placed antiaxially, which can therefore be considered the plesiomorphic state. *Protofeaella* can be separated from Cybellinae by having trichobothrium *st* level with *t*, the trochanteral horn with a broad base and the coxae of leg III meeting in the midline, the latter state being clearly plesiomorphic. It differs from Feaellinae in lacking pleural plates, in having the chemosensory setae situated antiaxially on the movable chelal finger and the position of trichobothrium *st* on the movable chelal finger. The character states shared with Cybellinae on the one hand, or with Feaellinae on the other, are either symplesiomorphic or of uncertain polarity. At the same time, *Protofeaella* shows two plesiomorphies that appear to place it outside the crown-group of Feaellidae: the absence of a tuberculate tooth at the base of each chelal finger and the relatively long chela of the palp (distinctly longer than femur). Based the limited evidence available at present, the most reasonable interpretation is that *Protofeaella* belongs to the stem-group of Feaellidae, though it is possible that it might prove to be closer to Cybellinae than to Feaellinae when polarity of trichobothrial positions and the arrangement of chemosensory setae become better understood.

Protofeaella sp.

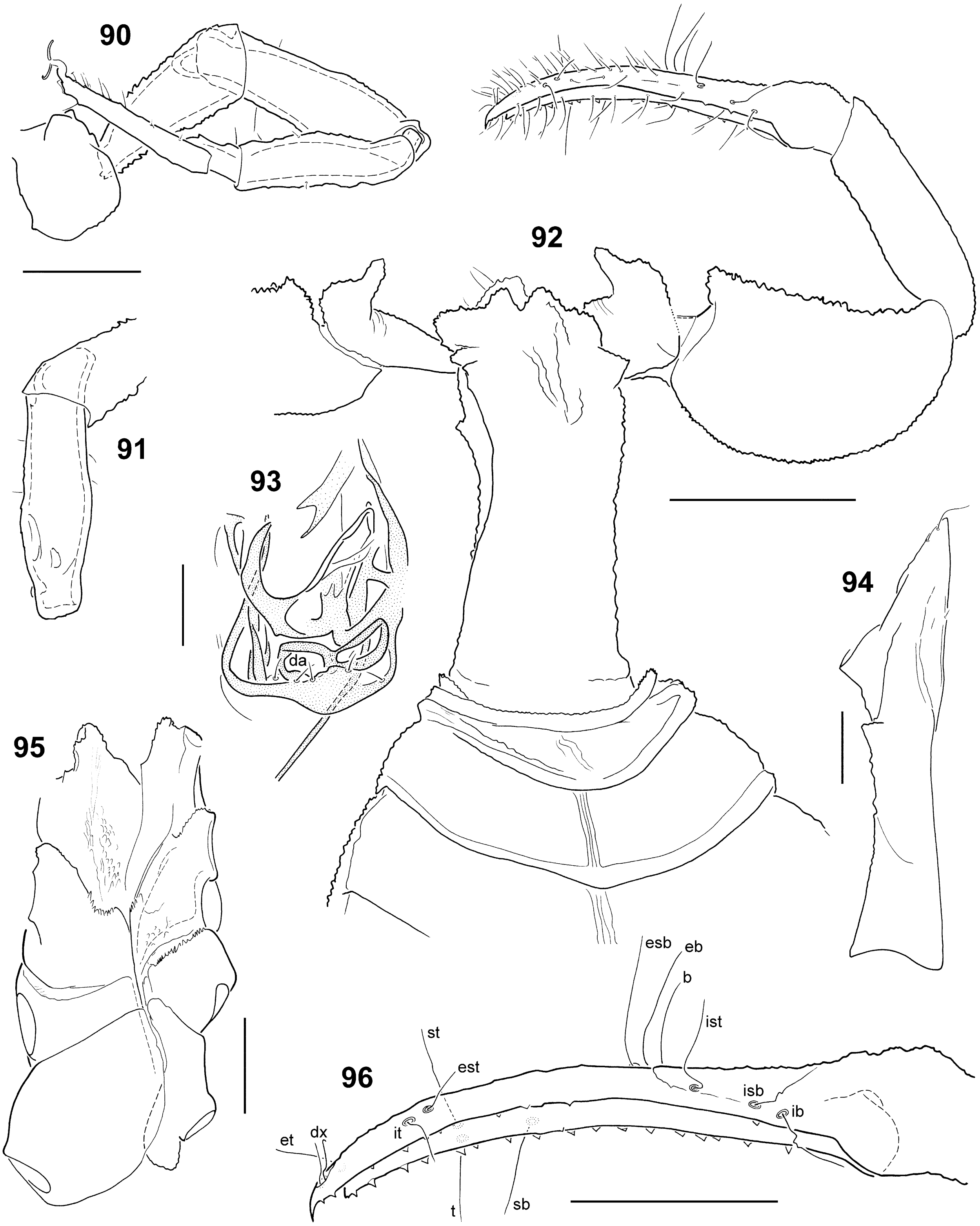
Figs 88–96

Material examined. Male in small piece (9.5×8.5×3 mm after preparation) of Burmese amber. Amber deep yellow, clouded by fine vegetal fragments; no other inclusions. Currently in J. Wunderlich collection (F2571/BU/CJW). Specimen intact, but strongly distorted (differential stretching or compression has occurred, giving parts unnatural proportions). The cuticle is very dark (perhaps as a result of heating) and reflects very little light, which presents an additional obstacle to observation. The amber piece was received in the form of a cabuchon (original size about 15×9×5 mm) that had been cut in two.



FIGURES 88–89. *Protofeaella* sp., male in Burmese amber. 88, habitus, dorsal view; 89, habitus, ventral view.

Description. Feaellidae of typical facies; cuticle of body and palps (except fingers) with honeycomb-like reticulation; legs scaly; setae minute, except on palp fingers, chelicera and manducatory process. Carapace (Fig. 92) distorted, strongly stretched longitudinally. Eyes not observed, but ocular region is raised. Anterior margin with 2 median projections, behind which is a pair of longitudinal ridges; expanded anterolaterally, but expansions not projecting anteriorly. Tergite I (Fig. 92) thin, undivided, covering base of carapace, tergites