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The genus *Eurytroma* from Sri Lanka: the homology of penial macrosetae in Podoctidae matches the gonyleptoid AE11 pattern (Opiliones: Laniatores: Epedanoidea)

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Abstract. A description of the pattern of structure and organization of the penial macrosetae was recently put forward for Gonyleptoidea Sundevall, 1833 and demonstrated to occur also in other families of Grassatores Kury, 2002, such as Assamiidae Sørensen, 1884, Epedanidae Sørensen, 1886 and Pyramidopidae Sharma, Prieto & Giribet, 2011. This set of homology hypotheses is herein called AE11 pattern. In this work, the monotypic Sri Lankan genus *Eurytroma* Roewer, 1949 of the family Podoctidae Roewer, 1912 (which is currently assigned to the Epedanoidea in the Grassatores) is studied. Male genitalia of *Eurytroma* are described for the first time and the first attempt is made to reconcile the chaetotaxy of ventral plate of podoctid species with the AE11 pattern. The podoctid genera *Hoplodino* Roewer, 1915, *Strandibalonius* Roewer, 1912 and *Santobius* Roewer, 1949 are also exemplified here; their set of macrosetae is described and the AE11 pattern is demonstrated to occur in all of them. Therefore, AE11 is more phylogenetically widespread in the Grassatores than previously thought. *Eurytroma pictulum* (Pocock, 1903) from Sri Lanka is redescribed. It is characterized by the presence of a meso-frontal stridulatory saw of denticles on the cheliceral hand and extreme reduction of mesotergal sutures. A further refinement is made on the current terminology system of cheliceral dentition of Podoctidae.

Keywords: Arachnida, harvestmen, Grassatores, Asia, Indo-Malaya, chaetotaxy

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The macrosetae inserted in the penis ventral plate in harvestmen of the suborder Laniatores (Arachnida: Opiliones) had never been compared in terms of structure, distribution and insertion until Kury & Villarreal (2015) proposed what we may call the “AE11 pattern” for the predominantly Neotropical superfamily Gonyleptoidea. Their hypothesis recognizes a typically constant number of 11 macrosetae grouped into 5 classes, called A to E. According to the AE11 configuration, typical for most species of Gonyleptoidea, the macrosetae are as follows: 3 A (latero-proximal), 1 B (ventro-latero-proximal), 3 C (latero-distal), 2 D (dorso-medial, often associated with the base of glans) and 2 E (ventro-lateral-distal, often forming a ventral rectangle).

Among the families of Gonyleptoidea, the AE11 pattern is clearly recognizable, in spite of deletions, additions and migrations of individual setae or groups of setae, depending on the taxon. However, there are more than a few examples of extreme supernumerary sets of macrosetae, obscuring the original pattern, such as in the cranid *Phalangodus* Gervais, 1842 (Villarreal & García 2016), the askawachids *Askawachi* Kury & Carvalho, 2020 and *Oxapampeus* Roewer, 1963 (Kury & Carvalho 2020), the ottilioleptid *Otilioleptes* Acosta, 2019 (Acosta 2019), several stygnopsids such as *Panzosus* Roewer, 1949 and *Philora* Goodnight & Goodnight, 1954 (Cruz-López & Francke 2016, 2019) and the sandokanid *Biantoncopus* Martens & Schwendinger, 1998 (Schwendinger & Martens 2002).

After the original proposal, the AE11 pattern has been routinely applied by different research groups to species descriptions in the families Cosmetidae (e.g., Damron et al. 2018; Friedrich & Lehmann 2020), Epedanidae (e.g., Zhang & Martens 2018), Gonyleptidae (e.g., Hara et al. 2018; Acosta

2020; Araujo-da-Silva et al. 2020) and Stygnopsidae (e.g., Cruz-López & Francke 2016, 2019, 2020). Kury & Villarreal (2015) suggested that the AE11 pattern may also occur in other superfamilies of Laniatores, such as Assamioida and Epedanoidea (*sensu* Fernández et al. 2017), but the authors did not further pursue this matter.

In this work, we formally investigate whether the AE11 pattern also applies to other families of Laniatores beyond those originally cited (Kury & Villarreal 2015). More specifically, we focused on the Podoctidae, a Palearctic family currently assigned to the superfamily Epedanoidea (e.g., Fernández et al. 2017) that includes 132 valid species, 70 of which were described by Roewer (Kury et al. 2020). The described diversity of Podoctidae is highest in Indonesia (25 valid species), Papua New Guinea (18 species) and Malaysia (17 species). In connection with a redescription of *Eurytroma pictulum* (Pocock, 1903), known by a single species from Sri Lanka, we attempt the recognition of the AE11 pattern in three other podoctid genera: *Hoplodino* Roewer, 1915, *Strandibalonius* Roewer, 1912 and *Santobius* Roewer, 1949. The four genera studied here were chosen because they are not especially closely related to each other within Podoctidae (Kury & Machado in prep.) and possess somewhat different genital morphology.

METHODS

Each genus studied here is represented by one species: *Eurytroma pictulum* from Sri Lanka; *Hoplodino continentalis* Roewer, 1915, from Singapore; *Strandibalonius esakii* (Suzuki, 1941), from Micronesia; and *Santobius annulipes* (Sørensen, 1886), from Fiji.

Table 1.—Diagnostic features for the Sri Lankan genera of Podoctidae.

Features	Genera			
	<i>Eurytromma</i> Roewer, 1949	<i>Eupodoctis</i> Roewer, 1923	<i>Ceylonositalces</i> Özdikmen, 2006	<i>Neopodoctis</i> Roewer, 1912
Cheliceral fingers, angle with hand	180°	180°	ca. 80°	45°
Cheliceral bulla, length and shape	short, swollen	short, swollen	short, swollen	indistinct
Basichelicerite, length	short	short	short	elongate
Pedipalpal femur, basal shape	cylindrical	cylindrical	bottle	cylindrical
Dorsal scutum outline	zeta	unknown	eta	zeta
Interocular mound, spear, dorsal process (DPS)	present	absent	absent	absent
Interocular mound, tower, dorsal spikes (TS1, TS2)	absent	present	absent	absent
Interocular mound, spear, antero-posterior inclination	almost erect	almost erect	strongly tilted forward	strongly tilted forward
Interocular mound, tower granulation	sparse	sparse	dense	dense
Tarsal formula	3, 9, 5, 5	3, 8, 5, 5	3, 5, 5, 5	4, 9, 5, 5

Morphological terminology for podoctids follows Kury & Machado (2009, 2018). Terminology of penial macrosetae follows Kury & Villarreal (2015). Terminology of scutal outline follows Kury & Medrano (2016). Terminology of cheliceral dentition follows Kury & Machado (2009) with some new expansions to account for displaced teeth: in addition to molars, canines and incisors on each finger, the new **posterior incisiviform tooth (pi)** category is created here for teeth situated outside the main blade, on the distal posterior surface of each cheliceral finger. The distal setiferous region of penis is herein called the ventral plate in a loose sense, because it is not a laminar region in the sense of Gonyleptoidea.

Descriptions of colors use the standard names of the 267 Color Centroids of the NBS/IBCC Color System (online at <http://people.csail.mit.edu/jaffer/Color/Dictionaries#nbs-isc>) as described in Kury & Orrico (2006). Scanning Electron Microscopy was carried out with a JEOL JSM-6390LV at the Center for Scanning Electron Microscopy of the Museu Nacional/UFRJ. Geographic locations on Earth are given in decimal coordinates, which do not use cardinal directions (north, east, south, and west), rather a minus sign for locations west and south of the Prime Meridian and Equator respectively. All measurements are in mm.

