

RESEARCH PAPER

Rehabilitation of *Mormoschema* (Hemiptera: Heteroptera: Pentatomidae): generic status restituted and tribal placement revised

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Accepted:
13th November 2023

Published online:
28th December 2023

Abstract. *Tolumnia immaculata* Distant, 1900 (Hemiptera: Heteroptera: Pentatomoidea: Pentatomidae: Pentatominae) is redescribed based on the study of primary types and additional specimens from India and Sri Lanka. This species is found to not be congeneric with the rest of *Tolumnia* Stål, 1868, including the type species. This verifies the original opinion of BREDIN (1909), which was subsequently rejected by DISTANT (1918) but without argumentation. As a result, the monotypic genus *Mormoschema* Breddin, 1909, stat. restit., is removed from synonymy with *Tolumnia*, and the combination *Mormoschema immaculatum* (Distant, 1900) is restituted. The male and female genitalia of *Mormoschema immaculatum* are described in detail. The tribal placement of *Mormoschema* is discussed; the genus is excluded from Cappaeini and transferred to Eysarcorini. *Buddleja asiatica* and *Scrophularia* sp. (Scrophulariaceae) are recorded as feeding plants for *M. immaculatum*.

Key words. Hemiptera, Heteroptera, Pentatomidae, Cappaeini, Carpocorini, Eysarcorini, Scrophulariaceae, food plant, genitalia, lectotype, tribal placement, India, Oriental Region

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Introduction

The Pentatomidae is the third most diverse family of Heteroptera, which includes nine subfamilies, 950 genera and nearly 5000 described species (RIDER et al. 2018, ROCA-CUSACHS et al. 2022). The taxonomic research within this family has faced two main obstacles: i) lack of well-supported hypotheses about infrafamilial phylogenetic relationships, and ii) shortage of revisionary works that enable identification of genus- and species-group taxa, especially in the fauna of the Old World tropics and Australia. The first obstacle was recently addressed by GENEVCIOUS et al. (2021), ROCA-CUSACHS et al. (2022) and YE et al. (2022), in phylogenetic analyses that incorporated broad taxon-sampling and Sanger sequence data. These were complemented by several papers on mitochondrial genomes of selected target species, which assessed their phylogenetic position (e.g. CHEN et al. 2021, LI et al. 2021, XU et al. 2021, ZHAO et al. 2021, GONÇALVES et al. 2022, MU et al. 2022, DING et al. 2023, JIA et al. 2023, WANG et al. 2023). The taxonomic works on New World Pentatomidae

have been comparatively plentiful since the 1950s to the present, including several taxonomic papers over the last three years (BARROS et al. 2021a,b; BIANCHI 2021; BIANCHI et al. 2021a,b; BITAR et al. 2023; CAMPOS & FERNANDES 2022; CORREIA et al. 2021; CUNHA et al. 2022; DELLAPÉ & FUENTES 2021; EGER 2021; FAÚNDEZ et al. 2021; FERNANDES & SILVA 2021; GRAZIA et al. 2022; LÓPEZ et al. 2023; MENDONÇA et al. 2021, 2023a,b; NUNES et al. 2022; PAIM et al. 2022; ROELL et al. 2021a,b; ROSSO & CAMPOS 2021; SAMPAIO & CAMPOS 2023; SAMPAIO et al. 2023; SILVA & CAMPOS 2021; SILVA & FERNANDES 2022a,b; THOMAS 2021).

Despite the recently revived interest in the taxonomy of the Old World Pentatomidae, the number of published papers does not approach the taxonomic outputs for the Americas (viz KMENT et al. 2021a,b, 2023; RÉDEI & TSAI 2021; ROCA-CUSACHS et al. 2021; SALINI et al. 2021a,b, 2023a,b; SALINI & KMENT 2021; SALINI & ROCA-CUSACHS 2021; SILVA et al. 2021; EGER 2022; GAPON 2023a,b). In the previous decades, the knowledge of Afrotropical Pentatomidae was enhanced significantly, in a series of valuable



papers by the late Rauno E. Linnavuori, published in the 1970s and 1980s (e.g., LINNAVUORI 1982). In contrast, the number of papers on the Pentatomidae of the Oriental Region, especially for taxa from the Indo-Pakistan sub-continent, by Imtiaz Ahmad and his students, issued from 1970a to 2000s, is substantive (e.g. AHMAD & KAMALUD-DIN 1977, AHMAD & ZAIDI 1989, HASAN & AHMAD 1988, HASAN 1993, ZAIDI 1994). Although these papers adhered to orthodox taxonomic practices and often cladistic in nature, they are problematic for several reasons. The first is that they largely underestimate intraspecific variability, with species (re)descriptions often based on a single specimen or at best a few specimens. These treatments often over-rely on fine differences that are either artefactual or variable, such as the relative lengths of the labial and antennal segments, and the shape and number of ductuli on the apical receptacle of the spermatheca. They are also compromised by biased taxon sampling (e.g. ignoring taxa described from former Soviet Central Asia) and the lack of study or incorrect interpretation of the pertinent types (for details see e.g. SALINI 2019, SALINI & KMENT 2021, KMENT et al. 2021a, GAPON 2023b). Insufficient knowledge of the taxonomy of Old World Pentatomidae taxa hampers correct identification of species, which is most concerning in the case of significant invasive pest species such as the brown-marmorated stink bug, *Halyomorpha halys* (Stål, 1855) (KMENT et al. 2021a, SALINI et al. 2021c), and the yellow-spotted stink bug, *Erthesina fullo* (Thunberg, 1783) (KMENT et al. 2023).

As part of our taxonomic revision project focused of the genus *Halyomorpha* Mayr, 1864 and its relatives currently assigned to the tribe Cappaeini, we have undertaken research on the genus *Tolumnia* Stål, 1868. It currently contains 13 valid species, distributed in the Oriental Region from India, Sri Lanka and central China to the Philippines, and Indonesia: Sulawesi, and the Lesser Sunda Islands (Salini et al., in prep.), as follows: *T. antennata* Distant, 1902, *T. basalis* (Dallas, 1851), *T. elongata* Hasan & Ahmad, 1988, *T. gutta* (Dallas, 1851), *T. horni* Breddin, 1909, *T. immaculata* Distant, 1900, *T. latipes* (Dallas, 1851), *T. longirostris* (Dallas, 1851), *T. malayensis* Hasan & Ahmad, 1988, *T. maxima* Distant, 1902, *T. papulifera* Bergroth, 1922, *T. southwoodi* Hasan & Ahmad, 1988 and *T. trino-tata* (Westwood, 1837); the latter is the type species by subsequent designation (DISTANT 1902). The main papers published on this genus are DALLAS (1851) (descriptions of new taxa), DISTANT (1902) (review of Indian fauna), HASAN & AHMAD (1988) (revision of Malayan fauna), and ZAIDI (1994) (review of Indian species), but it has never been critically revised in total. During the process of revising *Tolumnia*, we concluded that one of the examined species was not congeneric with the type species and required its exclusion from the genus.

Tolumnia immaculata was originally described by DISTANT (1900) from a series of specimens collected in India (Nilgiri hills and Kotagira [corrected as Kotagiri by DISTANT (1902)]) and Sri Lanka. According to DISTANT (1900), this species was closely related to *Tolumnia latipes*, separated from it by the narrower and more attenuated

head, the absence of callose spots on the scutellum, and the ventral surface of the abdomen having a median longitudinal fascia. BERGROTH (1908) catalogued this species from India. BREDDIN (1909), however, studied specimens from Sri Lanka that he identified as ‘presumably belonging of *T. immaculata*’. BREDDIN (1909) was certain that this species had nothing to do with *Tolumnia*, erected a new genus for it, *Mormoschema*, established a new combination, *Mormoschema immaculatum* (Distant, 1900), redescribed the taxon in detail (including the external scent efferent system of the metathoracic scent glands and the outline of the male genital capsule), and noticed some differences between the specimens studied by him and the original description. Concerning the relationships of his new genus, BREDDIN (1909) wrote: ‘This little distinctive genus agrees in the form of the external openings of the thoracic gland with the American genus *Mormidea* Am. and Serv. and the Palaearctic *Codophila* M. and R., being set to their vicinity also because of their other characters. However, it differs considerably from the latter one due to the form of the pronotal margin, the almost absent grooving of the tibiae and the completely different colouration. The animal does not appear to have any close relationships to *Tolumnia* [translation from German]’. KIRKALDY (1909) accepted BREDDIN’s (1909) opinion in his World catalogue.

DISTANT (1918), however, synonymized the two genera by simply listing *Mormoschema* in synonymy of *Tolumnia* without mentioning any particular reason for the action. Later, CHATTERJEE (1934), CHANDRA (1953), and MATHUR & SINGH (1960) reported additional localities and the first associated plant records from south India. Finally, ZAIDI (1994) redescribed the species in his poor treatment of the Indian species of *Tolumnia*; he, however, completely omitted the paper by BREDDIN (1909), and he managed to overlook all of the important differences that distinguished this taxon from its supposed congeners.

In this work, BREDDIN’s (1909) opinion is confirmed. The genus *Mormoschema* is removed from synonymy with *Tolumnia* and is redescribed, including the structures of its male and female genitalia. Additionally, new feeding plant records for the species are provided.