II to at least IX divided. Observed in dorsal view, outline of pleurum without obvious indentations, suggesting that pleural plates are absent. Presence of pleural setae indeterminable (optical conditions poor). At least some sternites divided. Palp coxa (Fig. 94) very long, but probably distorted. Coxa I excavated medially (Fig. 95). Presence or absence of coxal spines not determinable because posterior part is obscured by coxa II. Coxa II appears to have secondary spines anteriorly, but these might be distorted granules because there are also tooth-like granules near posterior margin. Coxa III with strong, spine-like granules on anterior margin. Setae of manducatory process damaged, but appear to be simple. Coxa IV with small, rounded posterior projection (Fig. 95). Genitalia (Fig. 93) distorted, but clearly those of a male; internal genital setae present, but difficult to observe. Only distal setae of chelicera visible (chelicera retracted), these being long and damaged. Palp (Fig. 92) with a distinct process on trochanter. Chelal fingers distinctly curved in dorsal view. Complete dentition of chela not visible, but both fingers with spaced teeth on paraxial face; terminal tooth still clearly recognizable (not in a cluster of equally-sized teeth). Trichobothria (Fig. 96) with hairs thinner than those of setae of fingers. Duplex trichobothria situated in a dorsal depression near the fingertip; hair of x_2 curved at tip and thicker than x_1. Chemosensory setae of movable finger difficult to observe, but at least some situated on antiaxial face behind trichobothrium *st*. These seem to be grouped in a common depression, as in *Cybella*, but the distortion of the finger makes it difficult to be certain that this is the case. Legs normal, trochanter of leg IV very large. Presence or absence of a depression on patellae could not be determined; a depression can be seen towards the distal end of patella of leg I, but this might be due to damage.



FIGURES 90–96. *Protofeaella* sp., male. 90, right leg I, ventro-paraxial view; 91, patella and distal part of femur of right leg I, dorso-paraxial view; 92, carapace, palp and anterior tergites, near-dorsal view (slightly from left); 93, parts of genitalia (distorted), ventral view; 94, right palp coxa, ventral view; 95, leg coxae, right coxae seen in near-ventral view, left coxae in lateroventral view; 96, right chela, dorso-paraxial view. Abbreviation: *da*, dorsal apodeme. Other abbreviations are notations of chelal trichobothria. Scale lines 0.3 mm (Fig. 92), 0.2 mm (Fig. 96), 0.1 mm (Figs 90–91, 94–95), 0.05 mm (Fig. 93).

