published 31.xii.2005

Volume 45, pp. 21-50

# Revision of *Mahea* Distant, 1909, with a review of the Acanthosomatidae (Insecta: Heteroptera) of Madagascar and Seychelles

## Petr KMENT<sup>1,2)</sup>

<sup>1)</sup> Department of Entomology, National Museum, Kunratice 1, CZ-148 00 Praha 4, Czech Republic; e-mail: sigara@post.cz

<sup>2)</sup> Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic

Abstract. The genus *Mahea* Distant, 1909 (Heteroptera: Pentatomoidea: Acanthosomatidae: Acanthosomatinae) is revised. *Muschalea* Cachan, 1952, is corroborated as a junior synonym of *Mahea*. Five species are recognized: *Mahea sexualis* Distant, 1909, (Seychelles) and *M. andriai* (Cachan, 1952) (Madagascar) are redescribed based on examination of the type specimens; three additional species – *Mahea distanti* sp. nov., *M. durrelli* sp. nov., and *M. parvula* sp. nov. from Madagascar – are described. The lectotypes of *M. sexualis* and *Noualhieridia rufa* Cachan, 1952, are designated. A key to the known acanthosomatid species of Madagascar and Seychelles is given. Possible phylogenetic relationships among the genera *Mahea*, *Catadipson* Breddin, 1903, *Ibocoris* Roche, 1948, and *Uhlunga* Distant, 1892, are briefly discussed.

Key words. Heteroptera, Pentatomoidea, Acanthosomatidae, *Mahea, Muschalea*, *Catadipson, Irsmia, Ibocoris, Noualhieridia*, Madagascar, Seychelles, new species, phylogeny, key

# Introduction

The family Acanthosomatidae Signoret, 1863, is one of the least speciose families of the superfamily Pentatomoidea, including about 200 species from all zoogeographical regions of the world (SCHUH & SLATER 1995). The higher classification of the family was established by KUMAR (1974) who recognized 47 genera belonging to 3 subfamilies: the Ditomotarsinae Signoret, 1863 with the tribes Ditomotarsini Signoret, 1863 (9 genera), and Laccophorellini Kumar, 1974 (4 genera), the Blaudusinae Kumar, 1974, with the tribes Blaudusini Kumar, 1974 (10 genera), and Lanopini Kumar, 1974 (12 genera), and the Acanthosomatinae (13 genera). Later, three new Neotropical genera of the Ditomotarsinae were described: *Mazanoma* Rolston & Kumar, 1975; *Tolono* Rolston & Kumar, 1975; and *Rolstonus* Froeschner,

1997 (ROLSTON & KUMAR 1975, FROESCHNER 1997). FISCHER (1996) reexamined the genus Pseudobebaeus Distant, 1911, and excluded it from the Acanthosomatidae. Subsequently, Pseudobebaeus was recognized as senior synonym of Zorcadium Bergroth, 1918, belonging to the family Pentatomidae, subfamily Pentatominae, tribe Procleticini (RIDER & FISCHER 1998). AHMAD & MOIZUDDIN (1990), revising the Acanthosomatinae of the Indo-Pakistan area, described a new genus Ameenocoris Ahmad & Moizuddin, 1990 and resurrected the genera Anaxandra Stål, 1876, and Sastragala Amyot & Serville, 1843 (regarded as synonyms of Acanthosoma Curtis, 1824 by KUMAR (1974)). AHMAD & ÖNDER (1993) resurrected another West Palaearctic acanthosomatine genus, Cyphostethus Fieber, 1861 (synonym of Elasmostethus Fieber, 1860 according to KUMAR (1974)). Cyphostethus has been generally treated as a valid genus by recent authors (e.g., GÜNTHER & SCHUSTER 1990, 2000; KERZHNER 2003; YAMAMOTO 2003). The Eastern Palaearctic genus Lindbergicoris Leston, 1951, was completely omitted by KUMAR (1974) (cf. ZHENG & WANG 1995). Altogether 54 valid genera of the Acanthosomatidae are now recognized. A cladistic analysis of the Acanthosomatidae, testing the higher classification proposed by KUMAR (1974), has not been published. However, a new critical approach to this matter is badly needed (see also Discussion).

In the Afrotropical region, the Acanthosomatidae are represented by 11 genera, five of which are geographically limited to South Africa – Agamedes Stål, 1876, Aesepus Stål, 1876 (both Ditomotarsinae: Laccophorellini), Esbenia Jensen-Haarup, 1931 (Ditomotarsinae: Ditomotarsini), Abulites Stål, 1876 (Blaudusinae: Lanopini), and Xosa Kirkaldy, 1904 (Blaudusinae: Blaudusini). Four genera are distributed in tropical Central, East, and West Africa – Laccophorella Horváth, 1904 (Central East Africa; Ditomotarsinae: Laccophorellini), Uhlunga Distant, 1892 (Africa south of the Sahara), and Ibocoris Roche, 1947 (West and Central Africa) (both Ditomotarsinae: Ditomotarsini), and Catadipson Breddin, 1903 (South and West Africa, Madagascar) (Acanthosomatinae). Two additional genera, Noualhieridia Breddin, 1898 (Blaudusinae: Blaudusini), and Mahea Distant, 1909 (Acanthosomatinae), are endemic to Madagascar and the Seychelles (KUMAR 1974). The only review of the Madagascar fauna of the Acanthosomatidae was by CACHAN (1952). As he neglected DISTANT's (1909) description of Mahea sexualis Distant, 1909, he listed only three genera from Madagascar (Noualhieridia and two newly described genera Irsmia Cachan, 1952, and Muschalea Cachan, 1952) and five species, four of them new. Later, LESTON (1953) synonymized Irsmia with Catadipson, and KUMAR (1974) synonymized Muschalea with Mahea. No additional species have been described so far.

# Material and methods

Abbreviations of collections:

BMNH	Museum of Natural	History, London,	Great Britain	(curator M.	Webb);
------	-------------------	------------------	---------------	-------------	--------

- CUMZ Cambridge University Museum, Cambridge, Great Britain (W. A. Foster);
- MMBC Moravian Museum, Brno, Czech Republic (I. Malenovský);
- MNHN Muséum National d'Histoire Naturelle, Paris, France (D. Pluot-Sigwalt);
- NMPC National Museum, Praha, Czech Republic.

In the transcriptions of labels of the type material, the following marks are used: " – verbatim copy, / – end of row, // – end of label, [] – author's remark, hw – handwritten, p – printed. The lectotype and paralectotypes are designated in order to preserve the stability of nomenclature in this group, according to Article 74.7.3 of the Code (ICZN 1999).

Morphological terms follow mainly SCHUH & SLATER (1995); for structures associated with the metathoracic scent gland opening, the terms are used according to KMENT & DAVIDOVÁ-VILÍMOVÁ (in prep.).

Photographs were taken using a digital camera Olympus Camedia C-5050 ZOOM combined with a binocular microscope Olympus SZ X 12, or using a hand-held digital camera Nikon Coolpix 4500.

## Results

#### Mahea Distant, 1909

Mahea Distant, 1909: 32, pl. 4 (description, figures). Type species: Mahea sexualis Distant, 1909, by monotypy. Muschalea Cachan, 1952: 312 (description, figures). Type species: Muschalea andriai Cachan, 1952, by original designation (syn. KUMAR 1974).

Mahea: KUMAR (1974): 43-44 (diagnosis, taxonomy).

**Redescription.** Body deltoid in shape; head shorter than pronotum; pronotum arched, sloping posteriad, highest between humeral angles, then descending caudad; dorsum flat; ventral side convex. Body surface slightly shining, covered with coarse dark punctures.

Head (Fig. 1). Mandibular plates sinuated in front of eyes, apically curved inwards, never spinously produced; clypeus with apex narrowly exposed or completely enclosed (intraspecific variable character). Eyes large, protruding from head outline by most of its width; ocelli situated behind imaginary line through posterior margins of eyes; each ocellus nearer to eye than to each other. Antenniferous tubercles visible from above; antennae 4-segmented (Fig. 11); antennomere 1 (scape) short, not or only very slightly surpassing apex of head; antennomere 2 (pedicel) very long, not subdivided, with erect pubescence; antennomeres 3 and 4 subequal in length, together about as long as antennomere 2, without erect pubescence. Bucculae low, diverging posteriad; maxillary plate tubercle developed; rostrum long, reaching or surpassing metacoxae; first rostral segment not surpassing posterior margin of eyes, hidden between bucculae.

Pronotum trapezoidal (Fig. 28); anterior margin more or less slightly concave, anterolateral angles touching posterior margins of eyes; antero-lateral margins rounded, more or less diverging posteriad; humeral angles always very prominent and spinuously produced (Fig. 2); posterior margin skewed posteriad to antero-lateral scutellar angles, margin anterior to scutellum concavely sinuate. Scutellum triangular, longer than clavi. Hemelytra narrow; clavi narrowly triangular (anteriorly with two rows of punctures, posteriorly with one row); corium long, triangular, acutely attenuated posteriorly and reaching middle of membrane, its posterior inner margin concave; suture between corium and membrane brown; membrane large, long oval, slightly brownish infuscated, translucent, slightly surpassing (exceptionally nearly surpassing) apices of postero-lateral angles of abdominal sternum 7 (Fig. 14). Prosternum with deep median groove, flanked by longitudinal, prominently elevated carinae. Mesosternal carina flattened laterally, extending anteriorly between procoxae and reaching posterior margin of prosternal groove, posteriorly reaching between metacoxae. Metathoracic scent gland complex inconspicuous (Fig. 31); ostiole small, situated laterally between meso- and metacetabula; peritreme horizontal, slightly raised above metapleura, oval, shining; evaporatorium small, narrowly surrounding ostiole and peritreme. Metapleura swollen (Fig. 14) or not. Legs pale, ochraceous, with short to very short pubescence; femora twice as long as tibiae; tarsi 2-segmented; claws slender, long, straight, apically abruptly rectangularly curved; parempodia and pulvilli developed.