Material and methods

The specimens studied were collected as part of a survey conducted at Yercaud in the District Salem, Tamil Nadu, and within the subcampus of ICAR-NBAIR, Bangalore, Karnataka, India. The name bearing types and other materials available in the collections of European museums, with particular reference to those held in the Natural History Museum, London (coll. Distant) and Senckenberg German Entomological Institute in Müncheberg (coll. Breddin). External observations and dissections were made using a Leica S8 APO microscope, and measurements were made with a Leica M205A stereomicroscope. Photographs of type material were taken using a Canon EOS 5 DSR camera attached to a customized movable stand and dedicated system, and stacked images from multiple layers were merged using Helicon Remote (ver. 4.3.0 W) software (BMNH). Other materials were imaged using

a Leica DFC 420 camera mounted on a Leica M205A stereomicroscope and were processed using the software Automontage® (NIM). Uncoated specimens were examined with a Hitachi S-3700N environmental scanning electron microscope, housed in the Department of Palaeontology, National Museum of the Czech Republic in Prague. The images were edited using Adobe Photoshop CS (Version 8.0). The procedure used to dissect the male genitalia followed SALINI (2016). The female genitalia were dissected after placing the entire abdomen in hot 10% potassium hydroxide solution (KOH) for 10–15 minutes. The internal contents were cleared after thoroughly washing them in distilled water 2–3 times, and then with the help of fine forceps, the terminalia and spermatheca were carefully detached from the abdominal ventrites.

All measurements are given in millimetres and presented as median, with minimum and maximum values given in parentheses. The following dimensions were measured: Body length (from apex of mandibular plates to apex of membrane, anterodorsal view), head length (from apex of mandibular plates to anterior margin of pronotum, dorsal view), head width (width of head including compound eyes, dorsal view), interocular width (between inner margins of compound eyes, dorsal view), length of each antennomere, length of each labiomere, pronotum length (medially, from anterior to posterior margins of pronotum, dorsal view), pronotum width (maximum width between humeri, dorsal view), scutellum length (medially from base to apex, dorsal view) and scutellum width (maximum width at base between basal angles of scutellum, dorsal view). Morphological terminology follows TSAI et al. (2011), RÉDEI & TSAI (2021, 2022), and SALINI & KMENT (2021); specialised terms follow these papers: antennomeres – ZRZAVÝ (1990), external scent efferent system of the metathoracic scent glands – KMENT & VILÍMOVÁ (2010), filter processes of metathoracic spiracle – ZHANG et al. 2020, female external genitalia – ZHOU & RÉDEI (2020). The terminology concerning the plant associations follows BURCKHARDT et al. (2014). The distribution map was created using SimpleMapp (SHORTHOUSE 2010).

In quoting the labels of the material examined, a slash (/) is used to divide data on different rows of one label, a double slash (//) is used to divide the data on different labels, authors' comments are given in square brackets [], and the following abbreviations are used: [hw] = handwritten, [p] = printed. Unless stated otherwise, the described labels are off-white.

The specimens examined are deposited in the following collections:

BMNH	The Natural History Museum, London, United Kingdom;
ISNB	Institut Royal des Sciences Naturelles, Bruxelles, Belgium;
NHRS	Swedish Museum of Natural History, Stockholm, Sweden;
NHMW	Naturhistorisches Museum in Wien, Vienna, Austria;
NIM	National Insect Museum of Indian Council of Agricultural Research-National Bureau of Agricultural Insect Resources, Bangalore, India (ICAR-NBAIR);
NMPC	National Museum of the Czech Republic, Praha, Czech Republic;
SDEI	Senckenberg German Entomological Institute, Müncheberg, Germany;
UASB	University of Agricultural Sciences, Bangalore, India.

Taxonomy

Mormoschema Breddin, 1909, stat. restit.

Mormoschema Breddin, 1909: 269–270 (original description). Type species: *Tolumnia immaculata* Distant, 1900, by monotypy.

Mormoschema: KIRKALDY (1909): 365 (catalogue); DISTANT (1918): 130 (listed as synonym of *Tolumnia*).

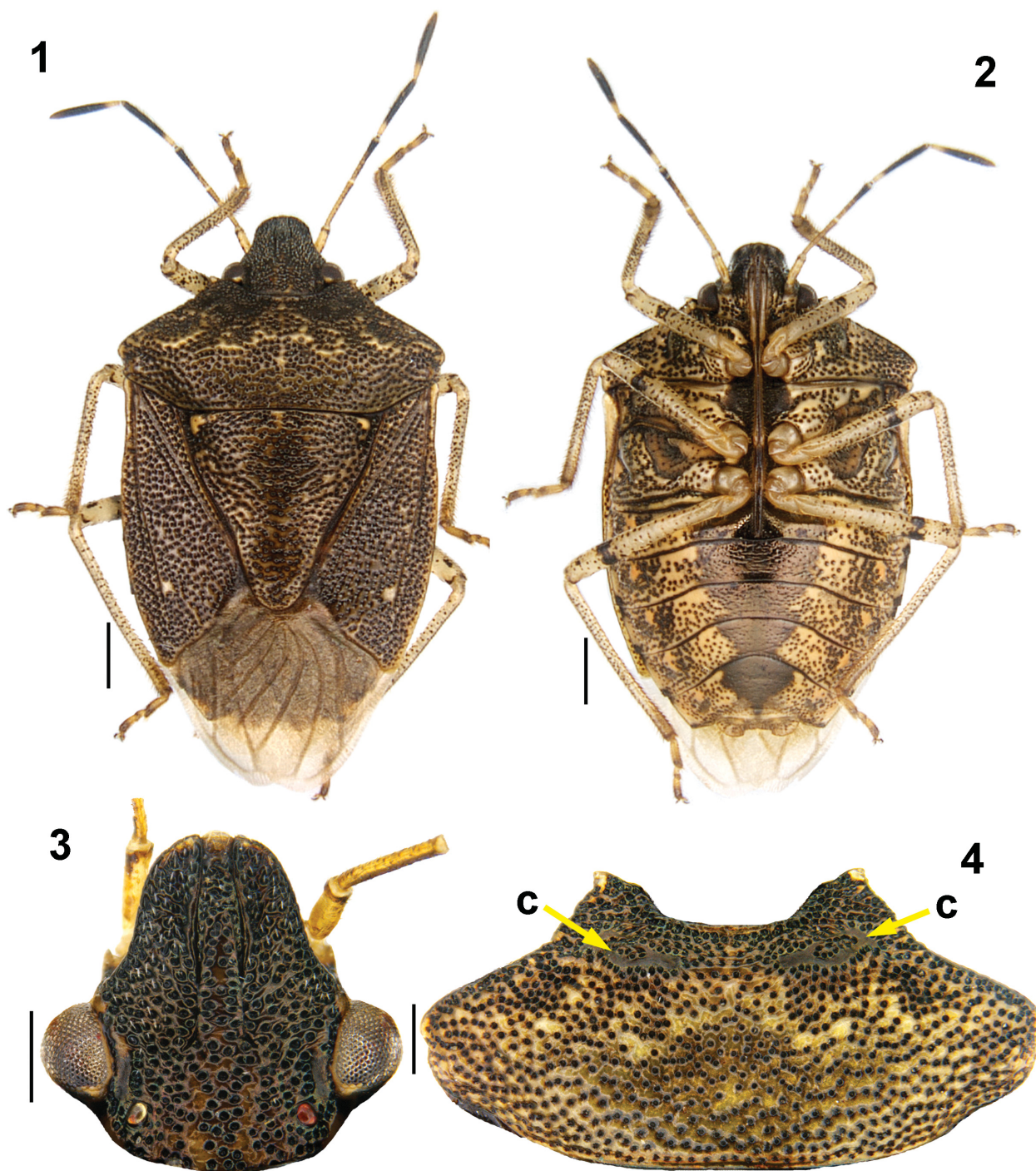
Redescription. Colouration, integument and vestiture. Dorsum as in Figs 1 and 5, with broad median stripe ventrally dark brown to black (Figs 2, 7), lateral margins of body venter, antennae in part, and legs whitish to ochraceous (for details see species redescription).

Body above including head, pronotum, scutellum, and hemelytra (except membrane) with dense, small but coarse, black punctures, uniformly distributed (Figs 1–4, 8–10). Head ventrally and propleuron (Fig. 9) with dense, coarse, black punctures; punctures on meso- and metapleuron (Fig. 13), and on abdomen (Fig. 2) sparse, black. All femora with sparsely distributed coarse, round, black spots (Fig. 2); all tibiae with dense, round, fine punctures. Posterior one third of genital capsule, including posterolateral projections, with uniformly distributed, moderately large, round, dark brown punctures (Figs 22–24).

Dorsum of body glabrous except the following: punctures on dorsum of head possess very short setae, few longer setae near apex of clypeus (Fig. 8), antennomeres I–IV with sparse, short, semi-erect setae, golden yellow. Legs and abdomen ventrally possessing very fine, short, golden setae. External male genitalia with median emargination of dorsal rim of genital capsule possessing moderately elongate sparse, golden-brown setae; ventral rim and infoldings of ventral rim with short golden setae; posterior half of genital capsule ventrally with moderately elongate, and anterior half with short, sparse, golden setae (Figs 16–18). External female genitalia (valvifers VIII–IX, laterotergites VIII–IX) dorsally with golden setae.

Structure. Head (Figs 3, 8) gradually narrowed towards apex; mandibular plates slightly concave in front of eyes, as long as clypeus; clypeus apically free. Antenniferous tubercles visible in dorsal view. Antennae pentamerous, slender. Antennomeres from shortest to longest: I < IIb < IIa < III < IV; scape (I) cylindrical, shortest and stoutest; antennomeres IIa, IIb and III cylindrical, slender; distiflagellum (IV) spindle-shaped (Figs 1–2). Bucculae (Fig. 9) short, low, rounded anteriorly, rectangular posteriorly. Labiomere I short, apical fourth surpassing posterior margin of bucculae and slightly surpassing anterior pronotal margin; apex of labium reaching ventrite III (Fig. 2).