Measurements (in mm, standard ratios in parentheses). Body 2.3×0.97. Carapace (strongly distorted) ca 0.77×0.32. Palp femur 0.55×0.29 (1.9), patella 0.33–0.47×0.13 (2.2–3.8), chela 0.62–0.70×0.11–0.12 (5.3–6.4), palm ca 0.13 (1.1–1.2), movable finger 0.57 (4.3–4.4).

Remarks. While it seems reasonable to suppose that the specimen studied here is congeneric with *P. peetersae*, it is not possible for the moment to determine whether they are conspecific. There appear to be some differences in the form of the carapace and size, but their significance is unclear. Henderickx & Boone (2016) described the carapace as having a central ridge, but this might not be a natural state because no such ridge is known in other Feaellidae or in their sister-group (Pseudogarypidae). Their drawing of the carapace (Henderickx & Boone 2016: fig. 1a) shows the anterior projections as spine-like, but because they only refer to 'traces' of the projections in their description, it may be that their reconstruction was partially inspired by the form seen in some extant Feaellinae. The movable finger is stated to lack teeth on the 'internal' (paraxial) side, but these would probably be difficult to observe from the orientations shown in their figures. Although the specimen described here is generally larger than the holotype of *P. peetersae*, no conclusion can be drawn from this because Henderickx & Boone (2016) did not determine the ontogenetic stage of the latter. According to H. Henderickx (in litt.), the paratype of *P. peetersae* is much larger than the holotype, hence it cannot be assumed that the holotype is an adult. Unfortunately, the holotype is not yet available for study, having been retained by H. Henderickx for additional studies (H. Henderickx in litt.). The paratype of *P. peetersae* has been donated to a private collector (H. Henderickx in litt.) and even if it were available for study, it would not be relevant to the identification of the present specimen.

Discussion of morphological characters

Homology and function of the genital setae of pseudoscorpions. The setae of the male posterior genital plate—hereafter referred to simply as 'genital setae'—are found in most pseudoscorpions of the superfamilies Chthonioidea (Chamberlin 1931; Vachon 1938a; Legg 1973), Feaelloidea (Chamberlin 1923; Heurtault-Rossi & Jézéquel 1965), Neobisioidea (Chamberlin 1923, 1931, 1952; Dashdamirov 2012; Legg 1975a; Muchmore 1973a, 1973b, 1982a, 1982b; Harvey & Edward 2007; Harvey & Volschenk 2007), Garypoidea (Harvey 1987; Harvey & Muchmore 1990; Harvey & Leng 2008; Harvey & Šťáhlavsk 2010), Cheiridioidea (Vachon 1938b; Benedict 1978) and Sternophoridae (Harvey 1985). However, there has long been a doubt as to whether they are homologous in all cases.

Vachon (1938a) argued that the genital setae of Chthonioidea were not homologous with those of other pseudoscorpions because they serve as the openings of the posterolateral glands, but his study did not include any Feaelloidea. Harvey (1986, 1992) interpreted the presence of setae in the male genital atrium as a synapomorphy for Chthonioidea and Feaelloidea, but did not consider them homologous with the genital setae of Neobisiidae, Hyidae or Parahyidae, writing that "Certain neobisioid species apparently possess male internal setae of a somewhat analogous nature, but I feel that this can confidently be attributed to convergence" (Harvey 1986: 757–758).

Legg (1973) showed that the lateral glands, which open through the genital setae, produce the liquid droplet on the stalk of freshly-deposited spermatophores of *Chthonius* C.L. Koch, 1843 (Chthoniidae). Similar droplets have been observed on the spermatophores of Neobisiidae, Geogarypidae, Larcidae, Cheiridiidae, Chernetidae and Cheliferidae (Weygoldt 1969, 1970). However, Legg (1974) did not find equivalent glands in the British species of Neobisiidae and Cheiridiidae, and he was unable to determine the source of the droplet on their spermatophores. Legg (1975b) suggested that the droplets of Chernetidae and Cheliferidae "could be derived from the median genital sac or even the prostatic reservoir", although the latter seems unlikely because the prostatic reservoir is normally filled with encysted spermatozoa and these have not been observed in the droplet.

Harvey & Volschenk (2007) stated that "the male genital atrium of most pseudoscorpions is furnished with several pairs of glandular setae". This would seem to suggest homology of the genital setae across all groups, but the examples they give all belong to Neobisioidea. Harvey & Volschenk (2007) did not provide evidence for a secretory function in non-chthonioid taxa, but the term 'glandular' has started to be applied to these setae in some taxonomic descriptions in families such as Ideoroncidae (Villegas-Guzmán & Francke 2009), Syarinidae (Harvey & Edward 2007), Olpiidae (Harvey & Leng 2008; Harvey & Šťáhlavský 2010; Nassirkhani & Vafai Shoushtra 2014; Nassirkhani 2015) and Garypinidae (Nassirkhani *et al.* 2016).