Abdomen with median carina well developed on sterna 3-6 in males (Fig. 4) and on sterna 3-4 in females (Fig. 5), produced anteriad as abdominal spine reaching between metacoxae, resting against mesosternal carina. Connexiva (especially its posterolateral corners) with more or less prominent spines (variable between species and sexes) (Figs. 4-5, 14, 16); especially postero-lateral angles of sternum 7 in males conspicuously produced; sternum 8 slightly incised posteromedially.

Male genitalia. Pygophore subquadrate (Figs. 7, 17, 25), more or less dorso-ventrally flattened (Figs. 6, 16, 24); margins of external opening setose; dorso-lateral angles slightly produced, with tuft of conspicuous setae; proctiger large, convex, exposed; hypophyses of parameres exposed from pygophore (Figs. 7, 17, 25); parameres flat, head enlarged, not bifurcate, bearing setae (Figs. 18, 26); vesica of aedeagus long, deeply sinuated (Fig. 19) or looped (Fig. 27).

Sexual dimorphism strongly developed. Body of females behind humeral angles less narrowed; metapleura only slightly swollen; abdomen broader, median carina short, posterior part of abdomen flat; connexival spines with more than one spine per sternum, especially on sterna 5-7; Pendergrast's organ not developed. Hind femora and tibiae are most probably sexually dimorphic in some/all species; I cannot confirm that given the lack of material.

**Differential diagnosis.** According to KUMAR (1974), the presence of both abdominal spine and mesosternal carina places *Mahea* as a member of the subfamily Acanthosomatinae. Within the Acanthosomatinae, *Mahea* and *Catadipson* are the only genera with 4-segmented antennae. *Catadipson* differs from *Mahea* in the following characters: elongate oval species; head very broad, slightly broader than two thirds of pronotal width; apex of clypeus free; mandibular plates projected as conspicuous apical spines; humeral angles of pronotum not produced, rounded; metathoracic scent gland complex as in Fig. 32; connexival margins without apparent spines; head and pronotum with very large black punctures.

**Distribution.** This genus is known only from Madagascar (four species) and the Seychelles (Island of Mahé) (one species).

**Comments.** KUMAR (1974) noticed the resemblance in the descriptions of *Mahea* and *Muschalea* and considered them to be synonymous. He, however, did not examine Cachan's type specimens of *Muschalea*. This synonymy is herein confirmed based on the study of type material.

#### Mahea sexualis Distant, 1909

(Figs. 1-7, 31, 40-41)

Mahea sexualis Distant, 1909: 32-33, pl. 4 (description, figure of female). Mahea sexualis: KUMAR (1974): 44 (taxonomy, invalid lectotype designation).

## Type locality. Seychelles, Mahé.

**Type material.** LECTOTYPE:  $\bigcirc$ , 'Seychelles / Mahe / H P.T. 1906 [p] // Mahea / sexualis / Dist. [hw] // University Museum of / Zoology, CAMBRIDGE [p] // LECTOTYPUS / MAHEA / SEXUALIS / Distant, 1909 / des. P. KMENT 2005' [p, red label] (CUMZ), here designated. The lectotype is glued onto the tip of a pentagonal piece of card, with the pygophore removed and mounted on the same piece of card. The original piece of card is pinned under the new one. Antennomeres 3 and 4 of both antennae, right middle and hind legs, and all tarsi from left legs of the lectotype are missing. PARALECTOTYPES: 1  $\bigcirc$  and 1  $\bigcirc$ , 'Seychelles / Mahe / H P.T. 1906 [p] // Distant Coll. / 1911-383 [p] // SYN- / TYPE [p, white circle with blue margin] // PARALECTOTYPUS / MAHEA / SEXUALIS / Distant, 1909 / des. P. KMENT 2005' [p, red label] (BMNH). The male paralectotype is pinned, its antennomeres 2-4 (left) and 3-4 (right), all left legs (except hind femur), right hind leg, apical part of scutellum and pygophore missing, and it has a large pinpoint in the scutellum. The female paralectotype is mounted on the tip of a pentagonal piece of card, with one separate leg glued on the same piece of card. Rest of legs and antennae are missing, right pronotal spine broken, and abdomen ruptured ventrally on the left side.

Redescription. Body slightly shining; basic colour ochraceous, with coarse dark punctures.

Male (lectotype) (Fig. 40). Length 7.5 mm, width of pronotum between humeral angles 4 mm. Head (Fig. 1) pale ochraceous with coarse brown punctures forming more or less apparent rows (two rows on each mandibular plate, posteriorly coalescent, forming a figure resembling an 8 next to each eye; two rows on clypeus, partly coalescent medially, reaching to posterior margin of head, on frons surrounded by two rows forming an incomplete circle). Head shorter than wide (1 : 1.35), its width about half that of pronotum between humeral angles (1 : 2.08). Mandibular plates basally almost parallel, suddenly curved inwards apically, not meeting; apex of clypeus free (Fig. 1). Eyes large, ochraceous; ocelli ochraceous, situated behind eyes, near anterior pronotal margin. Each antenniferous tubercle with black longitudinal spot laterally; antennae castaneous; antennomere 1 pale, basally ochraceous; antennomere 2 with erect pubescence, hairs slightly shorter than diameter of antennomere; length of antennomeres: 1 - 0.4 mm, 2 - 2.3 mm (ratio 1 : 5.75). Head ventrally pale ochraceous, without punctures; apex of rostrum blackened, reaching middle of sternum 4.

Pronotum ochraceous with thick brown punctures; punctures on posterior half more dense than on anterior half; pronotal spines and narrow median line ochraceous; anterior margin concave; antero-lateral margins widening posteriad; humeral angles prominent, each abruptly produced into long, narrow spine directed laterad (Figs. 2-3). Scutellum triangular, ochraceous, anterior part medially brownish, with brown punctures; anterior part arched, sloping posteriad; posterior part flat, apex blackened, triangular. Hemelytra ochraceous with brown punctures; suture between corium and membrane brown; membrane slightly brownish, translucent, slightly surpassing postero-lateral angles of sternum 7.



Figs. 1-5. *Mahea sexualis* Distant, 1909. 1 – head, dorsal view; 2 – pronotum, dorsal view; 3 – pronotum, posterior view; 4 – abdomen of male (lectotype), ventral view; 5 – abdomen of female (paralectotype), ventral view.



Figs. 6-7. *Mahea sexualis* Distant, 1909. Pygophore (lectotype). 6 – posterior view; 7 – ventral view. Scale bars 0.5 mm.

Thorax ventrally with coarse brown punctures, which are more sparse on metapleura; peritreme ochraceous. Metapleura swollen, its postero-lateral corners visible in dorsal view.

Legs ochraceous, apices of tibiae and tarsomeres 2 slightly blackened; hind femur and tibia with inner margin granulated, femur slightly swollen and curved inwards, tibia straight. Abdomen with only connexival spines visible from above; ventrally ochraceous, sterna 3-6 each with small black spot on each side near middle; median carina on sterna 3-6 well developed; postero-lateral angles of sterna 3-5 with small spines, sternum 6 with long postero-laterally directed spine on each side; sternum 7 parallel-sided, postero-lateral angles strongly produced posteriad; posterior margin of sternum 8 slightly incised medially (Fig. 4).

Pygophore (Figs. 6-7) brownish, dorso-ventrally flattened, postero-lateral angles each with tuft of long setae; parameres apically pointed, ventrally with setigerous punctures.

Female (paralectotype) (Fig. 41). Length 8.2 mm, width of pronotum between humeral angles approximately 4.1 mm (right spine missing); punctures on body reddish; metapleura only slightly swollen, less prominent in dorsal view; abdomen (Fig. 5) less narrowing posteriad, more flattened, unicolorous, without black round spots, median carina developed only on sterna 3-4; connexival spines as in Fig. 5.

**Variability.** Male paralectotype differs from the lectotype in having the clypeus completely enclosed by mandibular plates; body length 7.4 mm, length of antennomere 2 equal to 2.4 mm. **Differential diagnosis.** *Mahea sexualis* differs from *M. andriai*, *M. distanti* sp. nov., and *M. parvula* by having each humeral angle abruptly produced into a long spine, not conical. From *M. durrelli* sp. nov. it differs by having the lateral pronotal margins regularly sinuated, the humeral spines not raised (Figs. 2-3), the metapleura distinctly swollen, differently shaped connexival spines (Figs. 4-5), and apex of each paramere pointed (Figs. 6-7) (see also the key). **Bionomy.** Unknown.

Distribution. Island of Mahé (Seychelles). Known only from the type series.

**Comments.** DISTANT (1909) described *M. sexualis* based on both sexes, but he did not mention the number or the location of syntypes. The type locality was given unambigously as 'Locality. Mahé', but on the next line DISTANT (1909) wrote: 'Dr. Schouteden has kindly sent me a male specimen of this species from Madagascar.' The description was accompanied by a figure of a female from Mahé and a male from Madagascar.

KUMAR (1974) examined three specimens of *M. sexualis* deposited in the BMNH – one male and one female from Mahé, and one male from Madagascar. He wrote: '... the Madagascar male is a distinct species, quite different from Mahé specimens. ... Distant's description covers both species and his type label is affixed to the Madagascar specimen. In these circumstances, I have taken the Madagascar specimen to be the type and have placed a label on it indicating this is the holotype. The species represented by the specimens from Mahé is being described elswhere.' The Madagascar specimen, however, did not originate from the type locality, and thus it cannot be a syntype of *M. sexualis* either by DISTANT (1909) or KUMAR (1974). The lectotype designation by KUMAR (1974) is therefore unjustified and in valid.