Pronotum (Figs 4, 10). Anterolateral angles rectangular with minute laterally directed denticle; anterolateral margins slightly and broadly concave in middle; anterior half of anterolateral margins slightly granulated. Humeral angles narrowly rounded, more-or-less conspicuously notched apically, bent slightly downwards; posterolateral angles broadly rounded, posterior margin of pronotum nearly straight. Pronotal disc with anterior half flat, inclined, in same plane with dorsum of head; posterior half of pronotal disc horizontal. Pronotum submedially on anterior half with pair of calli, bearing conspicuous black unpunctured cicatrices (Fig. 4: c).



Figs 1–4. *Mormoschema immaculatum* (Distant, 1900), stat. restit., India: Karnataka: 1–2 – habitus (1 – dorsal view, 2 – ventral view); 3 – head (dorsal view); 4 – pronotum. Lettering: c – cicatrix. Scale bars: 1 mm (1–2), 0.5 mm (3–4). Photo: Salini.

Scutellum (Fig. 1). Lateral margins slightly concave in frenal portion; apex of scutellum narrowly rounded. Disc of scutellum slightly gibbose prefrenally, postfrenal portion nearly flat.

Hemelytra. Membrane translucent, broadly rounded apically, distinctly surpassing apex of abdomen, bearing 6 prominent, simple, brown veins, without reticulate venation.

Thoracic sterna and pleura. Mesosternum with low median longitudinal carina, mesosternum flat (Figs 12–13: mc). Ostioles small, oval, each directed laterad, accompa-

nied by deep periostolar depression (Fig. 14). Peritremes short, spout-shaped, each with apex distinctly elevated above surrounding metapleuron (Figs 13–14, 34: p). Evaporatoria (Figs 13, 34) well-developed on metapleura, each forming a broad triangular patch, emarginated by sharp ridge sublaterally, extending onto mesopleuron, forming only a narrow band along anterior margin of metathoracic spiracle, not reaching lateral margin of mesopleuron (Fig. 13). Metathoracic spiracle long, protected by reticulate filter processes (Figs 13: s, 15).

Legs. Outer (dorsal) surface of tibiae with narrow,



Figs 5–7. *Mormoschema immaculatum* (Distant, 1900), stat. restit., syntype from India: Kotagiri. 5 – habitus (dorsal view); 6 – labels; 7 – habitus (ventral view). Scale bars: 1 mm (5, 7). Photo: Salini.

indistinct longitudinal groove. All tarsi with tarsomere II shortest and tarsomere I longer than III.

Pregenital abdomen. Abdominal ventrites medially rounded, neither keeled or grooved (Fig. 2), ventrite III only slightly produced anteromedially, not surpassing over metapleuron (Fig. 12). Posterolateral angles of each connexival segment III–VII, angular, without denticle (Fig. 2). Spiracles on ventrites III–VII whitish, surrounded by narrow brown circle, without any adjacent callosities (Fig. 11). A pair of trichobothria present on each side of ventrites III–VII posteriad of spiracle (Fig. 11: t).

Male genitalia (Figs 16–31). **Genital capsule** (Figs 16–19, 22–24) slightly longer than wide, subquadrate with well-developed posterolateral (= caudal) lobes. Dorsal rim (Figs 16, 22: dr) deeply, concavely excavated, with narrow median emargination. Ventral rim (Figs 17, 23: vr) with narrow medial rectangular notch as wide as posterolateral lobes (Figs 17, 23: pl); infoldings of ventral rim moderately developed with narrow, short, V-shaped notch medially. **Paramere** (Figs 20–21, 25–27) with large bilobed crown, one lobe slightly smaller with apex twisted mesad, other lobe larger, with short, triangular projection directed mesad, stem broad, short. **Phallus** (Figs 28–31). Phallosome nearly of uniform width in

ventral view with base slightly constricted, hinges not well-developed, dorsal wall convex basally, ventral wall concave medially, slightly convex basally. Three conjunctival processes, a short one dorsally (Figs 30, 31: cpd) and a pair of obovate ventral conjunctival processes (Fig. 30: cpv). Processes of aedeagus absent. Aedeagus (Figs 29–30, 31: ad) elongate tube-like.

Female genitalia (Figs 32–33). **Terminalia** (Fig. 33). Valvifers VIII (vlf8) rectangular, with mesial margins slightly concave medially. Valvifers IX (vlf9) nearly trapezoidal. Laterotergites IX (lt9) elongate subtriangular, each with posterior apex arcuately rounded. Laterotergites (lt8) triangular. **Gynatrium** with inverted U-shaped sclerite surrounding spermathecal opening (Fig. 32: us), ring sclerites absent. **Spermatheca** (Fig. 32). Spermathecal dilation long with proximal one third opaque, at its base twisted upwards; intermediate portion of spermatheca short, proximal flange narrower than distal flange; apical receptacle orbicular without any ductules (Fig. 32: ar).

Differential diagnosis. This genus resembles members of *Eysarcoris* Hahn, 1834, or *Carbula* Stål, 1865, in the shape and size of the body, the short, spout-shaped peritremes, which do not reach the middle of the metapleuron, the bilobed crown of the parameres, and the

absence of finger-like processes on the apical receptacle of the spermatheca. *Mormoschema* is distinct in possessing the following characters: humeral angles slightly depressed or bending downwards, medially notched or incised, forming anterior and posterior lobes (Figs 1, 4–5, 10); anterior half of anterolateral pronotal margins with granulation; spermathecal dilation long with proximal one-third golden brown coloured, and the proximal end opaque, twisted upwards; ring sclerites absent; and the posterolateral lobes of the genital capsule arcuately rounded. **Etymology.** BREDDIN (1909) created the name combining the generic name *Mormidea* and the latinized Greek word *schema* (σχῆμα), meaning shape, figure, form, manner, or posture. The word *schema* could be treated as feminine in Latin or neuter in Greek. As BREDDIN (1909) combined this generic name with a species epithet using a neuter ending (*immaculat-um*), the gender of *Mormoschema* should therefore be considered as neuter (Article 30.1.2 of the ICZN 1999).

Included species. Monotypic.

***Mormoschema immaculatum* (Distant, 1900),
comb. restit.**

Tolumnia immaculata Distant, 1900: 168 (original description). Syntypes: Ceylon; India: Nilgiri Hills, Kotagira (BMNH).

Tolumnia immaculata: DISTANT (1902): 155 (original description repeated); BERGROTH (1908): 162 (catalogue); KIRKALDY (1909): 51 (catalogue, distribution); DISTANT (1918): 130 (original combination restored); CHATTERJEE (1934): 12 (faunistics, associated plant); CHANDRA (1953): 96 (faunistics); MATHUR & SINGH (1960): 66 (associated plant); ZAIDI (1995): 512 (key to species), 513: figs 1A–G (redescription; illustrations of habitus, external scent efferent system, genital capsule, paramere, penis, external female genitalia and spermatheca).

Mormoschema immaculatum: BREDDIN (1909): 270–271 (new combination); KIRKALDY (1909): 365 (catalogue).

Type material examined. SYNTYPES: **INDIA:** 1 ♀, ‘Kotagiri [hw] // Atkinson / Coll. / 92–6. [p] // NHMUK 013589968 [p] // ♀ [p] (BMNH, pinned; Figs 5–7); 1 ♀, ‘Kotagiri [hw] // Atkinson / Coll. / 92–6. [p] // ♀ [p] (BMNH, pinned); 1 ♀, ‘Nilgiris / (Hampson) [hw] // Distant Coll. / 1911–383 [p] // ♀ [p] (BMNH, pinned); 1 ♂, ‘*immaculata* / Dist. [hw] // Nilgiri / (Hampson [sic], p) // Distant Coll. / 1911–383 [p] // ♂ [p] (BMNH, pinned). **SRI LANKA:** 1 ♀, ‘Type [p, round label with red circle submarginally] // *Pundaloya / Ceylon* [p] II [hw] // Ceylon / Green Coll. / 91–26 [p] // *immaculata* / Dist. [hw] // 101 [hw, grey label] // BRIT. MUS. / TYPE No. / HEM [p] 993 [hw, pink label] // ♀ [p] (BMNH, pinned); 1 ♀, ‘101 [hw, grey label] // Ceylon / Green Coll. / 91–26 [p] // ♀ [p] (BMNH, pinned); 2 ♀♀, ‘Ceylon / (Lewis) [p] // Distant Coll. / 1911–383 [p] // ♀ [p] (BMNH, card-mounted); All the syntypes bear the following two labels: ‘SYNTYPUS / *TOLUMNIA / IMMACULATA* / Distant, 1900 stat. restit. / labelled: SALINI & KMENT 2023’ [p, red label] and ‘MORMOSHEMA / IMMACULATUM / (Distant, 1900) / det. SALINI & KMENT 2023’ [p].