Abbreviations of the repositories cited are: AMNH (American Museum of Natural History, New York, USA), BMNH (The Natural History Museum, London, UK), MNHN (Muséum National d'Histoire Naturelle, Paris, France), MNRJ (Museu Nacional, Rio de Janeiro, Brazil) and QM (Queensland Museum, Brisbane, Australia). Other abbreviations used: CL = carapace length, CW = carapace width, AL = abdominal scutum length, AW = abdominal scutum width, ID = interocular distance, Cx = coxa, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, MS = macrosetae, Mt = metatarsus, Ta = tarsus.

Tarsal formula: numbers of tarsomeres in tarsus I to IV, when an individual count is given; order is from left to right side (figures in parentheses denote number of tarsomeres only in the distitarsus I–II).

The basic set of macrosetae of the species of Podoctidae studied here was compared with the patterns previously described and interpreted for species of Assamiidae, Epeda-

nidae, Gonyleptoidea and Pyramidopidae (e.g., Kury & Villarreal 2015; Cruz-López & Francke 2020) and their most probable homology was mainly determined by topology and mutual exclusion.

Material examined.—*Eurytromma pictulum*: 5 ♂ 7 ♀ 4 juv. (MNHN SI 17222, 1 ♂ mounted for SEM), Sri Lanka, without further locality data, Gabb leg.

Hoplodino continentalis: 7 ♂ 29 ♀ (MNRJ 9257, 1 ♂ mounted for SEM), Singapore, Upper Pierce Reservoir Park, on tree trunks, 15.vii.2016, A. Giupponi & A. Kury leg.

Strandibalonius esakii: 9 ♂ 23 ♀ 2 juv. (AMNH AK 179, 1 ♂ mounted for SEM), Federated States of Micronesia, Ponape Isl., Nanpil, Nett District, Pacific Science Board, Ent. Survey of Micronesia, 27.ii.1948, Henry S. Dybas leg.; 11 ex. (AMNH AK 174), Micronesia, Ponape Isl., Mt. Kupuriso, summit, 2000 ft, beating vegetation, 10.iii.1948, Henry S. Dybas leg.

Santobius annulipes: 4 ♂ 13 ♀ (QM AK 001, 1 ♂ mounted for SEM), Fiji, Viti Levu, Nadarivatu Reserve, 850 m, 12.vii.1982, G.B & S.R. Monteith leg.

SYSTEMATIC BACKGROUND ON *EURYTROMMA*

Pocock (1903:448) described the new species *Podoctis pictulus* Pocock, 1903 from “probably Kandy”, Sri Lanka. He misspelled the generic name as “*Podactis*”. Pocock provided two illustrations: dorsal scutum in lateral view and the interocular mound in frontal view. In his description, he compared the species with *Podoctis armatissimus* Thorell, 1890, from Pinang, Malaysia.

Roewer (1912:206) created the new genus *Neopodoctis* Roewer, 1912 for *Podoctis pictulus* and a new species – *Neopodoctis ceylonensis* Roewer, 1912 – also from Sri Lanka. Roewer mentioned that he had not seen the type of *Podoctis pictulus*, but that the examination of this material by Stanley Hirst, the curator in BMNH, had allowed the erection of the new genus. Based on Roewer’s comments, this species was most certainly meant to be the type of the genus, and also because it was first numbered as it was Roewer’s habit.

After finally having personally examined Pocock’s type sent from London, Roewer (1949:280) was able to correct

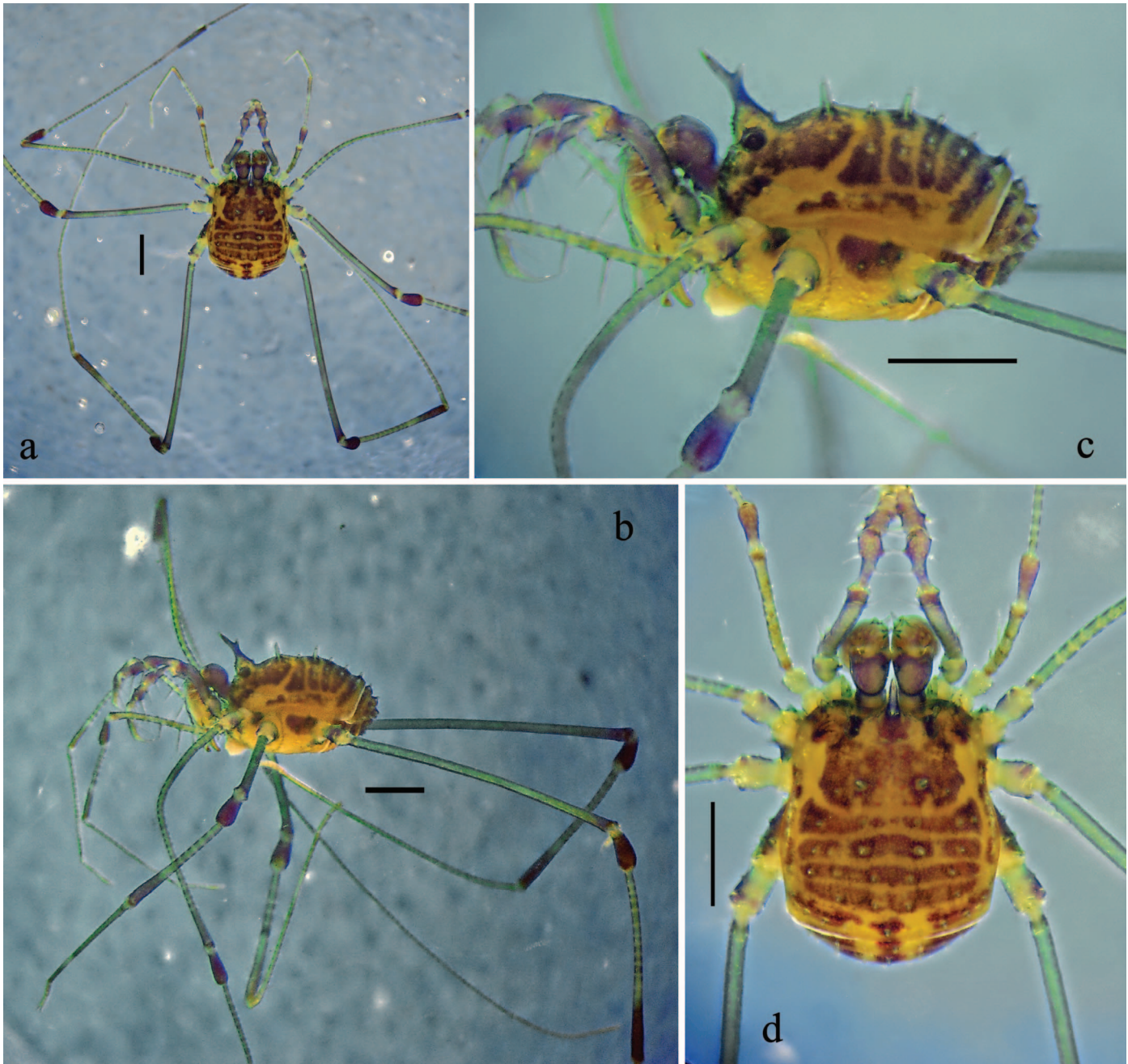


Figure 1.—*Eurytromma pictulum*, male (MNHN SI 17222), from Sri Lanka, habitus, showing color patterns of body and appendages: a. General aspect, dorsal view; b. Same, lateral view; c. Detail of body, lateral view; d. Same, dorsal view. Scale bars = 1 mm.

innumerable mistakes of Hirst's observation (virtually all relevant information was wrong according to Roewer) and created the new monotypic genus *Eurytromma* Roewer, 1949 for only this species. He provided illustration of the male cheliceral hand in frontal and mesal views and clearly depicted the stridulatory saw on the meso-frontal surface of cheliceral hand, explicitly calling it "eines Stridulationsorganes in Form einer feinen, dichten Zähnenreihe". The second species of *Neopodoctis* – *N. ceylonensis* – was then explicitly designated as type of *Neopodoctis*. Neither the genus *Eurytromma* nor the

species *E. pictulum* have been further referred to in the literature.