I had the opportunity to study three specimens of M. sexualis – one male and one female from BMNH, and one male from CUMZ – with the same locality labels and determination labels written most probably by the same hand (see Type material). Therefore, I regard all these specimens to be syntypes of M. sexualis. The male from CUMZ was choosen as the lectotype because it is better preserved and has the pygophore, which is lost in the male from BMNH. The Madagascar specimen designated as a lectotype by Kumar (1970) is currently described as M. distanti sp. nov.

#### Mahea andriai (Cachan, 1952)

(Figs. 8-10, 42)

*Muschalea Andriai* Cachan, 1952: 312-313, Figs. 193-194 (p. 311), 13 (Pl. XIV, p. 439) (description, figures). *Mahea andriai*: KUMAR (1974): 43-44 (diagnosis, taxonomy).

Type locality. South-east Madagascar, valley of Iantara by Ivohibe.

**Type material.** HOLOTYPE:  $\bigcirc$ , 'Valleé de l'Iantara [hw] / Inst. Scient. Madagascar [p] / 10-XI-50, A. R. [hw] // TYPIS [p, pink label] // Muschalea / andriai / Cachan [hw] // face side: HOLOTYPUS / Muschalea / andriai / Cachan 1952 / reverse: P. Kment 2005' [hw, red label] (MNHN). Holotype pinned; left antennomeres 3-4 and left middle and hind legs missing.

**Redescription.** Female (holotype) (Fig. 42). Body yellowish ochraceous. Length 9 mm, width of pronotum between humeral spines 6 mm.

Head yellowish ochraceous, margins and antenniferous tubercles laterally darkend; punctures on the head finer than in other species, slightly contrasting, their coalescence hardly intimated; slightly shorter than wide, less than 0.33 times as wide as pronotum. Mandibular plates sinuated before eyes, meeting in front of clypeus. Eyes black. Antennae dark brown, antennomeres 3-4 slightly paler; antennomere 2 with short pubescence (ca half of its diameter); length ratio of antennomeres -1: 5: 2.25: 2. Head ventrally ochraceous, with coarse and thick dark punctures; apex of rostrum blackened, reaching base of abdomen.

Pronotum coarsely and thickly punctate, punctures brown, darker on margins; anterior and posterior margins slightly concave; antero-lateral margins concave; each humeral angle



Figs. 8-10. Mahea andriai (Cachan, 1952). 8 – pronotum, dorsal view; 9 – pronotum, posterior view; 10 – abdomen, ventral view.

prominent, produced gradually into sharp, conical, black spine directed laterad and somewhat raised (Figs. 8-9). Scutellum triangular, with sparse concolorous punctures, basal angles slightly blackened; proximal part convex, apical part depressed laterally, with vague median carina; apex narrowly rounded, with black spot. Hemelytra with coarse concolorous punctation, membrane hyaline, translucent, apically distinctly surpassing abdominal apex.

Thorax yellowish brown similar to upper surface; pleura with dispersed small brown punctures. Legs ochraceous.

Abdomen ventrally without apparent punctures, with small black roundish spots near middle on each side of sterna 3-6; median carina on abdominal venter nearly obsolete; connexival spines as in Fig. 10.

**Differential diagnosis.** *Mahea andriai* differs from both *M. sexualis* and *M. durrelli* sp. nov. by having the lateral pronotal angles conically produced and gradually tapering to a spinose apex. From *M. parvula*, it differs by the larger body, more prominent lateral pronotal angles, and relatively narrower head. From *M. distanti* sp. nov. it differs by the following characters: Body almost uniformly yellowish ochraceous with small dark punctures (except darkened lateral corners of pronotum, apex of scutellum, antennae and paired black spots laterally on abdominal venter). Head with only indicated impressed rows of pale punctures. Apex of

scutellum more broadly rounded. Sternum without black punctures. Hairs on antennomere 2 shorter than its diameter. Thorax not swollen. Lateral connexival spines as in Fig. 10. **Bionomy.** Unknown.

Distribution. South-east Madagascar. Known only from the type locality (CACHAN 1952).

# Mahea distanti sp. nov.

(Figs. 11-19, 43)

Mahea sexualis (misidentification): DISTANT (1909): 33, pl. 4 (record, figure of male). Mahea sexualis (misidentification): KUMAR (1974): 44 (taxonomy).

#### **Type locality.** Madagascar, Tamatave [= Toamasina].

**Type material.** HOLOTYPUS:  $\langle \rangle$ , 'Type / H. T. [p, white circle with red margin] // Mahea / sexualis / type Dist. [hw] // Madagascar / Tamatave / XII. [hw] // Distant Coll. / 1911-383 [p] // SYN- / TYPE [p, white circle with blue margin] // HOLOTYPUS / MAHEA / DISTANTI / sp. nov. / det. P. KMENT 2005 [p, red label]' (BMNH). Holotype on micro pin; left antenna, right antennomere 4, left fore leg, right fore and middle tibiae and tarsi and both hind tarsi missing; pronotum ventrally detached from mesonotum, dorsally cracked on the right side, right humeral spine missing. The pygophore and male genitalia of the specimen had been dissected and stored in glycerol in a small glass microvial attached to the same pin.

**Description.** Male (Fig. 43). Length 8.2 mm. Body ochraceous, slightly shining, with thick coarse dark punctures.

Head pale ochraceous with coarse black or brown punctures, forming more or less distinct rows (two regular rows on each mandibular plate, rest of head with more irregular pattern than in *M. sexualis*, 'circular' figure on vertex not developed). Head shorter than wide across eyes (1 : 1.14), its width about half of pronotal width between humeral angles (1 : 2.75). Mandibular plates almost parallel basally, smoothly rounded apically, enclosing apex of clypeus. Eyes brownish; ocelli reddish, situated behind imaginary line through posterior margins of eyes, but more distant from anterior pronotal margin than in *M. sexualis*. Each antenniferous tubercle laterally with black longitudinal spot; antennomere 1 blackish brown; antennomere 2 pale castaneous, with erect pubescence, hairs slightly longer than diameter of antennomere; antennomere 3 castaneous; lengths of antennomeres: 1 - 0.4 mm, 2 - 2.9 mm, 3 - 1.3 mm (ratio 1 : 7.25 : 3.25) (Fig. 11). Head ventrally ochraceous with small brown punctures; rostrum ochraceous, apex blackened, reaching base of abdomen.

Pronotum ochraceous with uniform brown punctures, median carina not developed, humeral angles and spines reddish; anterior margin strongly concave, head more projected into pronotum than in *M. sexualis*; antero-lateral margins rounded, divergent laterad; each humeral angle conically produced into spine, directed laterad and slightly upwards (Figs. 12, 13). Scutellum triangular, its punctures finer than those on pronotum; anterior part only slightly arched, castaneous, only antero-lateral angles ochraceous; lateral margins slightly depressed medially; posterior part flat, ochraceous, with inconspicuous dark punctures; apex black, triangular. Hemelytra ochraceous with brown punctures; suture between corium and membrane brown; membrane with brownish tinge, translucent, slightly surpassing postero-lateral angles of sternum 7. Thorax ventrally ochraceous with coarse brown punctures; brown colour of punctures locally coalescent, forming small to large irregular spots on median parts of pleura; acetabula, peritreme and lateral margins of pleura ochraceous. Metapleura strongly swollen, produced laterad, its posterior margin introverted, both well visible in dorsal view (Fig. 14). Legs ochra-



Figs. 11-16. *Mahea distanti* sp. nov. 11 – antenna; 12 – pronotum, dorsal view; 13 – pronotum, posterior view; 14 – pleural margin and connexiva, dorsal view; 15 – hind leg (tarsomeres and claws missing); 16 – abdomen, ventral view.



Figs. 17-19. *Mahea distanti* sp. nov. 17 – pygophore, ventral view; 18 – right paramere, dorsal view; 19 – aedeagus (basal articulatory apparatus omitted). Scale bars 0.5 mm.

ceous, hind femora darkened apically, tarsi brown. Hind femora and tibiae slightly curved inwards, with granulation on inner margins (Fig. 15).

Abdomen ochraceous with thick brown punctures; sterna 3-4 broadly, sternum 5 narrowly reddish brown medially, sternum 6 with sparse brown punctures, sternum 7 with sparse brown punctures and large blackish brown spots on each side near anterior margin and before postero-lateral angles; median carina well developed on sterna 3-6, gradually disappearing on sternum 7, ochraceous, acutely produced anteriad as abdominal spine between metacoxae (Fig. 16); connexiva ochraceous, spines on postero-lateral angles of sterna 3-4 very small, on sternum 5 small, on sternum 6 long, narrow, directed posteriad, and on sternum 7 produced, widely triangular with parallel outer margins (Figs. 14, 16).

Pygophore brownish; dorso-ventrally flattened (Fig. 17); hypophysis of paramere roughly semicircular, apically rounded, not pointed, inner margin deeply incised (Fig. 18); vesica of aedeagus deeply sinuated, without loop (Fig. 19).

Female. Unknown.