Additional material examined. The material was identified by Salini unless stated otherwise. **INDIA:** **KARNATAKA:** Nandi Hills, 1478 m a.s.l., 13°38'N 77°70'E, 6.ix.2013, 1 ♂, T. Vinayaka lgt. (UASB); Coorg, Thadiyandamal hills, 12°33.729'N 75°37.479'E, 1328 m a.s.l., 12.iv.2011, 1 ♀, H. M. Yeshwanth lgt. (UASB); Bengaluru, Attur, 19.ix.2018, 5 ♂♂, ex. *Buddleja asiatica*, G. Prabhu lgt. (NIM); Yelahanka, Attur, 10.vii.2019, 1 ♀, Salini S. lgt. (NIM); Chikballapur, Mysore, i.1915, 1 ♂, T. V. Campbell coll., Pres. by Imp. Bur. Ent., Brit. Mus. 1921–494, B. Uvarov det., P. Kment revid. (BMNH); Chikballapura + KK + Nilgiris, Nilgiri Hills, v.1915, 3 ♀♀, T. V. Campbell, T. V. Campbell Coll., Brit. Mus. 1930–595, P. Kment det. (BMNH); South India, T. [?], iv.1915, 3 ♂♂ 3 ♀♀, T. V. Campbell Coll., Brit. Mus. 1930–595, P. Kment det. (BMNH); South India, T. [?], v.1915, 2 ♀♀, T. V. Campbell Coll., Brit. Mus. 1930–595,

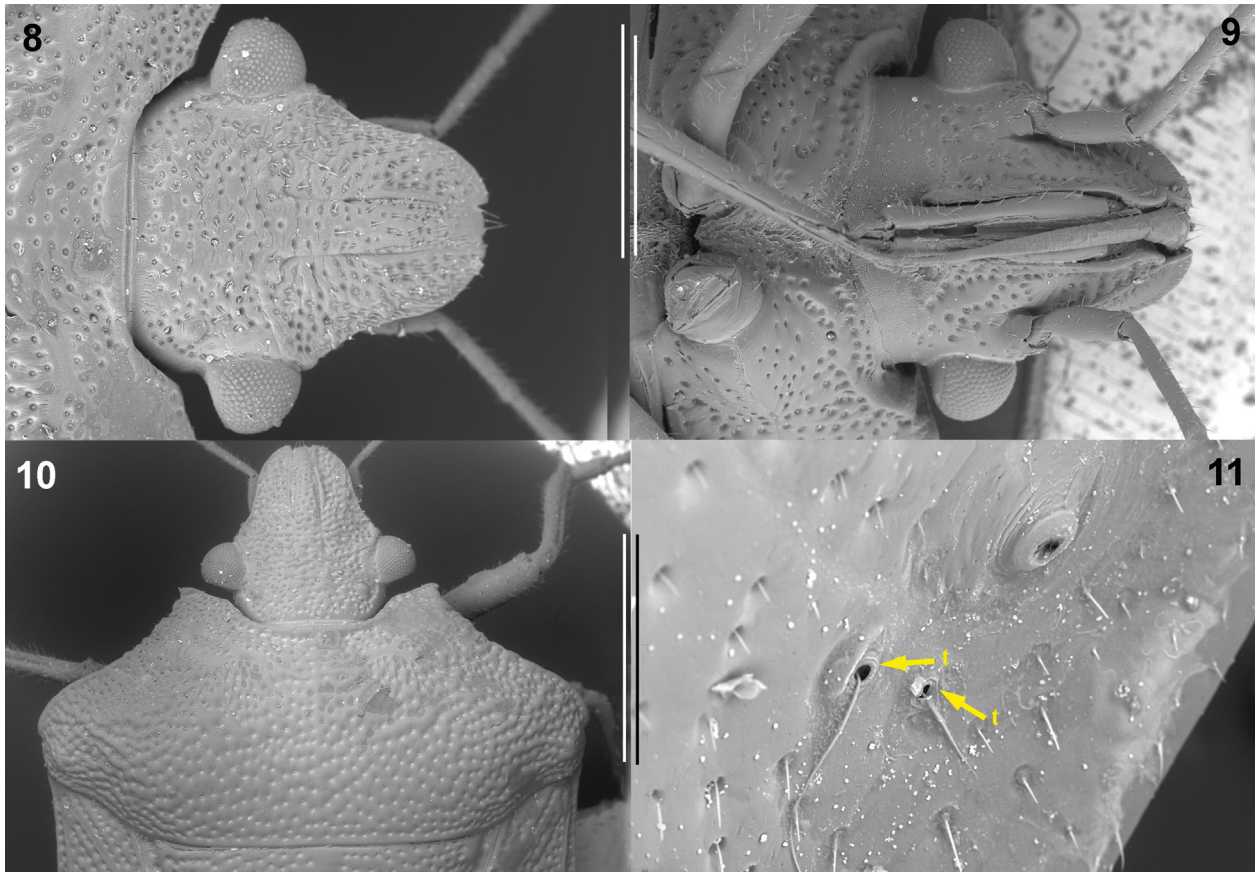
P. Kment det. (BMNH); South India, K.K., 5000 ft [= 914.4 m a.s.l.], v.1914, 1 ♂ 1 ♀, T. V. Campbell Coll., Brit. Mus. 1930–595, P. Kment det. (BMNH); South India, N. Dg. x.1913, 1 ♂ 2 ♀♀, T. V. Campbell Coll., Brit. Mus. 1930–595, P. Kment det. (BMNH); South India, N. Drug, x.1913, 1 ♂, T. V. Campbell Coll., Brit. Mus. 1930–595, P. Kment det. (BMNH). **TAMIL NADU:** Salem, Yeracaud, 28.ix.2021, 2 ♂♂ 2 ♀♀, ex. *Scrophularia* sp., K. V. Maruthi lgt. (NIM); Kodaikanal, Pullney Hills, 3 ♂♂, Distant Coll. 1911–383 (2 ♂♂ BMNH, 1 ♂ ISNB); S. India, Nilgiri Hills, 1 ♂ 8 ♀♀, 1903–63, P. Kment det. (BMNH); S. India, Nilgiri Hills, 1 ♂ 8 ♀♀, T. V. Campbell, Ex Coll. E. A. Butler, B. M. 1926–171, P. Kment det. (1 ♂ 7 ♀♀ BMNH, 1 ♀ NMPC); S. India, Nilgiri Hills, 1 ♀, T. V. Campbell, Distant det.?, P. Kment revid. (NHRS); S. India, Coromandel Coast, Tranquebar, iv.1947, 1 ♂ 1 ♀, P. S. Nathan lgt., P. Kment det. (NMPC). **SRI LANKA:** Ceylon, 1 ♀, Felder [lgt.] (NHMW); Colombo, 29.iii.1929, 9 ♂♂ 3 ♀♀, Pres. by Imp. Bur. Ent. Brit. Mus. 1930–197, P. Kment det. (8 ♂♂ 3 ♀♀ BMNH, 1 ♂ NMPC); Ceylon, Kandy, 5-09, 1 ♀, Distant Coll., B.M. 1911–383 (BMNH); Namunukuli, ii.1910, 1 ♂ 3 ♀♀, Distant Coll. 1911–383, P. Kment det. (BMNH); Ceylon, Nuwara Eliya, 6,234–8,000 ft [= 1900.1–2438.4 m a.s.l.], 8.–11.ii.[18]82, 3 ♂♂ 1 ♀, G. Lewis, 1910–320, P. Kment det. (Figs 8–21) (2 ♂♂ 1 ♀ BMNH, 1 ♂ NMPC); Ceylon, Anuradhapura, 1 ♂, W. Horn lgt., G. Breddin det., P. Kment revid. (SDEI); Ceylon, Colombo, 1 ♂ 1 ♀, W. Horn lgt., G. Breddin det., P. Kment revid. (SDEI); Ceylon, Horton Plain, 1 ♀, W. Horn lgt., G. Breddin det., P. Kment revid. (SDEI); Ceylon, Nalanda, 1 ♀, W. Horn lgt., G. Breddin det., P. Kment revid. (SDEI).

Redescription. Colouration. Body above (Figs 1, 3–5) dark brown to black except: antennae with scape (I), basipedicellite (IIa), basal half to two-thirds of distipedicellite (III), and basal one-fourth of basiflagellum (IV) and distiflagellum (V), lateral margins of pronotum, hypocostal lamina (Fig. 2), one small callose spot on each anterolateral angle of scutellum and a very small median callose spot along its anterior margin (spots on anterior margin of scutellum arranged in a line), a small round callose spot on disc of each corium (Fig. 1), and middle portion of each connexival segment, whitish to ochraceous; membrane infuscated, translucent.