Dashdamirov (2012) has discussed the internal genital setae with particular reference to Neobisioidea. According to this author, the droplet observed on spermatophores of "many species" (taxa not specified) is "released from the glands located at the base of setae (?), since at higher magnifications some of these setae show apical pores or furrows along the entire extent". He goes on to state that in the genus *Bisetocreagris* Ćurčić, 1983 the setae have become "glandular/hollow". In support of his interpretation, Dashdamirov (2012) states that "Harvey (2009) has shown the presence of glandular setae in a representative of the family Garypinidae". The reference to "Harvey (2009)" is an error for Harvey & Šťáhlavský (2010), but even so the latter gave no evidence for a glandular function and were probably just following Harvey & Volschenk's (2007) unsupported statement.

None of these observations is convincing. The unlabelled glands shown in Dashdamirov's (2012) drawings of the male genitalia of species of the genera *Halobisium* Chamberlin, 1930, *Microcreagris* Balzan, 1892 and *Neobisium* Chamberlin, 1930 clearly represent the posterodorsal glands, which produce the spermatophore stalk (Vachon 1938a; Legg 1973, 1975b). The genital setae of Neobisioidea are thin and acuminate and any furrows or terminal openings would probably not be resolvable with light microscopy, particularly for internal setae that, under normal circumstances (without dissection of the genitalia), are being observed through at least one layer of cuticle. The fact that the setae are hollow does not provide an indication that they are glandular because the ordinary setae of pseudoscorpions are also generally hollow. Dashdamirov's (2012) implication that the genital setae of *Microcreagris* and *Halobisium* are solid is erroneous (pers. obs.) and the same is presumably the case for the other genus mentioned, *Echinocreagris* Dashdamirov, 2012.

Later in his paper, Dashdamirov (2012) backtracks somewhat and writes of the genital setae of Neobisioidea (and, perhaps, other non-chthonioids) that they "are best to be termed pseudo glandular setae (*pgs*) before they are proven as being truly glandular or simple". The introduction of a new term to express doubt about function is an unnecessary complication. Until evidence is provided for the presence or absence of a secretory function for the genital setae of non-chthonioid groups, it is simpler to avoid describing them as glandular. The term 'pseudo glandular setae' is not appropriate because it implies either non-homology or the absence of a glandular function. Authors wishing to indicate an inferred secretory function would be better advised to describe them as putative glandular setae.

The most parsimonious interpretation is that the genital setae of Chthonioidea, Feaelloidea, Neobisioidea, Cheiridioidea and Sternophoridae are all homologous. The question of their function is not directly relevant to this homology. The only pseudoscorpion in which a secretory function has been demonstrated is *Chthonius ischnocheles* (Hermann, 1804), but it is safe to assume, on the basis of morphological similarities, that this function is shared by the genital setae of all Chthonioidea. The supposed correlation between the presence of genital setae and the presence of a liquid droplet on the spermatophore fails because a large droplet is present on the spermatophores of species of Cheliferidae and Chernetidae (Kew 1912; Weygoldt 1969; Proctor 1993) that lack internal genital setae.

Lyrifissures of the palp coxa in Feaellidae. The form of the median maxillary lyrifissures (*mml*) and the presence or absence of the posterior maxillary lyrifissure (*pml*) provide important characters for separating higher groups in the classification of pseudoscorpions (Chamberlin 1931; Harvey 1992). However, there has been some confusion concerning these lyrifissures in members of the Feaelloidea. Chamberlin (1923) described a circular maxillary lyrifissure in Pseudogarypidae, which he referred to as the "central elliptical lyriform fissure", but later (Chamberlin 1943) diagnosed Feaelloidea as lacking *mml*. Harvey (1992) considered *pml* to be absent in Feaelloidea and *mml* to be present in Pseudogarypidae but absent in Feaellidae, interpreting the latter as a secondary loss. However, Harvey *et al.* (2016) described *Iporangella orchama* Harvey, Andrade & Pinto-da-Rocha, 2016 as having a median maxillary lyrifissure (which they also referred to as the median 'manducatory' lyrifissure).