SYSTEMATICS

Eurytromma Roewer, 1949

Eurytromma Roewer 1949:280.

Type species.—*Podoctis pictulus* Pocock, 1903, by original designation.

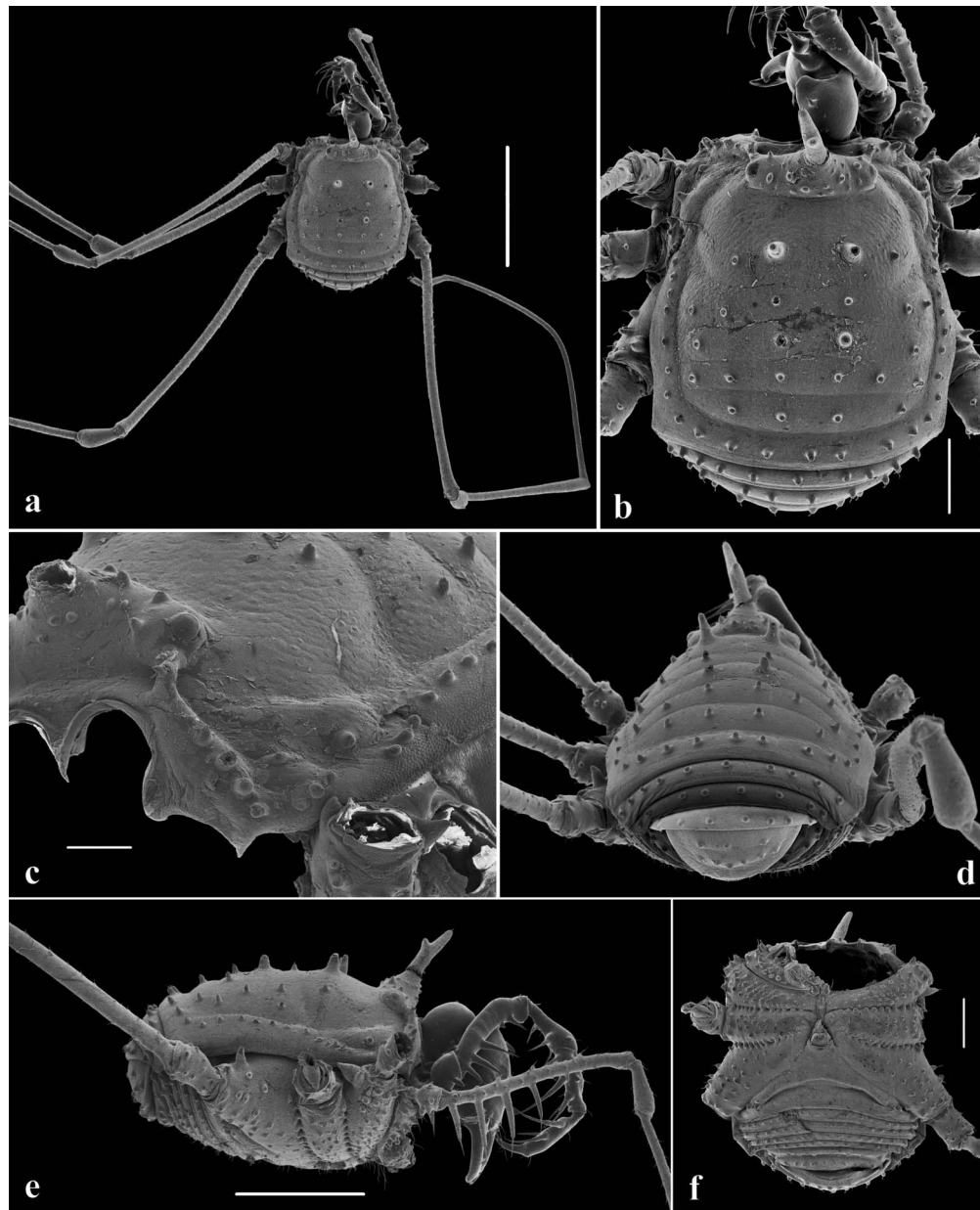


Figure 2.—*Eurytromma pictulum*, male (MNHN SI 17222), from Sri Lanka, body: a. Habitus, dorsal view; b. Dorsal scutum and coxae, dorsal view; c. Carapace, fronto-dorso-lateral view; d. Abdominal scutum and free tergites, posterior view; e. Habitus, dextro-lateral view; f. Coxae, sternum and sternites, ventral view. Scale bars: 2 mm (a); 1 mm (e); 500 μ m (b, d, f); 200 μ m (c).

Etymology.—*Eurytromma* from Greek εὖ (rightful, proper, good) + ῥότρος (globe-thistle, *Echinops viscosus*) + ὄμμα (eye). Gender neuter.

Diagnosis.—Not obviously related to any particular genus of Podoctinae. Interocular mound well-marked, without either zygomatic or cervical tubercular bridges; tower only moderately high; median spear with one dorsal process. Carapace and each mesotergal areas I to IV armed with a transverse row of tubercles. No tubercular bridges whatsoever on mesotergum. Cheliceral hand with meso-frontal stridulatory saw of denticles. Chelicera not especially robust, neither in basiche-licerite nor in hand. All pedipalpal podomeres armed with robust megaspines. Pedipalpal femur without any specially

incrassate part and sharply bent ventrally on distal fourth. Leg I with a row of 4 powerful ventral setiferous spines. Tarsal counts: 3(2)/9(3)/5/5. Setiferous region of penis not clearly defined as a proper ventral plate, and only slightly cleft at apex. Penial MS A, B, C, E clustered on distal region of truncus, with MS C fully apically inserted. Follis barrel-shaped, hugely developed, surpassing apical truncus in situ. For a comparison of *Eurytromma* with the other Sri Lankan genera, see Table 1.

Distribution.—Genus known only from Sri Lanka.

Eurytromma pictulum (Pocock, 1903)

Podoctis pictulus Pocock 1903: 448, pl. 12, figs. 3, 3a.