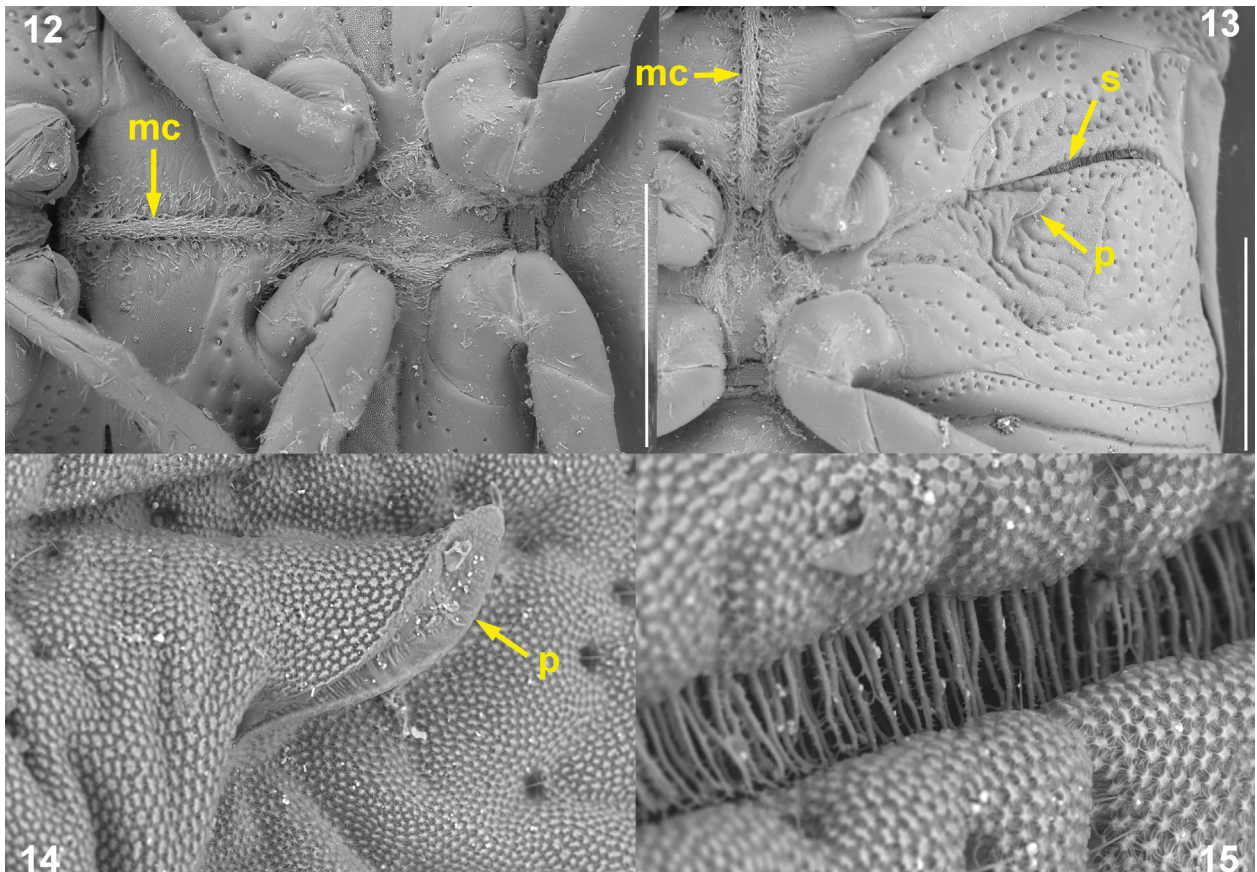
Ventral surface (Figs 2, 7) whitish to ochraceous except mandibular plates laterally, labiomere IV, pro-, meso-, and metasternum, broad median longitudinal spot on abdominal venter, gradually narrowing posteriad, undulated on ventrites V and VI, narrow ring around each spiracular opening, a broken ring on each femur near distal one-fourth, apical half of claws, and anterior and posterolateral angles of connexival segments, black.

Integument, vestiture and structure as in the generic redescription.

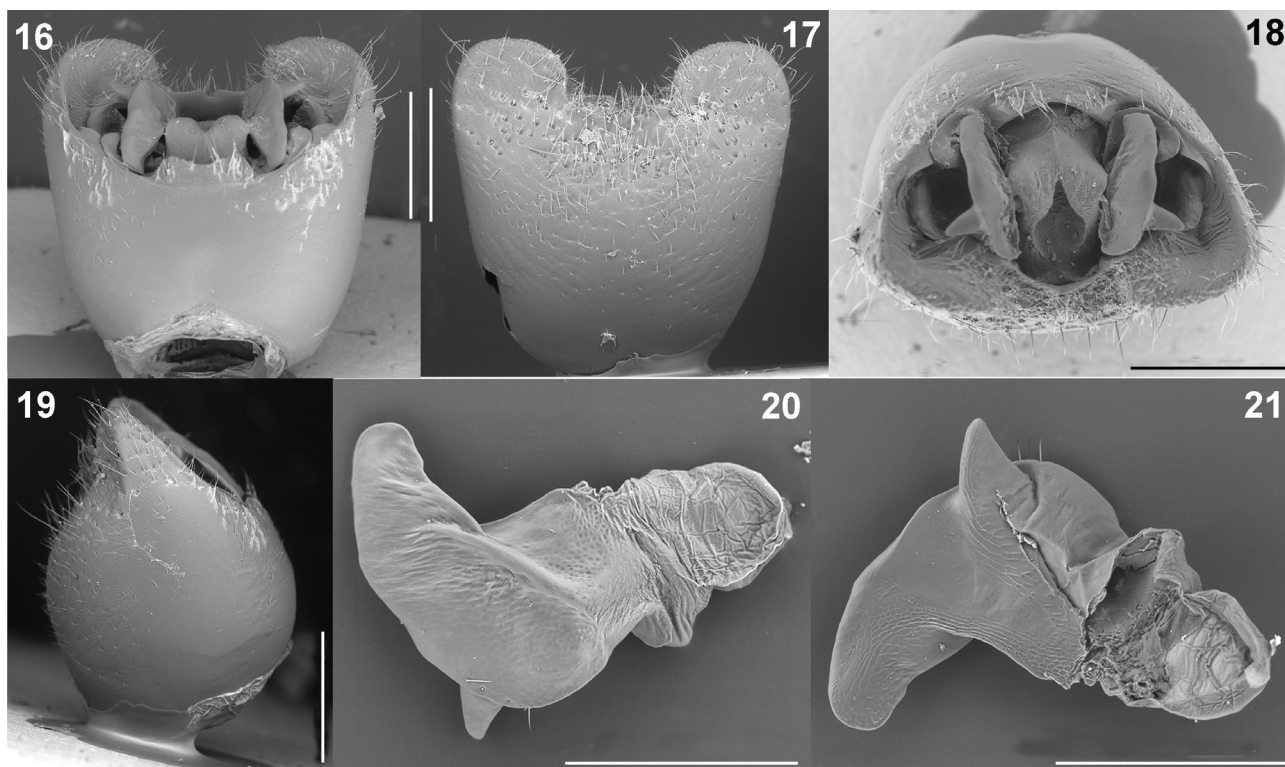
Male genitalia (Figs 16–31). **Genital capsule** (Figs 16–19, 22–24) slightly longer than wide, subquadrate with posterolateral (= caudal) lobes broad, well-developed, apices of posterolateral lobes arcuately rounded. Dorsal rim (Figs 16, 22: dr) deeply and concavely excavated with narrow median emargination; median emargination concave; infoldings of dorsal rim slightly developed with partially developed parameral sockets. Ventral rim (Figs 17, 23: vr) with narrow rectangular notch as wide as posterolateral lobes; infoldings of ventral rim moderately developed with narrow, short, V-shaped notch medially. **Parameres** (Figs 20–21, 25–27) with large bilobed crown, one lobe slightly smaller with apex twisted mesad, other lobe larger, with short, triangular projection directed mesad, stem broad, short. **Articulatory apparatus** (Fig. 28). Basal plate and support bridge complex, fused to form elongate subtri-



Figs 8–11. *Mormoschema immaculatum* (Distant, 1900), stat. restit., Sri Lanka: Nuwara Eliya: 8–9 – head (8 – dorsal view, 9 – ventral view); 10 – head and thorax (dorsal view); 11 – trichobothria on abdominal ventrite VII. Lettering: t – trichobothrium. Scale bars: 1 mm (8–9), 2 mm (10), 200 μ m (11). Photo: P. Kment.



Figs 12–15. *Mormoschema immaculatum* (Distant, 1900), stat. restit., Sri Lanka: Nuwara Eliya: 12 – meso-, metathorax and abdominal ventrite III; 13 – external scent efferent system of the metathoracic scent gland; 14 – detail of peritreme; 15 – detail of metathoracic spiracle with filter processes. Lettering: mc – mesosternal carina, p – peritreme, s – metathoracic spiracle. Scale bars: 1 mm (12–13), 100 μ m (14), 50 μ m (15). Photo: P. Kment.



Figs 16–21. *Mormoschema immaculatum* (Distant, 1900), stat. restit., Sri Lanka: Nuwara Eliya, male genitalia: 16–19 – genital capsule (16 – dorsal, 17 – ventral, 18 – caudal, 19 – lateral view); 20–21 – paramere (two different planes). Scale bars: 500 μ m (16–19), 300 μ m (20–21). Photo: P. Kment.

angular plate-like structure with roughly kidney-shaped capitate process attached through dorsal connectives. *Phallus* (Figs 29–31). Phallosome nearly of uniform width in ventral view with base slightly constricted, hinges not well-developed, dorsal wall convex basally, ventral wall concave medially, slightly convex basally. Three conjunctival processes present, dorsal process short, membranous, broadest apically, a pair of ventral conjunctival processes, obovate, bifid apically, each with two broad pigmented stripes dorsally, converging towards apex. Processes of aedeagus absent. Aedeagus elongate, tube-like, longer than ventral conjunctival processes, phallosome oblique.

Female genitalia (Figs 32–33). *Terminalia* (Fig. 33). Valvifers VIII rectangular with mesial margins slightly concave medially, inner posterior angles angular, not developed. Valvifers IX nearly trapezoidal. Laterotergites IX elongate subtriangular, each with posterior apex rounded. Laterotergites VIII triangular. *Gynatrium* (Figs 32–33) with a triangular sclerite surrounding spermathecal opening, ring sclerites absent. *Spermatheca* (Fig. 32). Proximal spermathecal duct longer than distal spermathecal duct; dilation long, with proximal one-third opaque, twisted upwards basally; distal invagination of spermathecal duct (= sclerotized rod) nearly of uniform width throughout except slightly broader apically; intermediate part of spermatheca short, proximal flange narrower than distal flange; apical receptacle orbicular without ductules (Fig. 32: ar).