The median maxillary lyrifissure is present in all the extant Feaellidae that I have examined. Based on a comparison with Pseudogarypidae, it is evident that it does not represent the posterior maxillary lyrifissure despite its very proximal position. The posterior maxillary lyrifissure appears to be absent Feaelloidea, as noted by previous authors. The posterolateral lyrifissure observed in *Cybella* occupies much the same position as *pml* in other pseudoscorpions. However, when *pml* is present, its form generally mirrors that of *mml*. Because the lyrifissure of *Cybella* is simple, in contrast to the circular form of *mml*, it is assumed here that it is a foraminal lyrifissure that has migrated to a more posterior position.

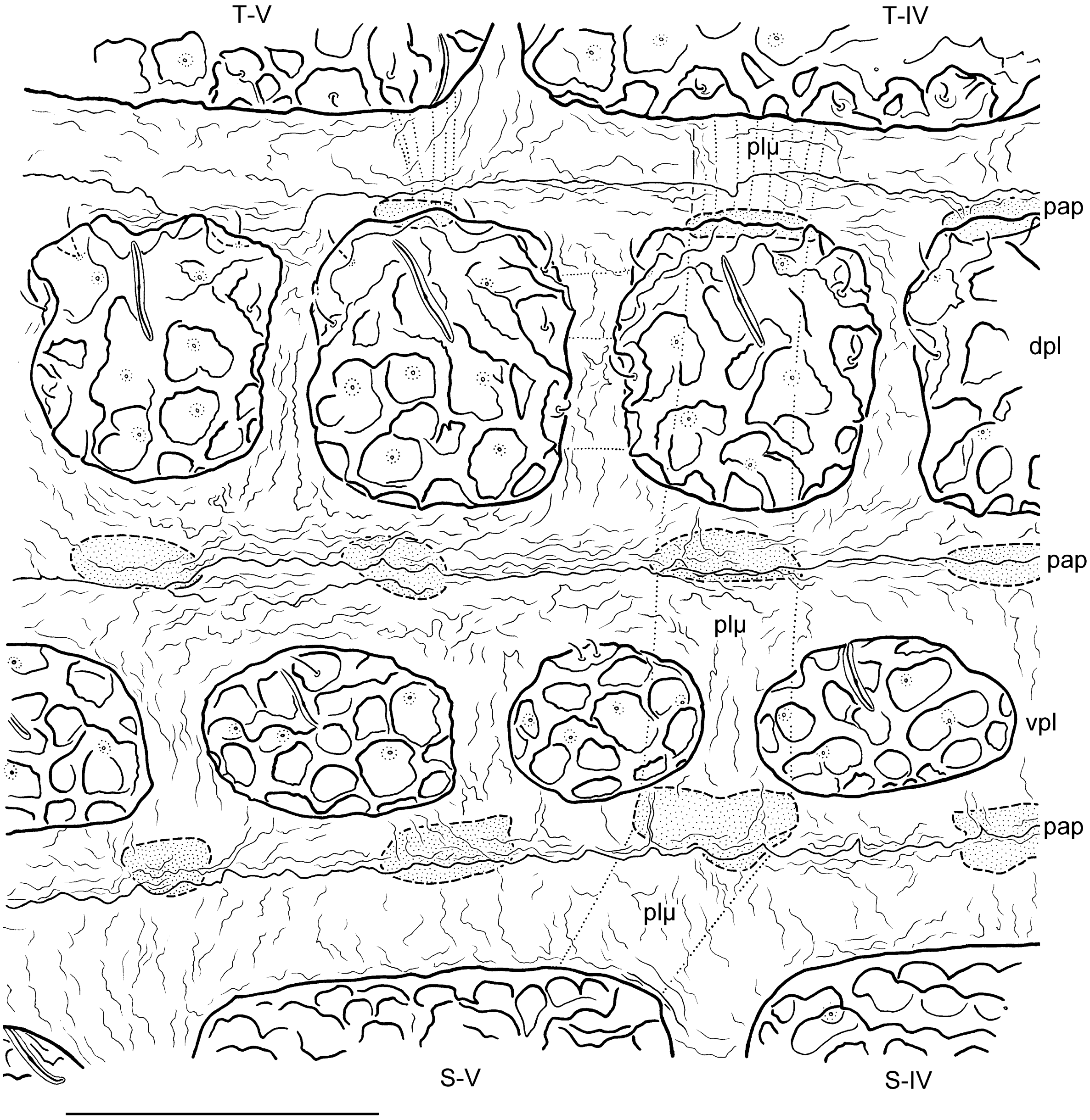


FIGURE 97. *Feaella leleupi* Beier, 1959, syntype male, pleural region of right side of opisthosoma at level of segments IV–V, lateral view, showing pleural plates, pleural apodemes and dorsoventral pleural muscles (latter only partially drawn). Abbreviations: *dpl*, dorsal pleural plate; *pap*, pleural apodeme; *pl*, dorso-ventral pleural muscle; *S-IV*, *S-V*, sternites IV and V; *T-IV*, *T-V*, tergites IV and V; *vpl*, ventral pleural plate. Scale line 0.1 mm.

Evolution of pleural plates in Feaellidae. The presence of two rows of pleural plates is one of the most striking features of the Feaellinae (Ellingsen 1906; With 1906; Chamberlin 1923, 1931), but it has not been clear how they arose. Morris (1948) described three rows of small "pleural plates" in the pseudogarypid *Neopseudogarypus scutellatus* Morris, 1948, which he treated as homologous with those of Feaellidae, although he stated that he was "not sure that these plates are the same as in *Feaella*". Similar structures were later found in the other genus of Pseudogarypidae, *Pseudogarypus* Ellingsen, 1909, by Benedict & Malcolm (1978), who also referred to them as pleural plates or sclerites. In addition to these, Muchmore (1981) found that the pleural membranes of species of *Pseudogarypus* bear 'tiny thickened plaques', which he speculated might represent the vestiges of the pleural setae observed for certain Garypidae. Finally, Mahnert (1982a) described *Feaella perreti* Mahnert, 1982 as having two rows of large plates in the pleurum as well as about three rows of smaller 'reduced' plates. A similar arrangement was described for *Feaella anderseni* Harvey, 1989, except that only two rows of smaller ‘platelets’ were observed (Harvey 1989). Harvey et al. (2016) referred to ‘platelets’ in the pleurum of *Iporangella*, but it is clear from their description and figures that these refer to the pleural plates, rather than to the ‘platelets’ of *F. anderseni*.