**Differential diagnosis.** *Mahea distanti* sp. nov. differs from both *M. sexualis* and *M. durrelli* sp. nov. by having the lateral pronotal angles conically produced and gradually tapering to a spinose apex. From *M. parvula*, it differs by the larger body, more prominent lateral pronotal angles, and relatively narrower head. From *M. andriai*, it can be separated by the following characters: Body more vividly coloured, covered with dark punctures; basic colour ochraceous, posterior part of pronotum with reddish tones; anterior part of scutellum reddish brown, antero-lateral angles and posterior part contrasting pale; apex of scutellum black, narrowly

rounded. Dark punctures on head, sternum and abdominal venter coalescent, forming conspicuous rows (usually impressed and darkened). Hairs of antennomere 2 as long as or slightly longer than its diameter. Thorax conspicuously swollen. Lateral connexival spines as in Figs. 14 and 16.

Etymology. This species is named in honour of William Lucas Distant (1845-1922), wellknown English entomologist, who described many heteropteran taxa, including Mahea. Bionomy. Unknown.

Distribution. East Madagascar (Toamasina). Only the holotype is known. **Comments.** See comments under *M. sexualis*.

## Mahea durrelli sp. nov.

(Figs. 20-27, 44)

Type locality. North-east Madagascar, Vohémar.

Type material. HOLOTYPE: 3, 'Vohémar / Madagascar [p] // Collectio / J.L.Stehlík / Moravské museum, Brno [p] // 3 [p] // HOLOTYPUS / MAHEA / DURRELLI / sp. nov. / det. P. KMENT 2005' [p, red label] (MMBC). The holotype is mounted with the pygophore glued on the same piece of card; I have dissected the aedeagus and left paramere and placed them in a plastic microvial with glycerol attached to the same pin. PARATYPE: 3, 'Vohémar / Madagascar [p] // COLLECTIO / NATIONAL MUSEUM / Praha, Czech Republic [p] // 3 [p] // PARATYPUS / MAHEA / DURRELLI / sp. nov. / det. P. KMENT 2005' [p, red label] (NMPC). The paratype is mounted on the tip of a pentagonal piece of card; left antennomere 2 broken, left antennomeres 3-4 missing, and right spine on sternum 6 broken; I have removed the pygophore and glued it on the same piece of card.

Note: The locality label 'Vohémar' is identical with those found in material collected in Madagascar by C. Lamberton in 1937 and housed in NMPC (see HOBERLANDT 1942).

**Description.** Body narrow, ochraceous with reddish-brown punctures, slightly shining.

Male (holotype) (Fig. 44). Length 6 mm, width of pronotum between humeral spines 3.1 mm. Head ochraceous with irregular rows and groups of coarse black or brown punctures (two

rows on mandibular plates less distinct than in other species, vertex with U-shaped figure). Head shorter than wide across eyes (1: 1.42), ratio of width of head : width of the pronotum between humeral angles equal to 1 : 1.97. Mandibular plates only slightly narrowing basally, apically arcuately curved inwards, not meeting in front of clypeus; apex of clypeus free, clypeus slightly shorter than mandibular plates. Eyes ochraceous with brownish spots; ocelli reddish, situated near anterior pronotal margin. Antenniferous tubercles each with black longitudinal spot laterally; antennae castaneous, antennomeres 1-2 basally paler; antennomere 2 with erect pubescence, some hairs longer than its diameter; lengths of antennomeres: 1 - 0.3 mm, 2 - 1.7mm, 3 - 1.0 mm, 4 - 0.9 mm (ratio 1 : 5.67 : 3.33 : 3). Head ventrally ochraceous with sparse reddish punctures and one pair of larger, blackish L-shaped spots postero-medially next to bucculae; rostrum ochraceous, apex blackened, reaching middle of metacoxae.

Pronotum ochraceous with thick, coarse, uniformly distributed reddish-brown punctures; two rows of black punctures in area of cicatrices; humeral angles reddish. Anterior margin of pronotum only slightly concave, almost straight medially; antero-lateral margins rounded,



Figs. 20-23. *Mahea durrelli* sp. nov. 20 – pronotum, dorsal view; 21 – pronotum, posterior view; 22 – hind leg (claws missing); 23 – abdomen, ventral view.

proximally almost parallel, medially abruptly curved laterad; humeral angles prominent, conically produced laterad and upwards, apically constricted, with long narrow spine (Figs. 20-21); posterior margin of pronotum medially more concave than in other species. Scutellum narrowly triangular, slightly sinuated medially, almost flat, only anterior part slightly sloping caudad; ochraceous, with reddish-brown punctures, colouration of neighbouring punctures locally coalescent in anterior part; apex narrowly triangular, with small black spot. Hemelytra narrow, suture brownish, membrane slightly brownish infuscate, not surpassing postero-lateral angles of sternum 7.

Thorax ventrally ochraceous with reddish-brown punctures; colouration of punctures especially on meso- and metapleuron coalescent, forming brown spots alternating with ochraceous unpunctured spots; acetabula, peritreme, and elevated unpunctured spots on pleura ochraceous. Metapleura not swollen, its margin only slightly visible from above. Legs ochraceous, tarsomeres 2 brownish. Hind femora and tibiae straight, lacking granulation on inner margins (Fig. 22).



Figs. 24-27. *Mahea durrelli* sp. nov. 24 – pygophore, posterior view; 25 – pygophore, ventral view; 26 – left paramere, ventral view; 27 – aedeagus (basal articulatory apparatus omitted). Scale bars 0.5 mm.

Abdomen ventrally ochraceous with small and shallow red punctures, sterna 3-6 with three pairs of small black spots: one oval spot on anterior margin next to median carina, one round spot medially on each side, one small, round, impressed spot laterally on suture between sterna; sternum 7 with pair of oval blackish spots on anterior margin, postero-lateral angles of sternum 7 black. Median carina well developed on sterna 3-6, only basally on sternum 7, disappearing caudad (Fig. 23). Connexiva ochraceous, postero-lateral angles without spines except sternum 6 with long spine curved postero-laterad; postero-lateral angles of sternum 7 lanceolate, produced postero-laterad (Fig. 23).

Male genitalia. Pygophore brownish; less dorso-ventrally flattened (Fig. 24); exterior opening with small triangular tubercle dorso-medially (Figs. 24-25); hypophysis of paramere oval, apically broadly rounded, not pointed, inner margin only slightly incised (Fig. 26); vesica of aedeagus long, looped medially (Fig. 27).

Female. Unknown.

**Variability.** Paratype male (length 5.9 mm, width of pronotum between humeral spines 3 mm, length of antennomeres: 1 - 0.3 mm, 2 - 1.5 mm, 3 - 0.9 mm, 4 - 0.9 mm) differs from the holotype by having the mandibular plates meeting in front of the clypeus, punctures on the head darker, and the pronotum with a vague ochraceous median line.

**Differential diagnosis.** *Mahea durrelli* differes from *M. andriai*, *M. distanti*, and *M. parvula* in having each humeral angle abruptly produced into a long spine. From *M. sexualis*, it differs by having the lateral pronotal margins deeply sinuated (Fig. 20); the humeral spines raised (Figs. 20-21); the metapleura not swollen; the shape of connexival spines; and the apices of parameres rounded, not pointed (Figs. 24-26) (see also the key).

**Etymology.** The species is named in honour of Gerald Durrell (1925-1995), the famous English 'amateur naturalist', nature conservator and writer who paid a lot of attention to the nature of Madagascar and adjacent islands.

Bionomy. Unknown.

Distribution. North-east Madagascar. Known only from the type locality.

#### Mahea parvula sp. nov.

(Figs. 28-30, 45)

### Type locality. Madagascar.

**Type material.** HOLOTYPE:  $\bigcirc$ , '4175 / 34 [hw; round label, upper side green without text, lower side with numbers 4175 (corresponding to the Accession book of MNHN) and 34 (= 1834)] // Plodyrensus Amyot – Ms. Paris. – .MADAGASCAR. [hw, mounted with sellotape] //  $\bigcirc$  [p] // HOLOTYPUS / Mahea / parvula / sp. nov. / des. P. Kment 2005' [hw, red label] (MNHN). Holotype pinned; antennae, all legs except right middle one, left hemelytra, and two apical segments of rostrum missing, right eye partly damaged, basal part of scutellum and sternum with puncture from original pinning.

**Description**. Female (holotype) (Fig. 45). Body ochraceous with dark brown punctures. Length 7.3 mm, width of pronotum between humeral angles 3.9 mm.

Head ochraceous, 2-3 dark brown spots laterally in front of each eye; dark brown punctures coalescent (two impressed rows on each mandibular plate; two rows on vertex coalescent basally on clypeus and following anteriad as single median row; vertex with two rows forming U-shaped figure, additional punctures mesad from eyes and on hind margin of vertex). Head slightly shorter than wide (1 : 1.15), width slightly less than one half of pronotal width. Mandibular plates only slightly narrowing basally, apically curved inwards, not meeting; apex of clypeus narrowly free. Eyes dark brown. Head ventrally ochraceous, dark brown spot on base of each buccula; two basal segments of rostrum ochraceous.

Pronotum ochraceous with dark brown punctures forming small irregular groups on anterior third of pronotum and almost regularly distributed on posterior two thirds of pronotum; humeral angles chocolate brown. Anterior and posterior margins slightly concave; antero-



Figs. 28-30. Mahea parvula sp. nov. 28 – pronotum, dorsal view; 29 – pronotum, posterior view; 30 – abdomen, ventral view.

lateral margins rounded, regularly concave, strongly widening posteriad; each humeral angle conically produced into obtuse spine directed laterad and slightly upwards (Figs. 28-29). Scutellum triangular, brownish with dark brown punctures, extreme apex black. Hemelytra of the same colour and puncturing as disc of scutellum; membrane hyaline, translucent, with about half its length surpassing apex of abdomen.

Thorax ventrally brownish with dark brown punctures; punctures laterally coalescent, forming irregular darker spots; pleuron along mesosternal carina dark brown, anterior half of carina ochraceous. Legs ochraceous.