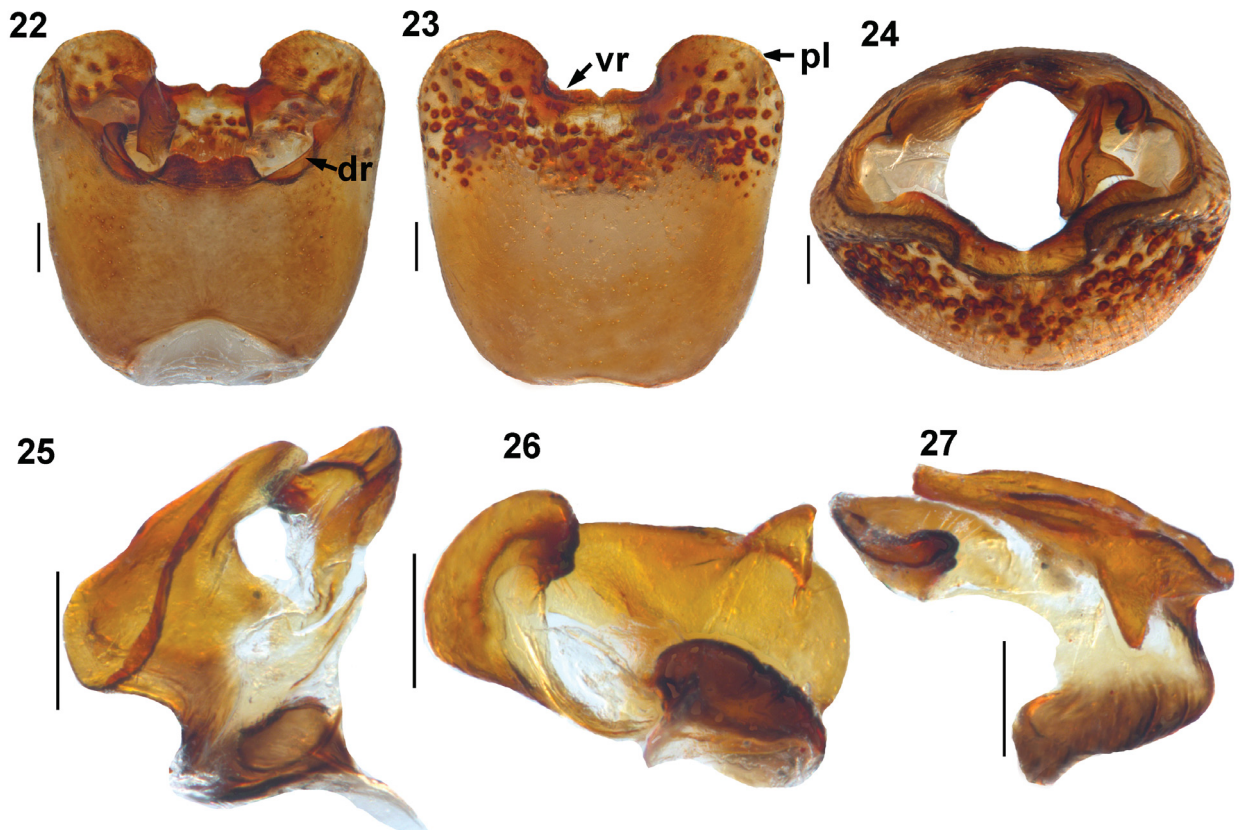
Measurements (mm). *Males* (n = 5; median (minimum–maximum)). Body length 8.72 (8.24–9.00); head: length 1.74 (1.63–1.86), width 1.81 (1.76–1.86), interocular width 1.10 (1.01–1.14); lengths of antennomeres: I – 0.49 (0.44–0.54), IIa – 0.74 (0.67–0.81), IIb – 0.65 (0.59–0.76),

III – 0.99 (0.92–1.09), IV – 1.07 (1.03–1.16); lengths of labiomeres: I – 0.99 (0.86–1.07), II – 1.55 (1.45–1.65), III – 0.65 (0.58–0.74), IV – 0.67 (0.64–0.70); pronotum: length 1.84 (1.70–1.91), width 4.78 (4.39–5.02); scutellum: length 3.08 (2.81–3.30), width 2.86 (2.48–2.97).

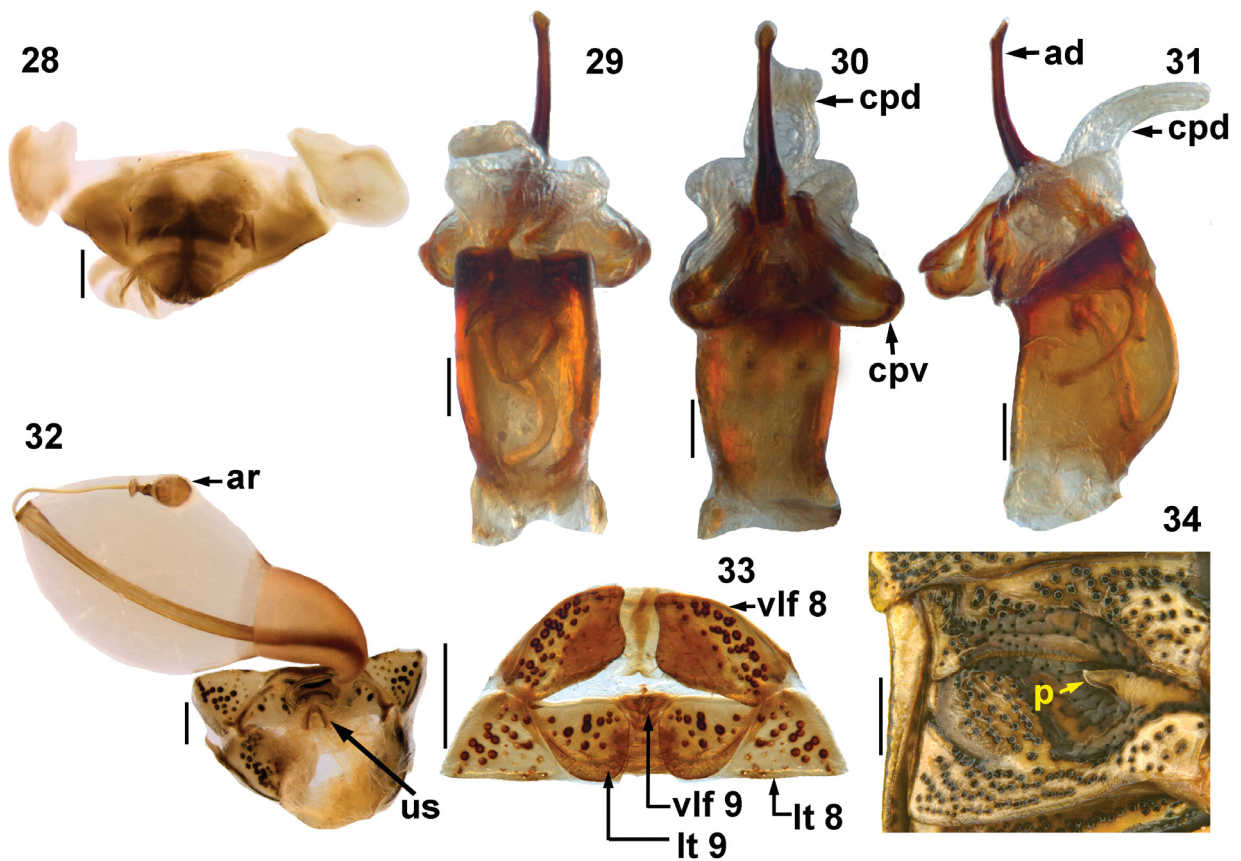
Females (n = 5; for labiomeres n = 4); median (minimum–maximum). Body length 9.41 (8.44–10.29); head: length 1.87 (1.69–1.96), width 1.93 (1.86–2.06), interocular width 1.17 (1.06–1.27); lengths of antennomeres: I – 0.54 (0.45–0.54), IIa – 0.77 (0.73–0.86), IIb – 0.64 (0.60–0.70), III – 1.04 (0.91–1.06), IV – 1.12 (1.08–1.16); length of labiomeres: I – 1.03 (0.94–1.11), II – 1.54 (1.43–1.83), III – 0.62 (0.61–0.67), IV – 0.71 (0.67–0.81); pronotum: length 1.99 (1.91–2.21), width 5.06 (4.70–5.73); scutellum: length 3.29 (3.02–3.48), width 3.22 (2.83–3.68).

Variation. The examined specimens vary in the following characters: Size and shape of the apical notch at the humeral angles, varying from distinct indentation to merely a shallow incision (Figs 1, 4–5, 10). Whitish callose spot on disc of corium well-developed (Fig. 1) or indistinct (Fig. 5). The specimens also differ in the shade of the brown dorsal colouration, in some specimens with distinct whitish markings on pronotum (Figs 1, 4), scutellum and exocorium, in some specimens the scutellum and exocorium distinctly paler than surrounding surface.

Bionomy. Usually found feeding on small herbs and shrubs in various ecosystems. Concerning plant associations, CHATTERJEE (1934) found the species repeatedly on *Santalum album* (Santalaceae) without further details. MATHUR & SINGH (1960) reported it feeding on sap of *Indigofera arrecta* (Fabales: Fabaceae). According to material we examined it was found feeding on *Buddleja asiatica* (Figs



Figs 22–27. *Mormoschema immaculatum* (Distant, 1900), stat. restit., India: Karnataka, male genitalia: 22–24 – genital capsule (22 – dorsal, 23 – ventral, 24 – caudal view); 25–27 – paramere (three different planes). Lettering: dr – dorsal rim, pl – posterolateral (= caudal lobes), vr – ventral rim. Scale bars: 0.2 mm. Photo: Salini.