Examination of a variety of Feaelloidea shows that there are three different types of structures involved (Fig. 97). The first are the true pleural plates, which are only found in Feaellinae. These are large, well sclerotized structures with well developed ornamentation, bearing dermal pores and setae. They are situated on the top (crest) of the folds of the pleurum and do not have attached muscles. The second are internal, sclerotized parts of the pleurum at the bottom of the troughs between the folds. These serve as attachment sites for dorsoventral pleural muscles and are therefore termed here the *pleural apodemes*. These apodemes correspond to the sclerites previously described in Pseudogarypidae and to the small plates noted in *Feaella perreti* and *F. anderseni*. Because the arrangement of the muscles is unlikely to vary within species, the apparent variation in the pleural apodemes observed by Benedict & Malcolm (1978) presumably just reflects differences in their degree of sclerotization between individuals and the difficulties in observing them when the pleural folds are retracted. Finally, the ‘plaques’ observed by Muchmore (1981) are the openings of dermal glands, similar to those found on the sclerotized parts of the body. These pores are not limited to Pseudogarypidae, being present in *Cybella* (Fig. 3) and Feaellinae (Fig. 97).

Based on outgroup comparison with Pseudogarypidae, the absence of pleural plates in *Cybella* is assumed to be a primitive state, rather than the result of secondary loss. Examination of the pleural folds of *Cybella* is therefore instructive concerning the evolution of the pleural plates in Feaellinae. To begin with, it is now clear that the plates arose *in situ*, through increased sclerotization of the pleural wall, rather than having split from the tergites or sternites. The arrangement of the pleurum into two folds running for most of the length of the opisthosoma is common to all Feaelloidea and thus forms part of the ground-plan of this group. A migration of fragments from the tergal and sternal plates can be ruled out because it would involve them moving into an intermediate position in the troughs between the folds, where they would serve no function. The simultaneous presence of pleural plates and apodemes in Feaellinae excludes homology between the two. Thus, although the pleural apodemes arose before the plates, they do not represent their precursors.