Abdomen flat, median carina present only on sternum 3 (Fig. 30); sterna 2-3 brown, abdominal spine ochraceous; sterna 4-5 brownish with dark brown, rounded spots laterally, sternum 6 brownish with large dark brown lateral spots connected with those on following sternum; sternum 7 entirely dark brown with two small pale spots medially on its anterior margin and one larger pale spot medially on its posterior margin. Connexival spines as in Fig. 30.

Male. Unknown.

**Differential diagnosis.** *Mahea parvula* differs from both *M. sexualis* and *M. durrelli* by having the lateral pronotal angles conically produced, each gradually tapering to a spinose apex. From *M. andriai* and *M. distanti*, it differs in having a smaller body, less prominent humeral angles, relatively broader head, and the connexival spines as in Fig. 30 (see also the key).

**Etymology.** Adjective parvulus (Latin) = 'little small', minute. The female of *M. parvula* is distinctly smaller than females of *M. andriai* and *M. sexualis*.

Bionomy. Unknown.

Distribution. Madagascar (no exact locality). Only the holotype is known.



Figs. 31-34. Pleura and metathoracic scent gland opening, most exposed view. 31 – Mahea sexualis Distant, 1909; 32 – Catadipson imernensis (Cachan, 1952); 33 – Noualhieridia rufa Cachan, 1952; 30 – Ibocoris ficivora Roche, 1947.

## Catadipson Breddin, 1903

Catadipson Breddin, 1903: 90 (description). Type species: Catadipson aper Breddin, 1903, by monotypy.
Catadipson: BREDDIN (1906): 198-199 (taxonomy).
Catadipson: BERGROTH (1908): 192 (catalogue).
Catadipson: KIRKALDY (1909): 170 (catalogue).
Irsmia Cachan, 1952: 310 (description, figures). Type species: Irsmia imernensis Cachan, 1952, by original designation (syn. LESTON 1953).

Catadipson: LESTON (1953): 124-125, Figs. 1-3, 5 (p. 125) (taxonomy, morphology).

Catadipson: KUMAR (1974): 43, Figs. 75-76 (p. 38), 77 (p. 50) (diagnosis, figures).

**Distribution.** Three described species are distributed in tropical Africa: *Catadipson aper* Breddin, 1903 from Equatorial Guinea (Fernando Póo Island) (BREDDIN 1903), Angola (LESTON 1953) and Ivory Coast (Schouteden 1964a); *C. sus* Breddin, 1906 from Togo (BREDDIN 1906) and Ivory Coast (Schouteden 1964a); and *C. imernensis* (Cachan, 1952) from Madagascar (CACHAN 1952).

# Catadipson imernensis (Cachan, 1952)

(Figs. 32, 46)

Irsmia imernensis Cachan, 1952: 310-312, Figs. 188-192 (p. 311), 5 (Pl. XIV, p. 439) (description, figures, bionomy). *Catadipson imernensis*: LESTON (1953): 123 (new combination).

**Type locality.** Central Madagascar, Tananarive [= Antananarivo].

**Type material.** HOLOTYPE:  $\bigcirc$ , 'Tananarive / Tsimbazaza [p] // I. S. Madagascar [p] / Sur Ficus (figuàr) [hw] / Mai 1947 A. R. [hw] // Ficusia imernensis Cachan [hw] // TYPIS [p, pink label] // Irsmia / imernensis / n. sp. / Cachan det. [hw] // face side: HOLOTYPUS / Irsmia / imernensis / Cachan 1952, reverse: P. Kment 2005' [hw, red label] (MNHN).

**Bionomy.** Collected from *Ficus* sp. (Moraceae) (CACHAN 1952). **Distribution.** Central Madagascar (Antananarivo env.) (CACHAN 1952).

#### Noualhieridia Breddin, 1898

Noualhieridia Breddin, 1898: 266-267 (description). Type species: Noualhieridia ornatula Breddin, 1898, by monotypy.

Noualhieridia: BERGROTH (1908): 191 (catalogue).

Noualhieridia: KIRKALDY (1909): 178 (catalogue).

Noualhieridia: CACHAN (1952): 308 (redescription, figures).

Noualhieridia: KUMAR (1974): 23-24 (diagnosis, figures).

**Distribution.** A genus endemic to Madagascar and including only three species – *N. marginata* Cachan, 1952, *N. ornatula* Breddin, 1898 and *N. rufa* Cachan, 1952.

## Noualhieridia marginata Cachan, 1952

(Fig. 47)

Noualhieridia marginata Cachan, 1952: 310, Fig. 187 (p. 311) (description, figure).

## Type locality. Madagascar.

**Type material.** HOLOTYPE: Q, 'Muséum Paris / Madagascar / Coll. Sicard 1930 [p] // TYPE [p, red label] // Noualhieridia / marginata / n. sp. / Cachan det. [hw] // face side: HOLOTY-PUS / Noualhieridia / marginata / Cachan 1952, reverse: P. Kment 2005' [hw, red label] (MNHN).

Bionomy. Unknown.

Distribution. Madagascar (no exact locality). Only the holotype is known.

#### Noualhieridia ornatula Breddin, 1898

(Fig 48)

Noualhieridia ornatula Breddin, 1898: 267-268 (description).

Noualhieridia ornatula: BERGROTH (1908): 191 (catalogue).

Noualhieridia ornatula: KIRKALDY (1909): 178 (catalogue).

Noualhieridia ornatula: CACHAN (1952): 309, Figs. 5 (Pl. VII, p. 275), 183-186 (p. 311), (redescription, figures, distribution).

Noualhieridia ornatula: KUMAR (1974): 24, Figs. 33-34 (p. 22) (lectotype designation, figures).

Type locality. Madagascar.

**Material examined. MADAGASCAR**, coll. Noualhier 1898, 3 335 200, Martin det. (part) or Cachan det. (part), P. Kment revid. (MNHN). Madagascar, 1 200, P. Kment det. (NMPC).

Bionomy. Unknown.

**Distribution.** Central Madagascar (Antananarivo) and West Madagascar (Maevatanana) (CACHAN 1952).

**Note.** *Noualhieridia ornatula* resembles (in body shape and colouration) another endemic Madagascar species, *Cloequeria bourgini* Cachan, 1952 (Pentatomidae: Pentatominae: Co-querelini), which differs by having 3-segmented tarsi, a different shape of the peritreme, no conspicuous round black spot on the mesopleura, and by other details of colouration.

## Noualhieridia rufa Cachan, 1952

(Fig 33, 49)

Noualhieridia rufa Cachan, 1952: 309-310 (description).

#### Type locality. Madagascar.

**Type material.** LECTOTYPE:  $\bigcirc$ , 'Muséum Paris / Madagascar / Coll. Sicard 1930 [p] // TYPE [p, red label] // Noualhieridia / rufa / n. sp. / Cachan det. [hw] // LECTOTYPUS / Noualhieridia / rufa / Cachan 1952 / des. P. Kment 2005' [hw, red label] (MNHN). PARALECTOTYPE:  $\bigcirc$ , the same labels as lectotype (MNHN). Here designated. The lectotype is pinned; the paralectotype is pinned on a shortened pin which is put onto a piece of card and regularly pinned. **Other material examined. MADAGASCAR** bor. or.: Maroansotra [= Maroantsetra] env., Ambodivoangy [= Ambodivoahangy], Institut Scientifique Madagascar, 1  $\bigcirc$ , P. Kment det. (MNHN). Sambava dct., R. N. XII – Marojejy, Ambatosoratra, 100 m, VIII-60, 1  $\bigcirc$ , P. Soga lgt., Institut Scientifique Madagascar, P. Kment det. (MNHN).

## Bionomy. Unknown.

Distribution. North-east Madagascar (Maroantsetra env., Sambava env.).