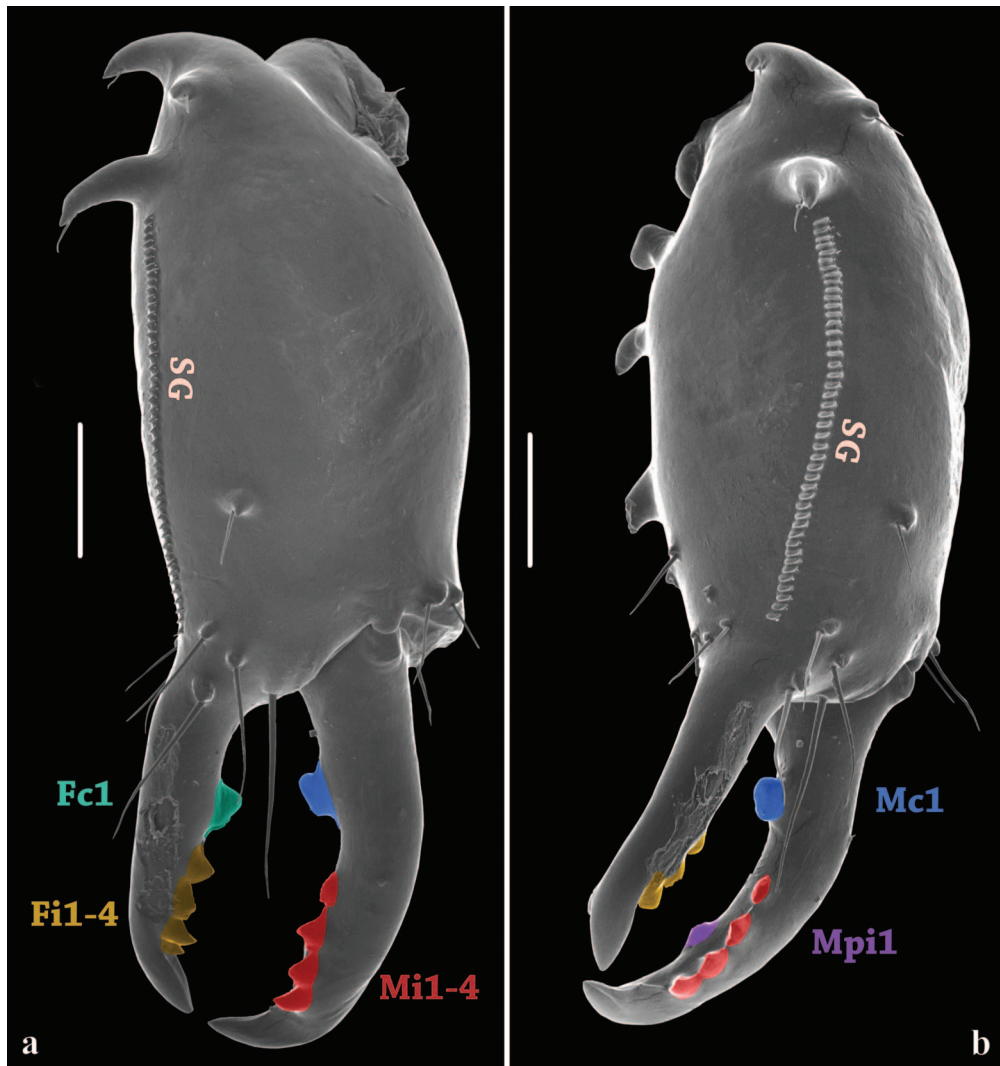


Figure 3.—*Eurytromma pictulum*, male (MNHN SI 17222) from Sri Lanka. Left chelicera: a. Frontal view; b. Mesal view. Abbreviations: c = caniniform tooth; F = dentiform projection (= tooth) of fixed finger; i = incisiviform tooth; M = dentiform projection (= tooth) of movable finger; SG = stridulatory grate. Scale bars = 200 μ m (a, b).

Neopodoctis pictulus: Roewer 1912: 207; Roewer 1923: 176, fig. 196.

Eurytromma pictulum: Roewer 1949: 280, figs. 81a–b.

Type data.—Male holotype (BMNH, examined), SRI LANKA, Kandy.

Description.—*Male* (MNHN SI 17222). Measurements: CL = 1.0; CW = 1.7; AL = 1.2; AW = 2.0; ID = 0.7; Leg I = 5.8 (Fe = 1.6; Ti = 1.2; Mt = 1.6); Leg II = 17.2 (Fe = 5.0; Ti = 4.5; Mt = 5.0); Leg III = 10.6 (Fe = 3.0; Ti = 2.2; Mt = 3.6); Leg IV = 12.7 (Fe = 3.9; Ti = 2.1; Mt = 4.6).

Body: Mid-sized podocetid (dorsal scutum 2.2 mm long), with elongate slender legs I–IV (Figs. 1a,b, 2a). Brown background of the body interrupted by two pairs of green/yellow flecks (Figs. 1a–d). Interocular mound with one dorsal secondary apophysis (Figs. 1c, 2e). Carapace, scutal areas and tergites each with transverse row of acuminate tubercles, the paramedian pair standing out, especially those on carapace and mesotergal area II (Figs. 2b, d, e). Tegument quite

smooth, except for the tuberculate-microgranulate taenidium (Fig. 2c). Setae of setiferous tubercles of dorsal scutum, free tergites, coxae and trochanters flattened in the typical fashion of the family (Figs. 2b–d). Dorsal scutum outline of type zeta (Kury & Medrano 2016), armed with a single row of acuminate, setiferous tubercles all around its rim (Fig. 2b). The set mesotergum plus carapace separated from lateral margins of scutum by deep groove; all other grooves are narrow and shallow (Figs. 2b, c, e). Interocular mound wide, tower only moderately high, flattened anteriorly, with few large tubercles, and connected with frontal border of carapace by a pair of lacrimal tubercular bridges, lacking other tubercular bridges. Median spear bearing a blunt dorsal process (DPS). Eye lumps embedded on interocular mound, bearing small superciliary spine (Figs. 2b, c, e). Carapace with five pairs of antero-lateral acuminate tubercles twice as long as each of the abdominal areas; with transverse row of four acuminate tubercles on post-ocular region, the inner pair much more prominent. The four mesotergal areas, scutal area

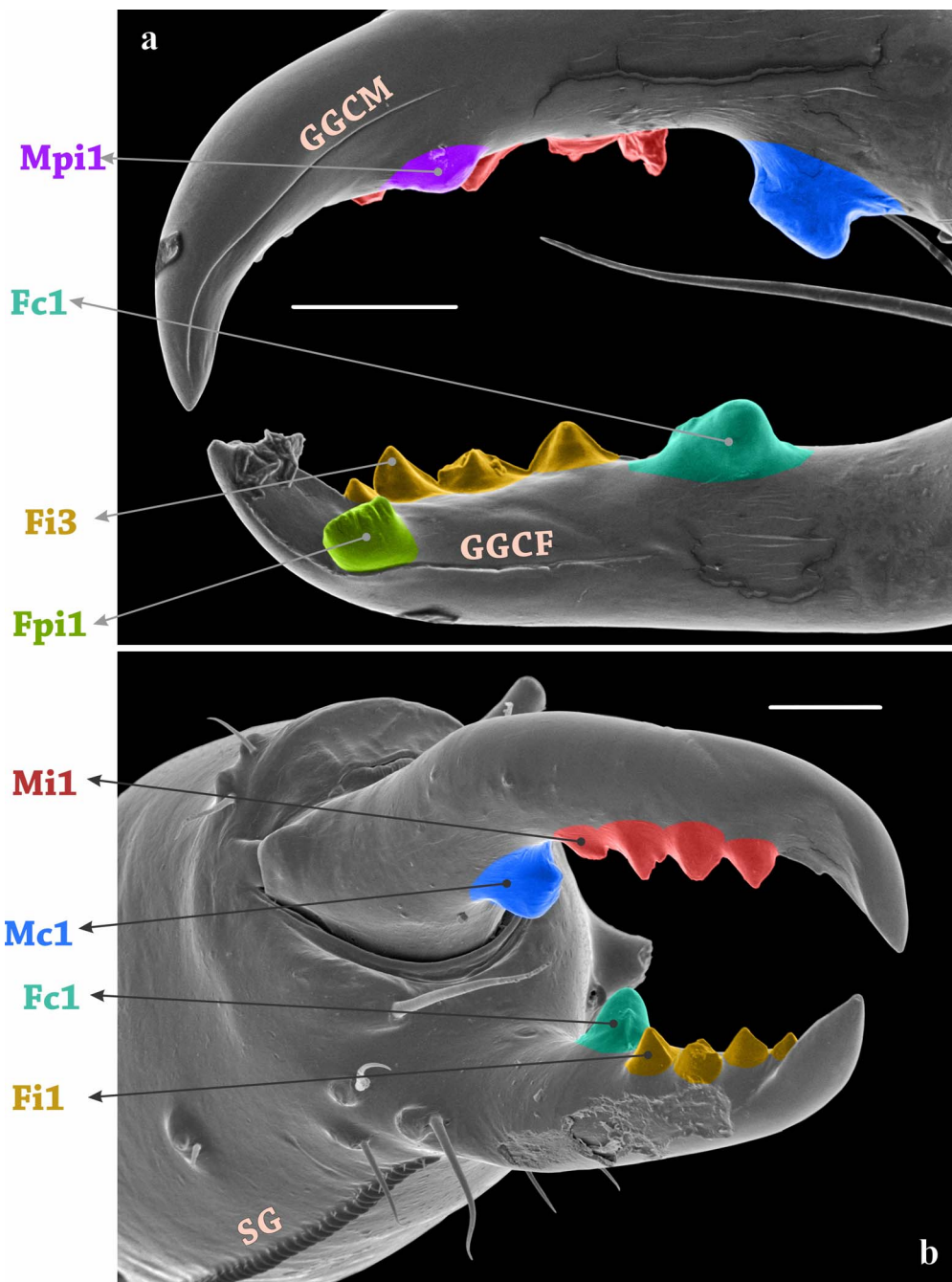


Figure 4.—*Eurytromma pictulum*, male (MNHN SI 17222) from Sri Lanka. Fingers of left chelicera: a. Posterior view; b. Antero-ventral view. Abbreviations: c = caniniform tooth; F = dentiform projection (= tooth) of fixed finger; GGCF = groove of cheliceral comb of fixed finger; GGCM = groove of cheliceral comb of movable finger; i = incisiviform tooth; M = dentiform projection (= tooth) of movable finger; m = molariform tooth; pi = posterior incisiviform tooth; SG = stridulatory grate. Scale bars = 100 μ m (a, b).