Of interest in *Cybella* is the arrangement of lyrifissures. These are aligned along the tops of the folds. Because the pleurum is slightly depressed around each lyrifissure, the folds are thus weakly divided into a series of raised regions. Although these raised parts are reminiscent of the plates of Feaellinae, the latter have the lyrifissures situated on the pleural plates. It is therefore assumed here that the arrangement seen in Cybellinae is not the result of a secondary reduction of pleural plates. However, it does result in a similar arrangement of the setae and it is conceivable that the plates of Feaellinae might have evolved through a progressive increase in the sclerotized cuticle around the bases of the setae, with a subsequent incorporation of the lyrifissures into the plates.

Intercoxal canal. The presence of a distinct intercoxal canal was first noted in pseudoscorpions by Judson (1998). This is a modified space between the coxae of the palps and legs I–III, through which the secretion of the coxal glands flows towards the oral region. Feaellidae show a particularly well developed canal between the coxae of the palps and legs I. At this point, the membrane between the coxae is invaginated to form an almost closed tube. Unfortunately, its extent is difficult to study without sectioning, because it is necessary to detach the palp coxae from the leg coxae, which inevitably results in its being damaged, as is the case in Fig. 57. Such a modification is probably related to the mobility between the palp coxae and the coxae of legs I. The function of the canal is presumably to prevent the secretion spreading over the coxae, hence a flexible tube at this articulation point would be an advantage.

Modification of coxa III in *Cybella*. A marked reduction in the size of coxa III is unique to *Cybella* within the Feaelloidea. Pseudogarypidae have the coxae progressively increasing in size posteriorly, while in Feaellinae the leg coxae are of roughly equal width, although coxa IV is expanded posteriorly. The coxae of *Protofeaella* seem to have the same form as those of Feaellinae. A reduction of coxa III is quite frequent in Neobisioidea and certain Garypoidea of the families Olpiidae, Garypinidae and Menthidae. In most of these cases the reduction is associated with an increase in mobility between coxae II and III, this being particularly strongly developed in Menthidae (Chamberlin 1931). However, the leg coxae of *Cybella* are immovable and there is no obvious reason for the decrease in size of coxae III. The arrangement of the coxae of *Cybella* is unique within pseudoscorpions in that all coxae except III meet in the midline. The internal form of coxa III of *Cybella* is particularly unusual because it has become oblique, lying over the anterior part of coxa IV. Because the leg coxae are immobile, it is difficult to understand what might be the advantage of this modification.

Ontogeny of *Cybella* species.

Although only the tritonymph of *C. deharvengi* **n. sp.** and the protonymph of *C. bedosae* **n. sp.** are known, the two species are so similar that these provide a general idea of the ontogeny of *Cybella*. An unusual feature of the growth of *C. deharvengi* **n. sp.** (and, presumably, *C. bedosae* **n. sp.**) is the small difference in size between the tritonymph and adult. This might be related to the small size of *Cybella* species compared to most other Feaellidae, although in *Feaella perreti*—which is even smaller than *C. deharvengi* **n. sp.**—adults are distinctly larger than tritonymphs (Mahnert 1982a). Because males are generally smaller than females in Feaellidae, it is likely that the difference in size between the tritonymphs and females will be more marked when the latter become known in Cybellinae. If the non-type tritonymph of *C. deharvengi* **n. sp.** recorded here is correctly identified, it is conceivable that there might be a dimorphism in the size of tritonymphs, with the paratype tritonymph being a female and the non-type specimen a male.

The presence of only one proximal sensillum (p_1) in the protonymph of *C. bedosae* **n. sp.** follows a pattern that seems to be typical of all pseudoscorpions. Sensillum (p_2) usually appears in the deutonymph, regardless of whether it is coupled with p_1 or separate (Gardini 1991, 1993; pers. obs.). Although not explained by Judson (2007a), the notations p_1 and p_2 were selected to reflect this ontogenetic sequence.

The trichobothria are evidently added in the same sequence and positions as those of Feaellinae, even if deutonymphs were not available. Thus Cybellinae do not provide any additional information about the remarkable rearrangements in position that characterize Feaellidae as a whole (Mahnert 1982b; Harvey 1992).

Age and distribution of Feaelloidea

Although it is generally considered that Feaelloidea must be an old group, doubts about their phylogenetic position have made it difficult to decide exactly how old they might be. Harvey (1992) treated Feaelloidea as the sister-group of Chthonioidea and attributed to the latter group the Devonian genus *Dracochela* Schawaller, Shear & Bonamo, 1991. Because sister-groups have the same age by definition (Hennig 1966), this implied a minimum age of 392 My for Feaelloidea. Murienne et al. (2008) argued from molecular data that Feaelloidea were instead the sister-group of all other pseudoscorpions, though they did not indicate whether or not *Dracochela* should be included in the latter group. Judson (2012) restudied *Dracochela deprehendor* Schawaller, Shear & Bonamo, 1991 and concluded that it belonged to the stem-group of Pseudoscorpiones, making it irrelevant to the question of the age of Feaelloidea.