Figs 28–34. *Mormoschema immaculatum* (Distant, 1900), stat. restit., India: Karnataka, male and female genitalia, external scent efferent system. 28 – articulatory apparatus; 29–31 – phallus (29 – dorsal, 30 – ventral, 31 – lateral view); 32 – spermatheca attached to ventral side of terminalia; 33 – terminalia (dorsal view); 34 – external scent efferent system. Lettering: ad – aedeagus, ar – apical receptacle, cpd – dorsal conjunctival process, cpv – ventral conjunctival processes, lt8–lt9 – laterotergites VIII or IX, p – peritreme, us – inverted U-shaped sclerite, vlf8–9 – valvifers VIII or IX. Scale bars: 0.1 mm (28–31), 0.5 mm (32–34). Photo: Salini.

35–36) and *Scrophularia* sp. (both Lamiales: Scrophulariaceae) especially during September coinciding with the flowering period (feeding plants sensu BURCKHARDT et al. 2014).

Distribution (Fig. 37). South India: Karnataka (CHATTERJEE 1934), Tamil Nadu (DISTANT 1900, 1902; CHATTERJEE 1934; CHANDRA 1953); Sri Lanka (DISTANT 1900, 1902; BREDDIN 1909). For details see Table 1.

Comment on types. DISTANT (1900) described the species *Tolumnia immaculata* based on an unspecified number of syntypes coming from three different localities and four different collections: Ceylon (E. E. Green – Brit. Mus., G. Lewis – Coll. Dist.); India: Nilgiri Hills (Sir G. F. Hampson – Coll. Dist.), Kotagira (Atkinson Coll. – Brit. Mus.). Despite this fact, ZAIDI (1995) cited the examined material as follows: ‘Holotype, South India: Nilgiri hills leg Hampson in NHM other materials 1 male, 1 female Srilanka: [sic!] Colombo 29.3.1929 in the same museum as holotype’. The specimen mentioned as holotype by ZAIDI (1995) is indeed a syntype, but the remaining specimens from Colombo do not belong to the type series. There is no evidence in ZAIDI (1995) that the author intentionally wanted to select the one of the syntypes as the only name bearing type, therefore we consider his action merely an incorrect use of the term holotype and not a valid lectotype designation (see ICZN 1999: Article 74.5). In our opinion all the syntypes we examined are conspecific and there is currently no need for a lectotype designation.

Discussion

Generic status and similarities. BREDDIN (1909) was the first to discover that *Mormoschema* is not closely related with *Tolumnia*. Despite the fact that he did not explicitly mention the differences between the two genera, he emphasized the structure of the external scent efferent system of the metathoracic scent gland, especially the short, spout-shaped peritremes, which he illustrated. In *Tolumnia*, the peritreme is ruga-shaped, long and apically pointed (HASAN & AHMAD 1988; Salini & Kment, pers. observ.).

DISTANT (1918) simply ignored BREDDIN’s (1909) evidence and synonymised *Mormoschema* with *Tolumnia* without giving any reason. The same fate met also the genus *Mycterizon* Breddin, 1909 synonymised by DISTANT (1918) and recently reinstated by SALINI et al. (2023b). A reasonable explanation is that Distant acted out of wounded pride. It is a well-known fact that William Lucas Distant (1845–1922) did not tolerate criticism of errors in his publications very well, for example, see the disputes with his main ‘censors’ E. E. Bergroth (e.g., BERGROTH 1911a,b versus DISTANT 1911a,b) and G. W. Kirkaldy (for details see DOLLING 1991).

The only person who studied *Tolumnia immaculata* prior to our revision was ZAIDI (1995). Though he identified the species correctly, his redescription is imprecise (e.g. the ratio of lengths of antennomeres do not fit our observations). As a result, ZAIDI (1995) overlooked important differences between *T. immaculata* and its supposed congeners.



Figs 35–36. *Mormoschema immaculatum* (Distant, 1900), stat. restit. Associated plant, *Buddleja asiatica* Lour. (Scrophulariaceae). Photo: Salini.

BREDDIN (1909) considered *M. immaculata* to have similar colouration and habitus to members of the genus *Eurinome* Stål, 1867 (presently classified in the Carpocorini, distributed mostly in Malesia), but he did not consider the two genera to be closely related. We verify both his conclusions based on the following observations. Species of *Eurinome* and *Mormoschema* share the basic colour pattern, with the dorsum dark brown, ventrally pale with a broad dark brown median stripe, and pale legs with dark punctures, as well as the anterolateral angles of the pronotum produced, with a denticle. However, species of *Eurinome* differ by usually being larger with a broader body, larger eyes, a transverse pale callous line on the pronotum between the humeral angles, the external scent efferent system of the metathoracic glands with large ostioles that are oriented posteriad, and the peritreme is ruga-shaped, relatively broad, reaching about the middle of the metapleuron (P. Kment, pers. observ.).

According to BREDDIN (1909), *Mormoschema* should be placed in the vicinity of *Mormidea* or *Codophila*, both of which have a short, spout-shaped peritreme. He did not mention any characters which would distinguish *Mormoschema* and *Mormidea*. *Mormidea* is a large genus, containing 36 described species, and is widely distributed in the New World, from southern Canada to Argentina (ROLSTON 1978, RIDER 2023). *Mormoschema* runs to *Mormidea* in the key to American genera by ROLSTON & McDONALD (1984), with the exception of a single character, the outer surface of the tibiae rounded for most of their length in *Mormidea* (as in the related genus *Lattinidea* Rider & Eger, 2008). Contrastingly, the outer surface of the tibiae is sulcate for most of their length in *Mormoschema*. The latter genus shares sulcate tibiae with the following two American

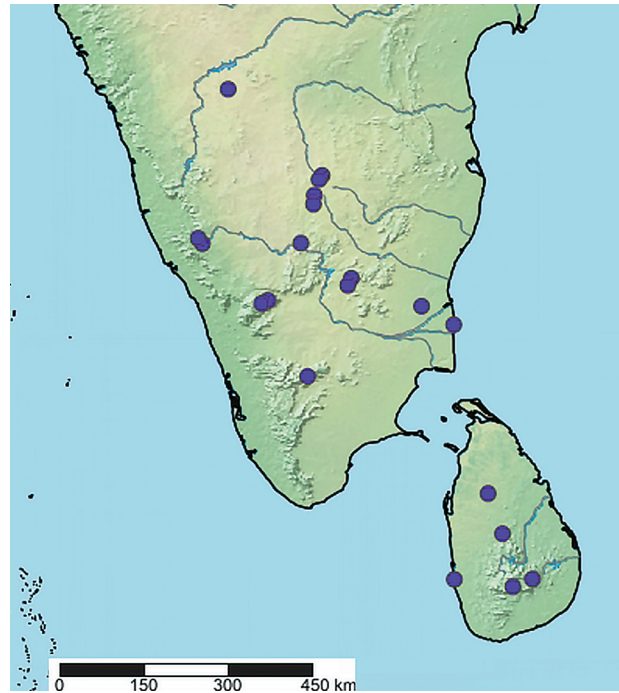


Fig. 37. Distribution map of *Mormoschema immaculatum* (Distant, 1900), stat. restit.

genera that are related to *Mormidea*: *Moromorpha* Rolston 1978 (differing from related genera by the presence of a small flat spine on each posterolateral angle of pronotum protruding over the scutellum) and *Lattinella* Rider & Eger, 2008 (differing by the metallic blue-green to black dorsal colouration of pronotum, scutellum, and corium, sharply contrasting with the pale yellowish head) (ROLSTON 1978, ROLSTON & McDONALD 1984, RIDER & EGER 2008).

Table 1. The known distribution of *Mormoschema immaculatum* (Distant, 1900).

Country / Region	Locality	Spatial coordinates	Reference
INDIA			
Karnataka	Bangalore	12.9716, 77.5946	this paper
	Chikkaballapur	13.4355, 77.7315	this paper
	Kodagu	12.3375, 75.8069	this paper
	Kottur	14.8267, 76.2218	CHATTERJEE (1934)
	Nandi hills	13.3702, 77.6835	this paper
	Thadiyandamal hills	12.4244, 75.7382	this paper
Tamilnadu	Yelahanka	13.1155, 77.6070	this paper
	Ayyur	11.3277, 79.3331	CHATTERJEE (1934)
	Jawalgiri	12.3459, 77.3913	CHATTERJEE (1934)
	Kotagiri	11.4218, 76.8617	DISTANT (1900)
	Nilgiri hills	11.3744, 76.7620	DISTANT (1900)
	North Salem	11.6643, 78.1460	CHANDRA (1953)
	Palani hills	10.2000, 77.5000	this paper
	Tharangambadi	11.0290, 79.8507	this paper
Yercaud	11.7794, 78.2034	this paper	
SRI LANKA			
	'Ceylon'		DISTANT (1900)
	Anuradhapura	8.3114, 80.4037	BREDDIN (1909)
	Colombo	6.9271, 79.8612	BREDDIN (1909)
	Horton Plains	6.8094, 80.8023	BREDDIN (1909)
	Nalanda	7.6639, 80.6355	BREDDIN (1909)
	Namunukula	6.9333, 81.1167	this paper

Based on our observation, *Mormoschema* also fits within the variation observed in *Mormidea* in most characters, including those of the peritremes and evaporatoria (see BARÃO et al. 2017: fig. 5B). It differs in the shape of the head, which is shorter in *Mormidea*, with the mandibular plates more strongly insinuate in front of the eyes, and usually with the clypeus surpassing the mandibular plates, the lateral margins of the pronotum are callose, and the structure of the parameres as illustrated in ROLSTON (1978) and RIDER & ROLSTON (1989).