## Key to the Acanthosomatidae of Madagascar and the Seychelles

-	Mesosternal carina well developed. Antennae 4-segmented, antennomere 2 very long. Metathoracic scent gland complex different (Figs. 31-32), mesopleura without lateral round black spot. Slender species, body more or
2.	less parallel
	of pronotum convex
_	Body dorsally, antennae and legs multicoloured. Antero-lateral margins of pronotum convex or concave with
	pale spot; base of corium with another pale spot laterally; postero-lateral angles of connexiva with black spots.
3.	Antero-lateral pronotal margins convex, with oval pale spot overlapping to pronotal disc; trochanters, apices of
	femora and entire tibiae, tarsi and antennae black
-	Antero-lateral pronotal margins slightly concave, with long narrow pale spot not overlapping to pronotal disc; legs and antennae entirely pale, only apical halves of antennomeres 3-5 blackened.
4.	Elongate oval species. Head very broad, slightly broader than two thirds of pronotal width. Apex of clypeus free,
	mandibular plates projected as conspicuous apical spines. Humeral angles of pronotum not produced, rounded.
	Metathoracic scent gland complex as in Fig. 32. Connexival margins without apparent spines. Head and pronotum
	with very large black punctures Catadipson Breddin, 1903: Catadipson imernensis (Cachan, 1952)
-	Not conspicuously elongate, parallel species. Head only as broad as ca one half to one third of pronotal width).
	Mandibular plates without apical spines, meeting or not in front of clypeus. Humeral angles of pronotum each
	with conspicuous spine. Metathoracic scent gland complex as in Fig. 31. Connexival margins spinous. Head
_	and pronotum with small dark punctures. <i>Mahea</i> Distant, 1908
5.	Humeral angles gradually narrowed, each produced into conical spine, not constricted basally
_	Humeral angles abruptly narrowed, constricted, each with long needle-like spine
6.	Smaller species (7.3 mm). Humeral angles of pronotum less prominent (Figs. 28-29). Head slightly narrower
	than half of pronotal width. Clypeus narrowly free apically. Lateral connexival spines as in Fig. 30.
	Larger species (S. 9 mm). Humani analog of grantum more graminant (Figs. 9.0, 12.12). Head as yide as
-	Larger species (> 8 mm). Humerar angles of pronotum more prominent (Figs. 8-9, 12-13). Head as wide as
	(Eig. 10)
7	(FIS. 10).
1.	proportium approximation of source light and paired black spots laterally on abdominal venter). Head with varue
	imprased rows of punctures. Apex of scutallum more broadly rounded. Sternum without black punctures. Hairs
	on antennomere 2 shorter than its diameter. Metanleura not swollen Lateral connexival spines as in Fig. 10
	Mahoa andriai (Cachan 1952)
_	Body more colourful covered with prominent black nunctures Basic colour ochraceous posterior part of prono-
	tum with reddish tones. Anterior part of scutellum reddish brown antero-lateral angles and posterior part con-
	trastly pale apex of scutellum black Dark punctures on head pleura and abdominal venter coalescent forming
	conspicuous rows (usually impressed and darkened). Apex of scutellum narrowly rounded. Sternum with black
	punctures. Hairs on antennomere 2 as long as or slightly longer than its diameter. Metapleura conspicuously
	swollen. Lateral connexival spines as in Fig. 16
8.	Larger, more robust species (7.5-8 mm). Humeral angles not raised upwards (Figs. 2-3). Male: metapleura
	swollen; hind femora and tibiae curved inwards; abdomen ventrally with only one row of black spots medio-
	laterally on sterna 3-7; connexiva as in Fig. 4; postero-lateral angles of sternum 7 triangular, not curved laterad
	(Fig. 4). Female: connexiva as in Fig. 5
_	Smaller, more slender species (5.9-6 mm). Humeral angles raised askew upwards (Figs. 20-21). Male: meta-
	pleura not swollen; hind femora and tibiae not curved inwards (Fig. 22); abdomen ventrally with three rows of
	black spots on each side of sterna 3-6; connexiva as in Fig. 23; postero-lateral angles of sternum 7 broadly
	lanceolate, distinctly curved laterad (Fig. 23). Female: unknown

# Discussion

KUMAR (1974) based his classification of the Acanthosomatidae on characters given in the following key:

- Abdominal spine absent; postero-lateral angles of sternum 7 never produced into process. Sternal carina usually absent, but when present it assumes the form of a thin, flat and poorly developed ridge. .... Ditomotarsinae Abdominal spine usually present; when absent, either postero-lateral angles of sternum 7 produced into pro-
- Sternal carina usually absent; when present, seldom more than a raised wedge at the junction of pro- and mesosternum, possibly extending slightly forward and backward; in some genera both pro- and mesosternal carina present but invariably poorly developed and never continuous; abdominal spine in such cases very well developed and sometimes reaching anterior end of prosternal carina.

However, KUMAR (1974) himself admitted the existence of exceptions in the Acanthosomatinae. In Proctophantasta, abdominal and sternal carina may be present or absent in different species; in Eupolemus, the sternal carina may be well developed or reduced or absent completely; in *Amphaces*, the abdominal spine and sternal carina may be completely absent in some species, though some remnants of a former carina can be seen in the midline of sterna 4-7 (KUMAR 1974). Various sternal carinae and abdominal spines (on sternum 3) also occur in many genera of the Pentatomidae in the subfamilies Asopinae, Edessinae, Pentatominae, and Discocephalinae (e.g., WAGNER 1966; ROLSTON & MCDONALD 1979, 1981; ROLSON et al. 1980; THOMAS 1992, 1994; RIDER 1994; SCHUH & SLATER 1995; FISCHER 1996) and in the Tessaratomidae s. l. in the Tessaratominae (KUMAR & GHAURI 1970) and the Oncomerinae (SINCLAIR 2000), usually with no more than a generic level value. Unfortunately, KUMAR (1974) did not give any additional characters supporting his classification. The metathoracic scent gland complexes as figured by KUMAR (1974) seem to be good distinguishing characters at the generic level, but insufficient for phylogenetic hypothesis. Evidence gained by the study of male and female genitalia is even more incomplete. KUMAR (1974) figured only the external male genitalia of a few species of Elasmucha Stål, 1864, Acanthosoma, and Anaxandra (all in the Acanthosomatinae). Also descriptions of external male genitalia in papers of other authors concern only the Acanthosomatinae: Acanthosoma (SINGH-PRUTHI 1925, AHMAD & MOIZUDDIN 1980, ZHENG & WANG 1995), Ameenocoris (AHMAD & MOIZUDDIN 1980), Cyphostethus (Leston 1953, Ahmad & Önder 1993), Elasmostethus (Baker 1931, Leston 1953, McDonald 1966, Ahmad & Moizuddin 1980, Ahmad 1997, Yamamoto 2003), Elasmucha (BAKER 1931, PIOTROWSKI 1950, MCDONALD 1966, AHMAD & MOIZUDDIN 1980), Lindbergicoris (ZHENG & WANG 1995), Microdeuterus Dallas, 1851 (AHMAD & MOIZUDDIN 1980), and Sastragala (AHMAD & MOIZUDDIN 1980). Internal male genitalia and female genitalia are even less well known (e.g., PENDERGRAST 1957; SCUDDER 1959; MCDONALD 1966; AHMAD & MOI-ZUDDIN 1980, 1985, 1990; AHMAD & ÖNDER 1993; AHMAD 1997; GAPUD 1991). Therefore, KUMAR's (1974) classification of the Acanthosomatidae seems to be more of a 'practical classification' facilitating the identification rather than a phylogenetic hypothesis. A cladistic analysis of the Acanthosomatidae, supported with molecular methods wherever possible, is badly needed.

KUMAR (1974) noted that the characteristically produced mandibular plates show affinities between the genera *Catadipson* (Acanthosomatinae) and *Ibocoris* (Ditomotarsinae), which he classified in different subfamilies based on the presence or absence of abdominal and sternal carinae. The genus *Ibocoris* includes two species distributed in tropical Africa – *I. ficivora* Roche, 1947 (Congo, Cote d'Ivory, Gambia, Kenya, Nigeria, Senegal, Tanzania – Roche 1947; Schouteden 1964a, 1964b; VILLIERS 1967; KUMAR 1974; LINNAVUORI 1982) and *I. orientalis* Schouteden, 1964 (Kilimanjaro: riv. Tsavo – Schouteden 1964b). According to KUMAR (1974), *Ibocoris* is closely related to *Uhlunga* distributed in South Africa, Kenya, and Ghana (DISTANT 1892, HESSE 1925, KUMAR 1974). All three genera – *Catadipson, Ibocoris*, and *Uhlunga* – are known to live on *Ficus* spp. (Moraceae) (Roche 1947, CACHAN 1952, KUMAR 1974).

I was able to compare the genera *Mahea* and *Catadipson* with *Ibocoris ficivora* (Figs. 34-39, 50-51; material examined: Senegal, Casamance, on *Ficus*, 15.xi.1983, 1  $\bigcirc$  2  $\bigcirc$  $\bigcirc$ ; 25.xi.1983, 1  $\bigcirc$ , I. Etienne lgt (MNHN)). This comparison revealed several other characters shared by *Mahea*, *Catadipson*, *Ibocoris*, and *Uhlunga*. The characters of *Uhlunga*, which were not available for my study, are based on descriptions by DISTANT (1892), HESSE (1925, including a figure of the habitus) and KUMAR (1974). I found similarities in the following characters:

i) Sexual dimorphism is more or less developed in all genera. In *Mahea*, the sexes differ in colouration, shape of the abdomen, swelling of the metapleura, development of the median abdominal carina, and the shape and distribution of the connexival spines. In *Ibocoris*, there are differences in colouration, the shape of the mandibular plates, and the shape of the connexiva. In *Uhlunga*, the sexes have different colouration, the abdomen of the female is much broader than that of the male and medially sulcate in the female, whereas it has an elevated median carina in the male, and humeral spines are present only in females (DISTANT 1892, KUMAR 1974). Almost nothing is known about the sexual dimorphism of *Catadipson*; CACHAN (1952) noted that the rostrum is longer in females than in males. Other authors studied only females of *Catadipson* (BREDDIN 1903, 1906; LESTON 1953; KUMAR 1974; this paper).

ii) Antennae 4-segmented, antennomere 2 (pedicel) not subdivided, very long in all four genera. This reversal character within the Pentatomoidea developed independently many times, and is known in many genera of the Scutelleridae, Tessaratomidae (Tessaratominae, Natalicolinae), Dinidoridae (Dinidorinae, Megymeninae), Cydnidae (Cydninae, Cephalocteinae), and Pentatomidae (Serbaninae, Pentatominae: e.g., Halyini, Memmini, Degonetini) (e.g., LESTON 1956, AZIM & SHAFEE 1984, LIS 1994); in the Acanthosomatidae this is present also in the Australian genus *Galgacus* Distant, 1899 (Blaudusinae) (KUMAR 1974).

iii) Spinous processes on mandibular plates present in both sexes of *Catadipson* and in males of *Ibocoris*; lacking in *Mahea*, *Uhlunga*, and females of *Ibocoris* (cf. DISTANT 1892, HESSE 1925, ROCHE 1947, CACHAN 1952, KUMAR 1974).

iv) Maxillary plate tubercle developed in all genera (cf. KUMAR 1974). Maxillary plate tubercle described by PENDERGRAST (1953a) was mentioned among the principal features of the Acanthosomatidae by LESTON (1953), but according to KUMAR (1974) it does not constitute