Harvey (1998) interpreted the distribution of Pseudogarypidae in North America, New Zealand and the Eocene of Europe as being the result of vicariance, from which he deduced that the family arose before the breakup of Pangaea. Their sister-group, Feaellidae, were characterized as a typically Gondwanan group by Harvey (1996a) and this interpretation appeared to be strengthened by the subsequent discovery of the first South American representative in Brazil (Andrade 2004; Harvey et al. 2016). However, the family Feaellidae must have originated before the breakup of Pangaea if it is the sister-group of Pseudogarypidae. The implication that Feaellidae would have been present in Laurasia is supported by the recent discovery of a feaellid, *Feaella* (*Tetrafeaella*) *groehni* Henderickx, 2014, in Baltic amber (Henderickx & Boone 2014). It is therefore difficult to understand why Henderickx & Boone (2016) continue to characterize Feaellidae as a "Gondwanan" group.

Evidently, the current distribution of Feaellidae, like that of Pseudogarypidae, is relictual, being the result of extinction over much of the Northern Hemisphere. Whether or not Cybellinae represent a Laurasian element is less clear, due to the complex geological history of Southeast Asia. Nevertheless, the presence of *Protofeaella* in Burmese amber shows that Feaellidae and Pseudogarypidae were already well differentiated by the Cretaceous, which suggests that both families could be considerably older. In this context, it is interesting to note that a carbonized fossil of Pseudogarypidae has been found in the mid-Cretaceous (late Albian–early Cenomanian) of the Rhenish Massif, Germany. It consists of a single, well preserved chela that can be readily assigned to this family by virtue of its shape, dentition, reticulate ornamentation and trichobothriotaxy. A scanning electron micrograph of the specimen was published in the German newspaper *Die Welt* (Lossau 2002), but it has not yet been described. Details of the dating and fossilization process of the material can be found in Viehofen *et al.* (2008).

FIGURE 98. Satellite image of Nui Bai Voi (Mo So Lon), Hon Chong, Vietnam, showing extent of quarrying at 25 January 2015, the position of the type locality of *Cybella deharvengi* **n. sp.** (circle) and the location at which the non-type tritonymph was collected (square). Scale line 300 m. Photograph copyright Google Earth 2016.

Threats to localities of Cybellinae

The cavity from which the types of *C. deharvengi* **n. sp.** were collected is situated in the same hill, Nui Bai Voi, as the Grotte-hôpital de Mo So, from which another pseudoscorpion, *Lagynochthonius fragilis* Judson, 2007, was described. This limestone hill is threatened by large-scale quarrying for the cement industry (Deharveng *et al.* 2005, 2009; Deharveng & Bedos 2012, 2016; Kiernan 2010). The 'grotte des Feaellidae' is close to the quarrying site at the western end of the hill (Fig. 98) and forms part of the mining concession. Although the IUCN and the company Holcim had drawn up a Biodiversity Action Plan to preserve at least part of the site (IUCN 2012), this has not yet been implemented and it might even be obsolete in view of recent developments. The concession was originally operated by Holcim Vietnam Ltd, which became LafargeHolcim Vietnam after the merger of the Lafarge Group and Holcim Ltd in 2015. In April 2016, the majority stakeholder, LafargeHolcim, announced that it was selling its part of LafargeHolcim Vietnam to the Siam City Cement Public Company Limited (LafargeHolcim 2016). Moreover, the Vietnamese government has recently announced that it will be privatizing 49% of the minority stakeholder, the state-owned Vietnam Cement Industry Corporation (Vicem) (Anonymous 2016). Because of these changes, it is difficult to predict what the future holds for the site, a situation that in itself gives serious cause for concern.

The type locality of *C. bedosae* **n. sp.** in Cambodia is not under imminent threat, but the entire hill forms part of a mining concession (again for limestone extraction for producing cement), meaning that its future is uncertain. The site has been fenced off and only accessible with permission from the company. As a result of this, the site is no longer grazed, resulting in significant regrowth of the vegetation, which is why the cave in which the types were found in 2005 could not be accessed in 2008.

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