V and three free tergites each with a row of well-marked tubercles (respectively 6, 4, 6, 4, 9, 10, 8 and 6), with inner pair of paramedian tubercles on scutal area II much more prominent (Figs. 2b, d).

Chelicera: Not especially robust/swollen/enlarged, neither in basichelicerite nor in hand. Basichelicerite with tapering peduncle and a bulla, armed ventrally with six setiferous tubercles. Bulla with two dorso-apical setiferous tubercles. Cheliceral hand with posterior groove of cheliceral comb

(GCC) on both fingers (Fig. 4a); mesally with a row of 44 curved dentiform processes, described by Roewer (1949) as a stridulatory device (Figs. 3a, b, 5a, b); armed mesally with three and ectally with four megaspines (Figs. 3a, b). Fixed finger without molariforms, with a strong caniniform (Fc1) slightly displaced posteriad that opposes Mc1 (Figs. 3a, 4a, b); with four acuminate incisors (Fi1–4) and a robust multicusp incisiviform tooth on posterior edge (Fpi1) that matches the apex of movable finger (Figs. 3a, b, 4a, b, 5c). Movable finger

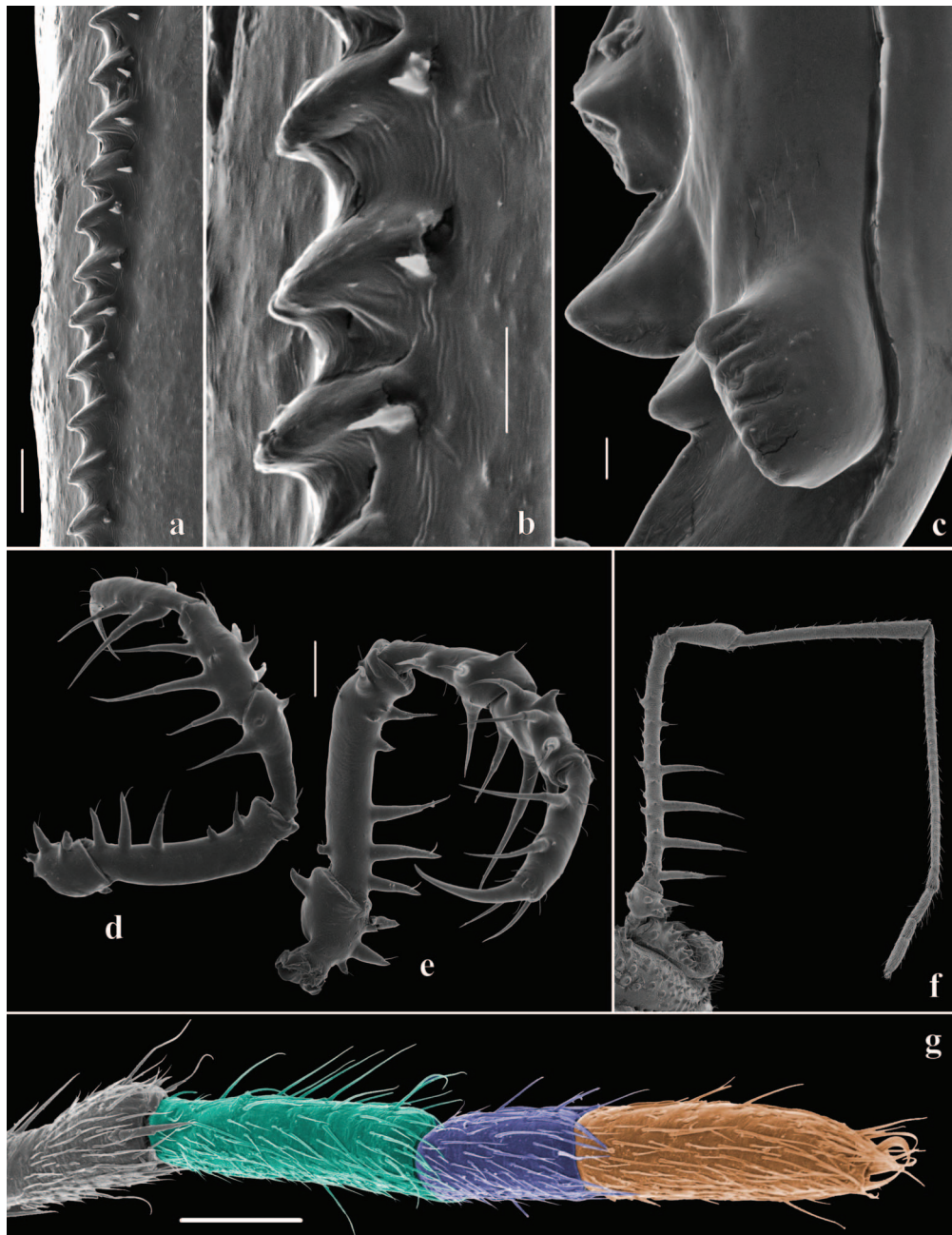


Figure 5.—*Eurytroma pictulum*, male (MNHN SI 17222), from Sri Lanka, appendages: a. Left chelicera, stridulatory grate, frontal (dorsal) view; b. Same, further magnified showing details of individual teeth with associated thorn; c. Left chelicera, detail of the cheliceral ridge, posterior (ventral) view; d. Left pedipalpus, ectal view; e. Left pedipalpus, mesal view; f. Right leg I, retrolateral view; g. Same, detail of tarsus (basitarsomere in green; distitarsomere 1 in blue; 2 in orange). Scale bars: 200 μm (d, e); 100 μm (g); 20 μm (a); 10 μm (b, c).

with one large truncated molariform (Mm1), no caniniforms, four acuminate incisories (Mi1–4) and one blunt posterior incisiviform tooth (Mpi1) (Figs. 3a, b, 4a, b).

Pedipalp (Figs. 2e, 5d–e): Robust, armed with stout megaspines. All 4 megaspines of Tr, the three most proximal of Fe and the dorsal ones on Pa and Ti bear small, subapical setae, while all others possess powerful terminal setae. Tr short, armed with three stout ventral and one dorsal megaspines. Fe cylindrical, sharply bent ventrally on distal fourth, with no special thickening of any portion, and bearing

a ventral row of five megaspines (arranged as 3 + 2 with clearly marked diastema) and a dorso-basal shorter and a meso-apical megaspine (surrounded by four setiferous tubercles). Pa moderately long, depressed ventrally, with thin cylindrical unarmed peduncle. Pa dorso-distally with a pair of short megaspines, armed mesally with two and ectally with one massive megaspines. Ti without peduncle, depressed ventrally, dorso medially with a pair of short megaspines, armed mesally with three and ectally with three massive megaspines. Ta elongate, cylindrical, with peduncle and not depressed, armed