Figs. 35-39. *Ibocoris ficivora* Roche, 1947. 35 – head and pronotum, dorsal view; 36 – pygophore, posterior view; 37 – pygophore, ventral view (setae ommited); 38 – left paramere, ventral view; 39 – aedeagus (basal articulatory apparatus omitted). Scale bars 0.5 mm.

a regular feature of the Acanthosomatidae, because it is missing in several genera (e.g. *Noualhieridia*). LESTON (1954) described a spur-like maxillary plate tubercle in *Brachycoris* Stål, 1870 (Pentatomidae: Pentatominae) without any note on its homology with that of the Acanthosomatidae.

vi) Bucculae very low, rostral segment 1 not protruding in *Mahea*, *Catadipson*, and *Ibocoris* (cf. BREDDIN 1903). There is no information on this character in *Uhlunga*.

vii) Humeral spines of pronotum present in both sexes in *Mahea*, *Ibocoris*, and some females of *Uhlunga*; absent in both sexes of *Catadipson* and males of *Uhlunga* (cf. HESSE 1925, ROCHE 1947, CACHAN 1952, KUMAR 1974).

viii) Mesosternal carina well developed in *Mahea* and *Catadipson*, in *Uhlunga* the mesosternum with a flat and thin median carina running from the middle of mesocoxae to the anterior ends of procoxae (KUMAR 1974, cf. HESSE 1925). In *Ibocoris*, the mesosternal carina is absent according to KUMAR (1974). However, I found in both sexes of *I. ficivora* a low and thin median mesosternal carina (anteriorly well developed and higher, almost obsolete posteriorly) which is normally covered by the rostrum and coxae and thus hidden.



Figs. 40-45. 40-41 – *Mahea sexualis* Distant, 1909. 40 – male, lectotype; 41 – female, paralectotype. 42 – *M. andriai* (Cachan, 1952), female, holotype. 43 – *M. distanti* sp. nov., male, holotype. 44 – *M. durrelli* sp. nov., male, holotype. 45 – *M. parvula* sp. nov., female, holotype. (Photo: J. Macek – Figs. 40-41, 43-44; P. Kment – Figs. 42, 45). Scale bar = 2 mm.

ix) Metathoracic scent gland complex with ostiole leading to a horizontal, disc-like peritreme; evaporatorium small, narrowly surrounding ostiole and peritreme developed only on the metapleura in *Mahea* (Fig. 31), *Ibocoris* (Fig. 34), and *Uhlunga* (KUMAR 1974); in *Catadipson* the peritreme vertical, evaporatorium larger and present also on the posterior margin of mesopleura (Fig. 32).



Figs. 46-51. 46 – *Catadipson imernensis* (Cachan, 1952), female, holotype. 47 – *Noualhieridia marginata* Cachan, 1952, female, holotype. 48 – *N. ornatula* Breddin, 1898, female. 49 – *N. rufa* Cachan, 1952, female, lectotype. 50-51 – *Ibocoris ficivora* Roche, 1947. 50 – male; 51 – female. (Photo: P. Kment – Figs. 46-49; J. Macek – Figs. 50-51). Scale bars = 2 mm.

x) Pendergrast's organ of female absent in all genera (cf. KUMAR 1974). This specialized feature of the Acanthosomatidae is missing in several genera in each of the three subfamilies (PENDERGRAST 1953b, KUMAR 1974).

xi) Abdominal spine on sternum 3 present in both sexes of *Mahea* and *Catadipson*, absent in *Ibocoris*. Median carina on abdomen in *Mahea* sexually dimorphic (Figs. 4-5). Abdominal

spine in *Uhlunga* missing according to KUMAR (1974). DISTANT (1892) wrote in the original description of *Uhlunga*: 'Abdomen in the male with a broad end elevated central longitudinal callosity, extending from base to anal appendage; in the female this is replaced by a broad, central, longitudinal sulcation.'

xii) Connexiva of both sexes of *Mahea* and *Catadipson* narrow, not expanded laterally. Connexival spines of *Mahea* sexually dimorphic, especially postero-lateral angles of sterna 6-7 in males conspicuously produced (see redescription and Figs. 4-5, 10, 16, 23, 30). Postero-lateral angles of sterna (especially the last one) denticulate in *Catadipson* (BREDDIN 1903, 1906; CACHAN 1952). In *Ibocoris*, connexiva in male narrow, not expanded, without spines, only postero-lateral angles of sternum 7 triangularly produced; in female very broad, expanded laterally, sternum 2 with a unique, long, pedunculate process directed antero-ventrad, which seems to be homologous with the connexival spines (cf. ROCHE 1947), postero-lateral angles of sterna 3-5 and 7 with long spines, those of sternum 6 only with a rudimentary spine. Connexiva well developed and exposed in *Uhlunga*, laterally expanded in female, without spines (DISTANT 1892, HESSE 1925). However, HESSE (1925) described *U. typica* var. *cornuta*, which differs from the typical form only by the 'acutely and characteristically produced posterior lateral angles of sixth abdominal segment'.

xiii) Vesica of aedeagus long, medially sinuated, or looped in *Mahea* and *Ibocoris*. A long vesica seems to be characteristic of several genera of the Acanthosomatinae (cf. SINGH-PRUTHI 1925, McDoNALD 1966, KUMAR 1974, AHMAD & MOIZUDDIN 1980, ZHENG & WANG 1995). However, there are important differences in the shape of the pygophore and parameres between *Mahea* and *Ibocoris* (see Figs. 6-7, 17-18, 24-26, 36-38). The male genitalia of *Catadipson* (except the line drawing of pygophore in ventral view by CACHAN 1952) and *Uhlunga* are unknown.

The above mentioned characters represent a mosaic which does not allow definitive conclusions about the phylogenetic relationships among the four genera without a further comprehensive study and a cladistic analysis of the entire family. In particular, the 4-segmented antennae and the lack of Pendergrast's organ are reversals, so it is hard to conclude if these characters are synapomorphic or homoplasious. LESTON (1953) supposed that the presence or absence of sternal and abdominal carinae are only generic characters, which may be confirmed by the presence of a rudimental mesosternal carina in *Ibocoris*. However, there are two alternative hypothesis for further consideration: i) the genera *Mahea*, *Catadipson*, *Ibocoris*, and *Uhlunga* form a monophyletic group (perhaps belonging to the Acanthosomatinae), or ii) characters shared by those genera are convergent, probably due to a similar bionomy on *Ficus*-trees (known for all genera except *Mahea*, whose bionomy is unknown).

## Acknowledgements

I am very obliged to Dominique Pluot-Sigwalt (MNHN) for her help and hospitality during my stay in Paris, and to Mick Webb (BMNH), William A. Foster (CUMZ), and Igor Malenovský (MMBC) for loans of material. Special thanks are also to I. Malenovský who kindly translated French literature for me, to Jan Macek (NMPC) who prepared some of the photographs, to Pavel Štys (Charles University, Praha) for important comments concerning the nomenclature and to David A. Rider (North Dakota State University, USA), Carl W. Schaefer (University of Connecticut, USA), and J. Vilímová (Charles University, Praha) for critical reading of the manuscript. This work was partly supported by grants of the Ministry of Culture (MK) 00002327201 (to National Museum, Praha) and the Ministry of Education (MSM) 0021620828 (to Charles University, Praha) and a grant from the Grant Agency of Charles University (GAUK) 113/2002 B/BIO/PrF.

# References

- AHMAD I. 1997: A revision of the genus Elasmostethus Fieber (Hemiptera: Acanthosomatidae) from Western Palaearctic, with a new record from Turkey and their cladistic relationships. *Proceedings of the Pakistan Congress of Zoology* **17**: 63-71.
- AHMAD I. & MOIZUDDIN M. 1980: Revision of Acanthosomatidae (Hemiptera: Pentatomomorpha: Pentatomoidea) from Indo-Pakistan area with a cladistic analysis of the genera. *Oriental Insects* **24**: 267-304.
- AHMAD I. & MOIZUDDIN M. 1985: Aspects of anatomy of two species of Sastragala Amyot & Serville (Pentatomoidea: Acanthosomatidae) of Pakistan with reference to phylogeny. *Karachi University Journal of Science* 13: 65-70.
- AHMAD I. & MOIZUDDIN M. 1990: Aspects of internal anatomy of Ameenocoris pakistanensis Ahmad and Moizuddin (Pentatomoidea Acanthosomatidae) from Pakistan with reference to phylogeny. *Karachi University Journal of Science* 18: 165-171.
- AHMAD I. & ÖNDER F. 1993: A review of status of Cyphostethus Fieber (Hemiptera: Acanthosomatidae) from western Palaearctic region. *Pakistan Journal of Entomology Karachi* 8: 55-62.
- AZIM M. N. & SHAFEE S. A. 1984: Degonetini trib. n. (Heteroptera: Pentatomidae). Current Science 53: 1094-1095.
- BAKER A. D. 1931: A study of the male genitalia of Canadian species of Pentatomidae. *Canadian Journal of Research* **4**: 148-179, 181-220.
- BERGROTH E. 1908: Enumeratio Pentatomidarum post Catalogum bruxellensem descriptarum. Mémoires de la Société Entomologique de Belgique 15: 131-200.
- BREDDIN G. 1898: Studia hemipterologica III. Entomologische Nachrichten (Berlin) 24: 262-268.
- BREDDIN G. 1903: Catadipson n. gen. Acanthosominorum (Hemiptera Heteroptera). Societas Entomologica 18: 90-91.
- BREDDIN G. 1906: Rhynchotographische Beiträge. Zweites Stück. Wiener Entomologische Zeitung 25: 188-200.
- CACHAN P. 1952. Les Pentatomidae de Madagascar (Hemipteres Heteropteres). Mémoires de l'Institut Scientifique de Madagascar, Série E 1(2): 231-462.
- DISTANT W. L. 1892: Notes on Ethiopian Rhynchota. Entomologist's Monthly Magazine 28: 237-239.
- DISTANT W. L. 1909: The Percy Sladen trust expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner. Volume II. No. IV. "Sealark" Rhynchota. *Transactions of the Linnean Society of London, Zoology* 13(1): 29-47 + 1 pl.
- FISCHER Ch. 1996: On the systematic position of Pseudobebaeus goyazensis Distant, 1911 within the Pentatomoidea (Heteroptera: Pentatomidae). *Deutsche Entomologische Zeitschrift* **43**: 83-87.
- FROESCHNER R. C. 1997: Rolstonus rolstoni, new genus and new species of Acanthosomatidae from Argentina (Heteroptera: Pentatomoidea: Ditomotarsini). *Journal of the New York Entomological Society* **103(4)**(1995): 360-363.
- GAPUD V. P. 1991: A generic revision of the subfamily Asopinae, with consideration of its phylogenetic position in the family Pentatomidae and superfamily Pentatomoidea (Hemiptera-Heteroptera). Parts I and II. *Philippine Entomologist* **8**: 865-961.
- GÜNTHER H. & SCHUSTER G. 1990: Verzeichnis der Wanzen Mitteleuropas (Heteroptera). Deutsche Entomologische Zeitschrift, N. F. 37: 361-396.
- GÜNTHER H. & SCHUSTER G. 2000: Verzeichnis der Wanzen Mitteleuropas (Insecta: Heteroptera) (2. überarbeitete Fassung). *Mitteilungen des Internationalen Entomologischen Vereins* **7**(**Suppl.**): 1-69.
- HESSE A. J. 1925: Contributions to the knowledge of the fauna of South-West Africa. IV. A list of the Heteropterous and Homopterous Hemiptera of South-West Africa. Annals of the South African Museum 23(1): 1-190 + 7 pls.