In the case of *Codophila*, BREDDIN (1909) wrote that *Mormoschema* was distinct from it by the structure of the pronotal margins, the near absence of a furrow on the tibiae, and the different colouration. The two species of *Codophila* are usually much larger and always broader, the anterolateral angles of the pronotum lack a denticle, the humeral angles lack a notch, the peritremes are short and grooved (with the peritremal surfaces in the same plane as the surrounding metapleura), large ostioles that are oriented ventrally, and the genital capsule and the parameres differ in shape (cf. TAMANINI 1958, RIBES & PAGOLA-CARTE 2013, SALINI et al. 2023a).

Mormoschema keys out between Carpocorini and Eysarcorini in the illustrated key for Pentatominae tribes from southern India by SALINI & VIRAKTAMATH (2015). Couplet number 60 states, ‘Large bugs measuring 1.0–1.5 cm; connexivum explanate and exposed well beyond hemelytra; connexivum incisures black; mesosternum with median, longitudinal carina (tribe Carpocorini in part).’ This gives an indication that *Mormoschema* does not belong to the Carpocorini, and better fits the alternative solution in the couplet (with slight modification). The alternative couplet is as follows: ‘Small bugs measuring 0.45–0.70 cm; connexivum not explanate and almost unexposed beyond hemelytra, if slightly exposed, then connexivum concolourous with dorsal body surface; mesosternum with median, longitudinal furrow, sometimes with indistinct carina (tribe Eysarcorini in part)’. The body size of *Mormoschema immaculatum* is slightly larger, ranging from 8.72 to 9.01 mm, but the connexivum is partially exposed, and the mesosternum has a narrow, central longitudinal carina. In the Indian fauna, this genus appears to be most similar to *Eysarcoris* and/or *Carbula* (Eysarcorini), mainly due to the combination of the characters given in the Differential diagnosis (see above). However, *Mormoschema* is distinct from both of them in several respects (e.g., absence of a constriction in the spermathecal dilation, and the shape of the parameres with broad lamellate lobes of the parameral crown).

Our investigation fully supports the judgement of BREDDIN (1909) and we resurrect *Mormoschema* stat. restit. as a valid genus, rendering single species, *Mormoschema immaculatum* comb. restit.

Tribal placement. *Tolumnia immaculata* was until recently placed in the tribe Cappaeini, based on its misplacement in *Tolumnia*. The Cappaeini is a taxon-rich tribe, containing 24 genera and 150 species, distributed mainly in the Afrotropical, eastern Palaearctic and Oriental Regions, reaching as far east as the Solomon Islands and New Cale-

donia (RIDER et al. 2018; KMENT et al. 2021a,b). This tribe is defined by a combination of putatively homoplasious characters but no synapomorphies (e.g., body shape often broadly rounded, somewhat robust, convex below; head subtriangular, mandibular plates and clypeus subequal in length; prosternum shallowly to distinctly sulcate medially; mesosternum carinate medially; metasternum flat; peritremes ruga-shaped, quite elongate and sharply acuminate apically; abdominal venter unarmed basally; female spermatheca receptacle ball-shaped without diverticula, or with 1–3 diverticula (e.g. LINNAVUORI 1982, HASAN & AHMAD 1988, VÉTEK et al. 2014, RIDER et al. 2018)). Cappaeines share some characters with members of the Carpocorini and past authors have sometimes included cappaeine genera in Carpocorini (e.g. AHMAD & ZAIDI 1989, ZAIDI 1995). *Tolumnia* may be related to *Cappaea* Ellenrieder, 1862 and *Halyomorpha*, with all three possessing the main diagnostic characters of the tribe, including elongate and apically pointed ruga-shaped peritremes. Conversely, a short, spout-shaped peritremes, the bilobed parameral crown, and the globular apical receptacle of the spermathecal pump devoid of ductules, negate the placement of *Mormoschema* in Cappaeini based on current criteria.

Using the illustrated key of SALINI & VIRAKTAMATH (2015), *Mormoschema* keys to either Carpocorini or Eysarcorini, although it best fits the latter tribe (see above). Carpocorini is the largest tribe in Pentatominae, including 127 genera and ca. 503 species distributed worldwide (RIDER et al. 2018). Carpocorini is in all likelihood a convenience group. It is not surprising that ROCA-CUSACHS et al. (2022) found it to be non-monophyletic based on an analysis of a multigene partition.

The diagnosis of Carpocorini is as follows: general colouration yellowish to brownish, sometimes mottled; no spine or tubercle at the base of the abdomen; mandibular plates and clypeus usually subequal in length (occasionally mandibular plates are little longer but not meeting in front of clypeus); peritremes not more than half the length of the metapleura (in the Old World Carpocorini, the peritremes tend to be somewhat longer and angulate apically, with the apices attached or detached from the metapleuron) (RIDER et al. 2018). Most New World carpocorine genus groups are diagnosed by: peritreme much shorter and more auriculate, with apices often detached from metapleuron (BARÃO et al. 2017); prosternum usually flat to shallowly concave; mesosternum usually with a well-defined medial carina; metasternum usually flat to shallowly concave; and scutellum more triangular (RIDER et al. 2018). The following male genitalic characters were documented by GROSS (1976) for Australian representatives of the Carpocorini: parameres strong and thick, F-shaped, with sculptured lateral surfaces; aedeagus usually robust, often sclerotized and sometimes quite long. The spermathecal receptacle tends to be simple, ball-shaped, and without diverticula or ductules (RIDER et al. 2018).

The tribe Eysarcorini is also a species-rich tribe, with 19 genera and 230 species from the Old World (RIDER et al. 2018). There are also New World carpocorine genera that have a similar habitus, including *Cosmopepla* Stål, 1864

(cf. KMENT & RÉDEI 2018), *Mormidea*, and allied genera (BARÃO et al. 2020). It is difficult to characterize and separate Eysarcorini from some members of the Carpocorini (RIDER et al. 2018), whereas Eysarcorini appears to be a monophyletic group, as given in the recently published phylogenetic analyses of Pentatominae (ROCA-CUSACHS & JUNG 2019, ROCA-CUSACHS et al. 2021).

The members of the tribe Eysarcorini are usually small to medium in size but more robust in shape, with brown to dark brown colour. They are further characterized by callose, sharply delimited lateral margins of the pronotum; peritremes usually short and spout-shaped; fairly small evaporatoria; medially carinate mesosternum; parameres usually strongly F-shaped; and the apical receptacle of the spermatheca simple, ball-shaped, lacking diverticula (LINNAUORI 1982, RIDER et al. 2018).

Male genitalic characters of several genera of Carpocorini from India (i.e., *Carpocoris* Kolenati, 1846, *Codophila*, *Dolycoris* Mulsant & Rey, 1866) usually possess a parameral crown which is simple with a main single lobe, and nearly C-shaped in lateral view. In contrast, members of the Eysarcorini (i.e., *Eysarcoris*, *Carbula*) usually have the parameral crown with two lobe-like structures (= biramous *sensu* LINNAUORI 1982), which are usually combined basally. In contrast, a few eysarcorine genera such as *Hermolaus* Distant, 1902, *Spermatodes* Bergroth, 1914 and *Sepontia* Stål, 1864, possess simple parameral crowns.

Mormoschema fits the *Carbula* group of LINNAUORI (1982) and Eysarcorini of RIDER et al. (2018), on the basis of its small body, a medially carinate mesosternum, a small spout-shaped peritreme, bilobate parameres, and the globular apical receptacle of spermatheca. Its classificatory position is however confounded by the current polyphyletic definition of the Carpocorini and possible monophyletic Eysarcorini, which will require further finer scale observations to disentangle its taxonomic position (cf. CHEN et al. 2021, LI et al. 2021, GONÇALVES et al. 2022, ROCA-CUSACHS et al. 2022, DING et al. 2023, JIA et al. 2023).

Acknowledgements

We are very grateful to David A. Rider (North Dakota State University, Fargo, USA) for helping with literature and access to his catalogue pertaining to the Cappaeini, as well as providing critical comments on the manuscript. Mick D. Webb (BMNH) is greatly acknowledged for facilitating the examination of type specimens. We acknowledge Chandrashekara A. Viraktamath (Department of Entomology, University of Agricultural Sciences, Bangalore, India) for providing specimens for this study, which were collected and preserved in the Department of Entomology, University of Agricultural Sciences Bangalore (UASB). The author is thankful to T. Shivalingaswamy (ICAR-NBAIR, Bangalore, India) for helping with the identification of host plants. Prabhu G. (ICAR-NBAIR) is acknowledged for the collection of the first lot of *Mormoschema immaculatum* for the present work. We are grateful to S. N. Sushil (Director, ICAR-NBAIR, Bangalore, India) for the facilities extended for this work. This work was supported from funding from the Australian Government Department

of Agriculture, Forestry and Fisheries, project 'Production of a Robust Classification and Identification Key of the *Halyomorpha* Complex and Allied Taxa'. The work of P. Kment was also financially supported by the Ministry of Culture of the Czech Republic (DKRVO 2019–2023/5.I.e, National Museum, 00023272).

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