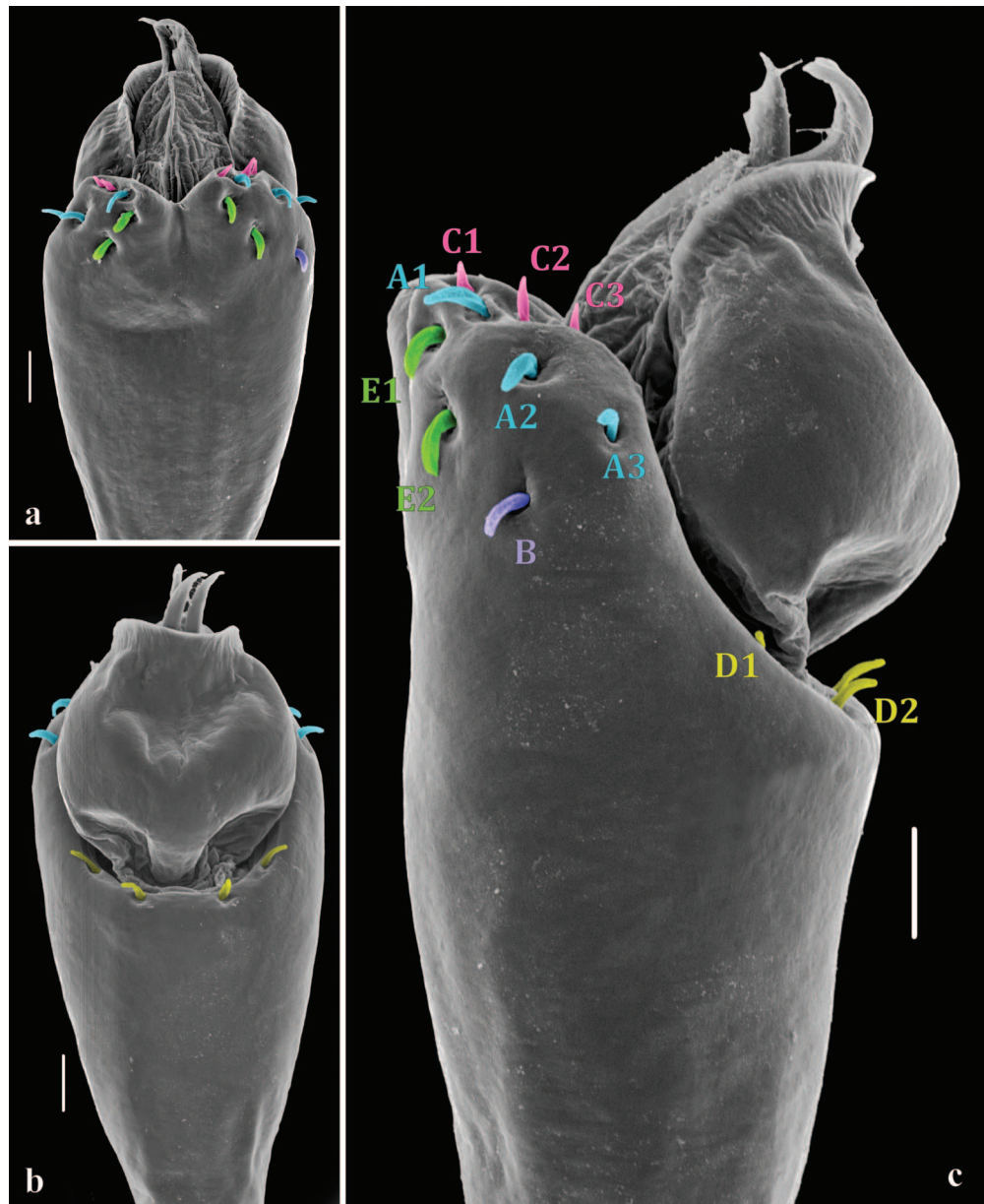


Figure 6.—*Eurytromma pictulum*, male (MNHN SI 17222) from Sri Lanka. Distal part of penis, with the macrosetae colorized to show the chaetotaxy: a. Ventro-apical view; b. Dorso-apical view; c. lateral view. Abbreviations: A to E = macrosetae clusters or groups A to E. Scale bars = 20 μ m.

mesally with two and ectally with two massive megaspines. Claw very robust, as long as Ti.

Legs: Legs I–IV elongate and slender, especially Fe IV, which is sexually dimorphic and longer in males (Figs. 1a, b). Only leg I with setiferous tubercles (setae terminally inserted). Tr I with four ventral setiferous tubercles, one much longer. Fe I substraight, with dorsal row of nine small setiferous tubercles, ventral row of five setiferous tubercles, the four proximal much longer and unarmed distal region (Fig. 5f). Tarsal claws unpectinated, without pseudonychium or scopula. Tarsal counts: 3(2)/9(3)/5/5 (Roewer gives 4(2) for leg I, but the basitarsomere appears to be undivided in the type specimen and clearly undivided in the specimens examined here; Fig. 5g).

Male genitalia (Figs. 6, 7, 8 a–c): Truncus club-like, abruptly thickened distally. Setiferous region of penis not clearly defined as a proper ventral plate, and only slightly cleft at apex. Follis barrel-shaped, very large, surpassing apical truncus in situ. Stylus flanked by a pair of laminar sigmoid spangen. Penial MS A, B, C, E clustered on distal region of truncus, with short straight MS C1–3 fully apically inserted. Short curved spatulate MS A1–A3 form a vertical lateral row, although distorted by the shortening of “ventral plate”. MS B identical in shape to A, displaced a little to ventro-lateral. MS D1–D2 short, curved, inserted fully dorsal, at the very base of follis. MS E1–E2 fully ventral, distal, forming a trapeze figure.

Color (in alcohol) (Figs. 1a–d): Body, chelicerae, pedipalps and Cx–Tr I–IV background dorsal and ventral predominant-