- HOBERLANDT L. 1942: Heteroptera Madagascariensia in Museo Pragensi. III. Ad Ploiariinarum cognitionem. Sborník Entomologického Oddělení při Zoologických Sbírkách Zemského Musea v Praze 20: 135-150 (in Czech and Latin).
- ICZN 1999: International Code of Zoological Nomenclature. Fourth Edition. International Trust for Zoological Nomenclature, London, 306 pp.
- KERZHNER I. M. 2003 : Notes on synonymy, nomenclature, and distribution of some Palaearctic Coreoidea and Pentatomoidea (Heteroptera). Zoosystematica Rossica 12: 101-107.
- KIRKALDY G. W. 1909: Catalogue of the Hemiptera (Heteroptera) with biological and anatomical references, lists of foodplants and parasites, etc. Vol. 1. Cimicidae. Felix L. Dames, Berlin, xl + 392 pp.
- KMENT P. & DAVIDOVÁ-VILÍMOVÁ J. in prep.: The external structures associated with the metapleural scent glands in the family Tessaratomidae (Heteroptera: Pentatomoidea).
- KUMAR R. 1974: A revision of world Acanthosomatidae (Heteroptera: Pentatomoidea): Keys to and descriptions of subfamilies, tribes and genera, with designation of types. *Australian Journal of Zoology, Supplementary Series* 34: 1-60.
- KUMAR R. & GHAURI M. S. K. 1970: Morphology and relationships of the Pentatomoidea (Heteroptera 2 World genera of Tessaratomini (Tessaratomidae). *Deutsche Entomologische Zeitschrift* 17: 1-31.
- LESTON D. 1953: Notes on the Ethiopian Pentatomoidea (Hemiptera). 14. An Acanthosomid from Angola, with remarks upon the status and morphology of Acanthosomidae Stål. *Publicações Culturais da Companhia de Diamantes de Angola* 16: 123-132.
- LESTON D. 1954: Brachycoris Stål and Saceseurus Breddin (Hem., Pentatomidae), with the description of an unusual maxillary plate tubercle in the former. *Idea* **10**: 9-10.
- LESTON D. 1956: The antennae of shieldbugs (Hem., Pentatomoidea). Entomologist's Monthly Magazine 92: 159-161.
- LINNAVUORI R. E. 1982: Pentatomidae and Acanthosomatidae (Heteroptera) of Nigeria and the Ivory Coast, with remarks on species of the adjacent countries in West and Central Africa. Acta Zoologica Fennica 163: 1-176.
- LIS J. A. 1994: A revision of the Oriental burrower bugs (Heteroptera: Cydnidae). Upper Silesian Museum, Bytom, 349 pp.
- McDONALD F. J. D. 1966: The genitalia of North American Pentatomoidea (Hemiptera: Heteroptera). Quaestiones Entomologicae 2: 7-150.
- PENDERGRAST J. G. 1953a: A projection on the maxillary plate in some Acanthosominae (Hem., Pentatomidae). Entomologist's Monthly Magazine 89: 215.
- PENDERGRAST J. G. 1953b: Setose areas on the abdomen in females of some Acanthosomatinae (Heteroptera, Pentatomidae). *Entomologist* (London) 86: 135-138.
- PENDERGRAST J. G. 1957: Studies on the reproductive organs of the Heteroptera with a consideration of their bearing on classification. *Transactions of the Royal Entomological Society of London* **109**: 1-63.
- PIOTROWSKI F. 1950: Sur la morphologie de l'appareil copulateur mâle des Hémiptères Hétéroptères, avec considération spéciale du groupe Pentatomoidaria Börner, 1934. Bulletin de la Sociéte des Amis Sciences et des Lettres de Poznan (B) 12: 237-274. (Not seen, fide LESTON (1953)).
- RIDER D. A. 1994: A generic conspectus of the tribe Procleticini Pennington (Heteroptera, Pentatomidae), with the description of Parodmalea rubella, new genus and species. *Journal of the New York Entomological Society* 102: 193-221.
- RIDER D. A. & FISCHER Ch. 1998: Zorcadium Bergroth, an objective junior synonym of Pseudobebaeus Fallou (Heteroptera: Pentatomidae). *Entomological News* **109**: 274-276.
- ROCHE P. J. L. 1947: A new genus and species of Pentatomidae (Hemiptera, Heteroptera) from Nigeria. *Proceedings* of the Royal Entomological Society of London, Series B, Taxonomy 16: 27-28.
- ROLSTON L. H. & KUMAR R. 1975: Two new genera and two new species of Acanthosomatidae (Hemiptera) from South America, with a key to the genera of the Western Hemisphere. *Journal of the New York Entomological Society* 82(1974): 271-278.
- ROLSTON L. H. & McDONALD J. D. 1981: Keys and diagnoses for the families of Western Hemisphere Pentatomoidea, subfamilies of Pentatomidae and tribes of Pentatominae (Hemiptera). *Journal of the New York Entomological Society* 87: 189-207.
- ROLSTON L. H. & McDONALD J. D. 1979: Conspectus of Pentatomini genera of the Western Hemisphere Part 2 (Hemiptera: Pentatomidae). *Journal of the New York Entomological Society* **88**: 257-272.

ROLSTON L. H., McDONALD J. D. & THOMAS D. B. Jr. 1980: Conspectus of Pentatomini genera of the Western Hemisphere. Part I (Hemiptera: Pentatomidae). Journal of the New York Entomological Society 88: 120-132.

SCHOUTEDEN H. 1964a: Pentatomides de la Côte d'Ivoire II. Revue de Zoologie et Botanique Africaine 70: 92-95.

- SCHOUTEDEN H. 1964b: Pentatomides de la Côte d'Ivoire III. Revue de Zoologie et Botanique Africaine 70: 188 208.
- SCHUH R. T. & SLATER J. A. 1995: *True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History.* Cornell University Press, Ithaca, London, 336 pp.
- SCUDDER G. G. E. 1959: The female genitalia of the Heteroptera: morphology and bearing on classification. *Transactions of the Royal Entomological Society of London* **111**: 405-467.
- SINCLAIR D. P. 2000: A generic revision of the Oncomerinae (Heteroptera: Pentatomoidea: Tessaratomidae). Memoirs of the Queensland Museum 46: 307-329.
- SINGH-PRUTHI H. 1925: The morphology of the male genitalia in Rhynchota. *Transactions of the Entomological Society of London* **1925**: 127-267 + 32 pls.
- THOMAS D. B. Jr. 1992: Taxonomic synopsis of the Asopine Pentatomidae (Heteroptera) of the Western Hemisphere. Entomological Society of America, Lanham, Maryland, 156 pp.
- THOMAS D. B. Jr. 1994: Taxonomic synopsis of the Old World asopine genera (Heteroptera: Pentatomidae). Insecta Mundi 8: 145-212.
- VILLIERS A. 1967: Contribution à la faune du Congo (Brazzaville). Mission A. Villiers et A. Descarpentries. LXVII. Hémiptères Pentatomidae. Bulletin de l'Institut Française d'Afrique Noire 29: 1784-1811.
- WAGNER E. 1966: Wanzen oder Heteropteren I. Pentatomomorpha. In: DAHL F. (ed.): Die Tierwelt Deutschlands und der angrezenden Meeresteile. Vol. 54. VEB Gustav Fischer Verlag, Jena, 235 pp.
- YAMAMOTO A. 2003: A revision of Japanese Elasmostethus Fieber (Heteroptera: Acanthosomatidae). Tijdschrift voor Entomologie 146: 49-66.
- ZHENG L.-Y. & WANG H.-J. 1995: Contribution to the taxonomy of Lindbergicoris Leston (Hemiptera: Acanthosomatidae). *Entomologica Scandinavica* 26: 17-26.