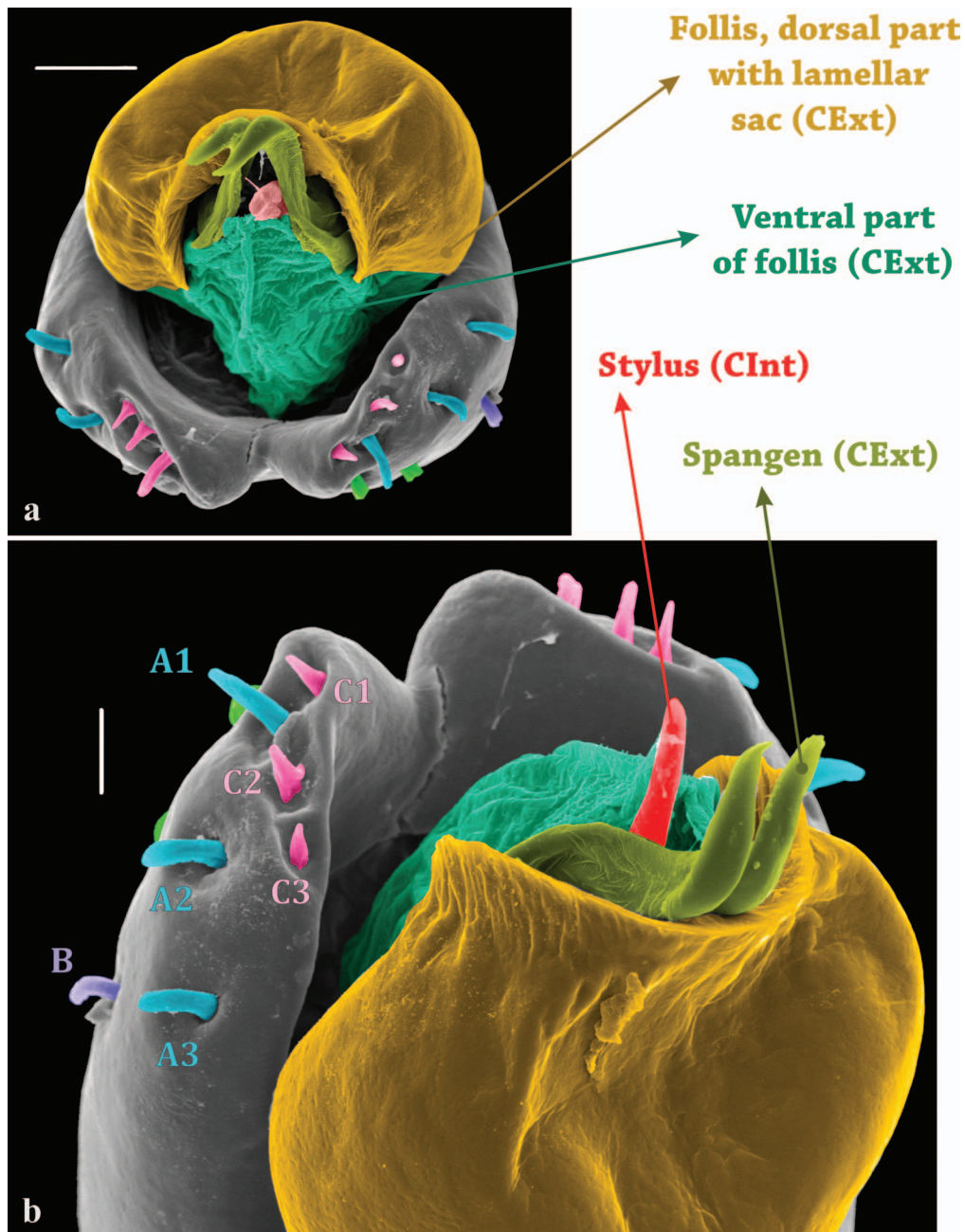


Figure 7.—*Eurytromma pictulum*, male (MNHN SI 17222) from Sri Lanka. Distal part of retracted penis, colored to show the structures and the chaetotaxy: a. Apical view; b. Dorso-latero-apical view. Abbreviations: A to E = macrosetae clusters or groups. Scale bars: 20 μm (a), 10 μm (b).

ly Strong Yellow (84). Dorsal scutum and free tergites with extensive darker areas of Moderate Brown (58): most of carapace, except for a pair of lateral areas on the lateral borders, all scutal areas and free tergites. Dorsally, the yellow background is clearly visible in the aforementioned laterals of carapace and another pair of paramedian yellow spots extending from area V to tergite III. Laterally and ventrally the yellow background predominates, except for a large elliptical spot of Cx IV. Chelicerae and pedipalps with dense moderate brown reticulation. Legs I–IV predominantly Brill-

iant Yellowish Green (130), except for Pt and distal tips of Fe and Ti, which are sharply contrasting Deep Red (13). Fe I–II and Ti I–IV with several lighter yellowish rings.

Penial macrosetae in *Hoplodino*, *Strandibalonius* and *Santobius*.—*Hoplodino continentalis* (Figs. 8d–f) has the distal region of truncus still more abruptly marked than *Eurytromma*. The ventral plate has a deep parabolic apical cleft, and the carenated MS C1–2 (reduced to two pairs) are lateral-subapical and MS A1–2 form a vertical lateral line. MS B is strongly reduced and displaced to ventral when compared with

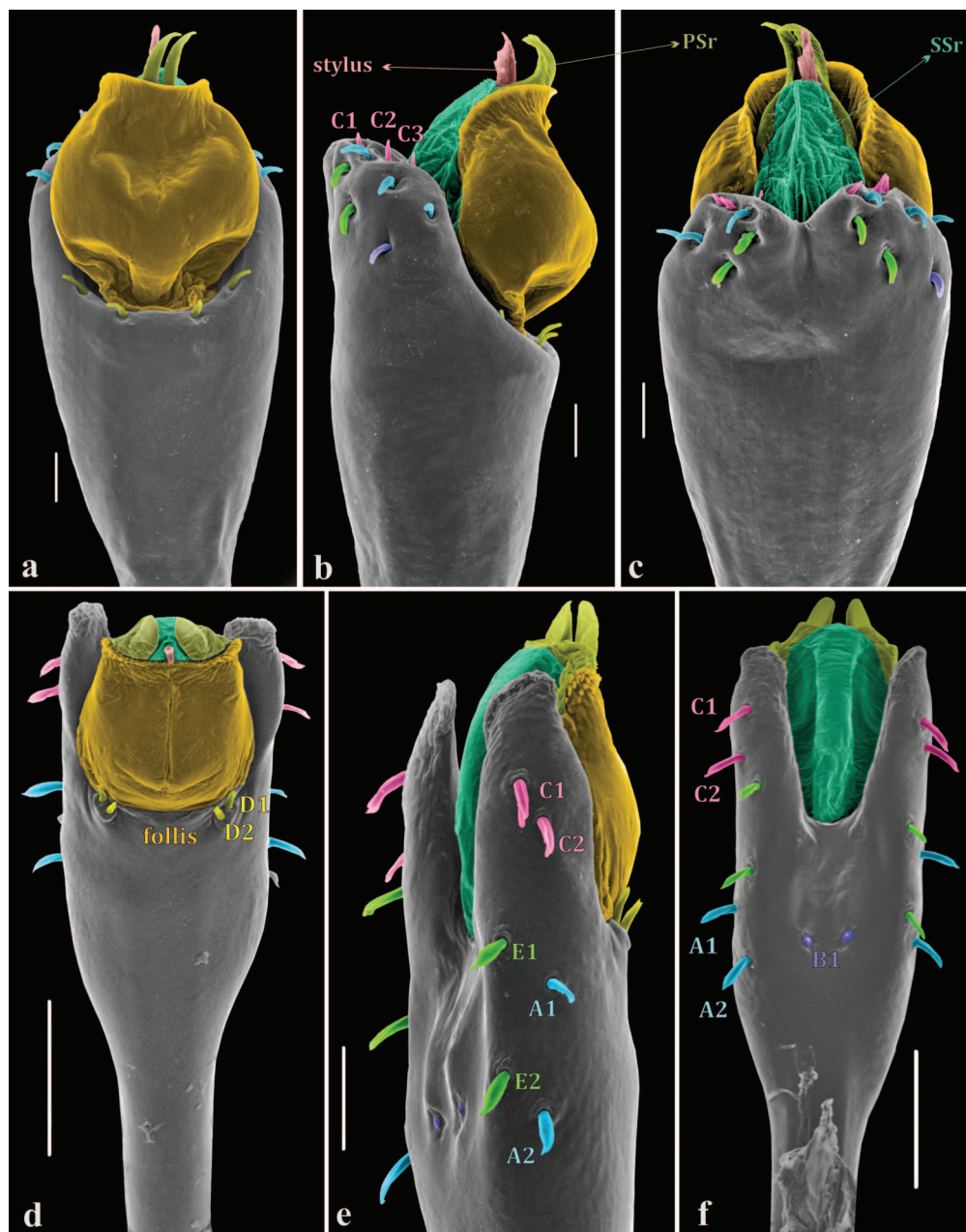


Figure 8.—Podoctinae. Male genitalia, pars distalis. a. *Eurytromma pictulum*, male (MNHN SI 17222) from Sri Lanka, dorsal view; b. Same, sinistrolateral view; c. Same, ventral view; d. *Hoplodino continentalis*, male (MNRJ 9257) from Singapore, dorsal view; e. Same, sinistrolateral view; f. Same, ventral view. Abbreviations: A to E = macrosetae clusters or groups; PSr = parastylar region; SSr = substylar region. Scale bars: 100 μ m (d, f); 50 μ m (e); 20 μ m (a, b, c).

the other podoctid species studied here. MS D1–2 are mid-dorsal at the base of follis. MS E1–2 form a more regular quadrangle, displaced to the edges by the cleft. *Strandibalonius esakii* (Figs. 9a–e) has the glans embedded in the ventral plate, which is shaped like a baseball glove with a deep ventral U-shaped cleft. MS A1–A3 form a vertical lateral line, and MS B are absent. MS C1–3 are disjunct, with C1 terminal, pointing apically and C2–3 clustered latero-distally. MS D1–2 are minute, almost concealed in the basal follis fold. MS E1–2 form a trapezoid and as in the previous species are displaced to

laterally by the cleft. *Santobius annulipes* (Figs. 10a–d) has the most defined ventral plate, hourglass-shaped, with strong mid-constriction, separated from the rest of the truncus by a striated region, and with an only moderately deep V-shaped cleft. All macrosetae but D are markedly ventral. MS A1–3 form a vertical lateral line, at the edge of the ventral surface of ventral plate. MS C1–3 are clustered subapically at the prongs of ventral plate. MS D1–2 are minute, inserted in the basal follis fold. E1–E2 form a ventral quadrangular shape. The small MS B are strongly displaced proximally.



Figure 9.—*Strandibalonius esakii* (MNRJ 5943), from Micronesia. Male genitalia, pars distalis: a. Dorsal view; b. Ventral view; c. Apical view; d. Sinistro-lateral view, detail; e. Dorso-apical view, detail showing macrosetae D1 and D2. Abbreviations: A to E = macrosetae clusters or groups. Color conventions as in Fig. 7. Scale bars: 50 μm (a, b); 20 μm (c, d); 10 μm (e).

DISCUSSION

If one simplifies the phylogenetic structure of the Podoctidae (Sharma et al. 2017; Kury & Machado in prep.) by considering a monophyletic Ibaloniinae core including the ovoid species from Philippines and Melanesia, a second clade formed by the Seychellan *Holozoster* and allies and a third clade formed by what is now roughly Podoctinae + Erecaninae, *Eurytromma* appears to be an early derivative of this third clade. *Eurytromma* displays a mix of a conservative body, similar to *Podoctis* for example, with genitalia entirely different, more akin to those of *Dongmoa* Roewer, 1927 or *Erecanana* Strand, 1911, which belong to the clade Podoctinae + Erecaninae.

The possible homology of the penial macrosetae in Grassatores is only starting to be scratched at the surface. Discounting the relatively few cases of extreme reduction or multiplication of macrosetae, in all families, almost always we can see three pairs of macrosetae C apical or subapical, sometimes migrated to dorsal distal to the glans. However, the distinction of macrosetae A as opposed to C is subtle and susceptible to subjectivity.

Concerning the four species of podoctids studied here, some features other than topology might come into play to help in the distinction of the macrosetae A and C: (a) In *Eurytromma pictulum* (Figs. 8a–c), A1–A3 are curved, blunt, longitudinally grooved, while C1–C3 are straight, acuminate and twisted along the main axis. (b) In *Hoplodino continentalis* (Figs. 8d–

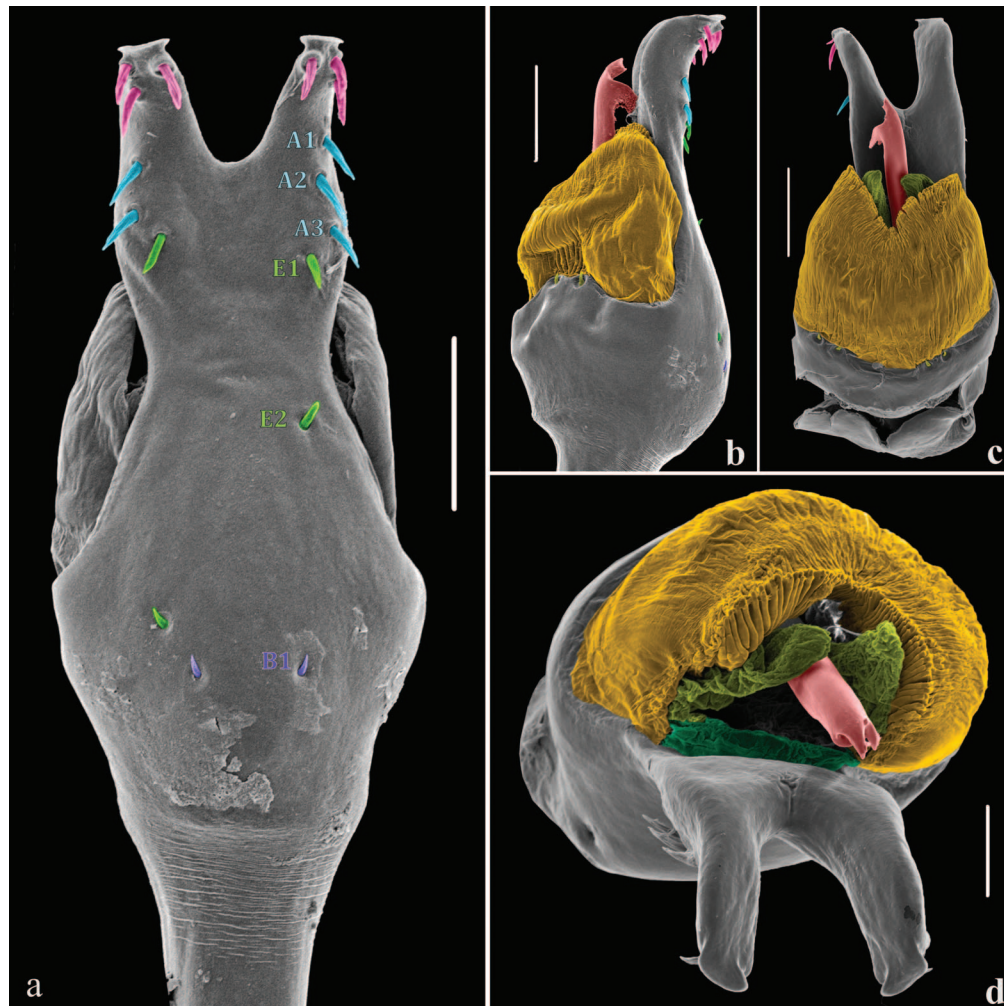


Figure 10.—*Santobius annulipes* (QM AK 001 [a, b]; AMNH AK 280 [c, d]), from Fiji. Male genitalia, pars distalis: a. Ventral view; b. Dextro-lateral view; c. Dorsal view; d. Apical view. Scale bars: 100 μm (a, b, c), 50 μm (d).

f), A1–A2 are lanceolate and slightly twisted on basal part, while C1–C2 are provided with three strong longitudinal carenae and are strongly twisted in the medial portion. (c) In *Strandibalonius esakii* (Figs. 9a–d), A1–A3 are plain spatulate, while C1–C3, besides being spatulate, also have an extra element, slightly smaller than the main element, with both elements separated only in the apex. Likewise, in C1–C3, there are two clearly separated regions: a peduncle, which abruptly widens in a distal flare, while in A1–A3, the slope is gradual. (d) In *Santobius annulipes* (Figs. 10a–c), all macrosetae A and C are very similar to each other, bearing longitudinal carenae. It appears that in C, however, the carenae are more strongly defined, making the distal half of the seta slightly lanceolate.

In contrast with A and C, the two pairs of macrosetae D can be easily recognized based exclusively on topology because they are most often dorsal, located more proximal, associated with the glans, sometimes migrating to dorso-lateral or even in extreme cases frankly lateral. The same happens with macrosetae E1–E2, which are very conservative, usually forming a ventro-distal quadrangle, and occasionally migrating to a latero-ventral flange. The one pair of macrosetae B is often associated with three pairs of macrosetae, and located more

proximal on the lateral of truncus, sometimes continuing the girdle formed by macrosetae D around the base of glans.

In conclusion, the AE11 pattern of penial setation described for Gonyleptoidea also occurs in Podoctidae. In spite of the widely diverse genital morphology in Podoctidae, the clustering of macrosetae D1–D2 in a dorsal position, basal to the follis occurs in all studied members of the family. This, along with a reduction in size of these macrosetae D1–D2 could be a possible synapomorphy for the family because these traits are presented in the four non-closely related species studied here.

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