Lilliputocorini, a New Tribe with Six New Species of *Lilliputocoris*, and a Cladistic Analysis of the Rhyparochrominae (Hemiptera, Lygaeidae)

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ABSTRACT

The Lilliputocorini, a new tribe based on the genus *Lilliputocoris* Slater and Woodward, is described and placed in the subfamily Rhyparochrominae. The relationships of the new tribe are discussed and it is assigned to a clade also containing the Antillocorini and Lethaeini. A discussion of wing polymorphism and of zoogeography is included. A key is given to the species of *Lilliputocoris*. *Lilliputocoris ghanaensis* (Ghana), *L. grossocerata* (Borneo), *L. neotropicalis* (Brazil), *L. seychellensis* (Seychelles Islands), *L. taylori* (Borneo), and *L. terraereginae* (Australia) are described as new. *Tomocoris punctatus* Woodward is transferred to *Lilliputocoris*, redescribed and reported from Queensland and Northern Territory (Australia) and Dauan Island (Torres Straits). Dorsal view illustrations of *Lilliputocoris neotropicalis*, *L. terraereginae*, *L. seychellensis*, *L. exiguis*, and *L. punctatus* are included as are illustrations of the nymph of *terraereginae*, of the genitalia and abdomen, and scanning electron photographs of the abdominal trichobothria, scent gland scars and spiracles.

A discussion of the cladistic relationships of the tribes of the Rhyparochrominae is included together with a cladogram and a character analysis.

INTRODUCTION

The genus *Lilliputocoris* was described by Slater and Woodward (1979) based on *Lilliputocoris exiguis* from Sri Lanka (Ceylon). At that time we noted that before us were additional species, from a number of widely separated localities. One of these had been described as *Tomocoris punctatus* Woodward (1959), the others are described in the present paper. At the time of the original description of *L. exiguis*, we tentatively placed *Lilliputocoris* in the tribe Antillocorini because of its concave apical corial margin, elongate buccular carinae, lack of basal iridescent areas on the dorsal head surface, ventral spiracles, and minute size. None of these reasons are very compelling. The nature of

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the concave apical corial margin in *Lilliputocoris* is quite different from that of the Antillocorini in that it encompasses most of the margin (figs. 11, 12, 17), whereas in most antillocorine species the concavity occurs as a more or less abrupt situation near the inner angle. Most other Rhyparochrominae, except the Lethaeini, lack iridescent basal head areas (although some have this surface area modified) and a great many have elongate buccular carinae.

The availability of considerable additional material and especially the opportunity to study a fifth instar nymph of *Lilliputocoris terraereginae*, new species, now makes it possible to interpret the systematic position of the genus in a more definitive manner.

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**LILLIPUTOCORINI, NEW TRIBE**

Polished, shining or subshining, minute insects less than 2 mm. in length. Body slightly flattened. Clothed above and on abdominal venter with elongate erect hairs. Pronotum, scutellum, and hemelytra coarsely punctate. Head porrect, lacking basal iridescent areas, sometimes with scattered punctures but frequently smooth across vertex, latter strongly convex. Bucculae joined mesally well behind base of labium. Eyes separated from pronotum by less than one-half eye length. Interocellar distance approximately three times ocellar width. First antennal segment exceeding apex of tylus, often greatly so; segments two and three robust and clavate; segment four broadly fusiform; all segments with long erect and suberect hairs. Pronotum of macropterous form broadened posteriorly with rounded humeral angles; lateral margins sinuate, frequently with crenulate edges; meson often depressed; calli shining, large, impunctate or nearly so. Scutellum broader than long, lacking a median elevation. Mesosternum anteriorly usually with a short, low, median carina. Hemelytra with clavus broad; a distinct commissure present; lateral corial margins sinuate, often crenulate on proximal third; apical corial margins evenly and shallowly concave for most of length. Membrane of hemelytron without cross veins. Hind wing (when present) lacking veins in cubital sector and anal lobe. Abdomen with well-developed dorsal abdominal scent gland scars between terga three and four and four and five; lacking a scent gland scar between terga five and six (fig. 6). Inner laterotergites absent.

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All abdominal spiracles ventral (fig. 7). Abdominal suture between sterna four and five usually incomplete, occasionally complete. Trichobothria of sternum five either with one trichobothrium anterior to spiracle and two placed together behind it (fig. 23) (plesiomorphic condition) or lacking two posterior trichobothria on sternum five. Suture between sterna three and four sometimes incomplete dorsolaterally and that between five and six often nearly or completely obliterated. Metathoracic scent gland auricle somewhat scimitar-shaped, curving strongly anteriorly (fig. 20); often elevated along outer margin to form rim of evaporative area. Fore femora mutic. Tarsi two segmented (fig. 8). Ovipositor reduced, scarcely laciniate, second valvifers fused across midline; no suture present between ninth tergite and ninth paratergite; first valvifers lightly sclerotized distally; first and second valvulae membranous; tenth segment solidly sclerotized, tenth tergum closely applied to ninth tergite, the two separated by a suture but not by a membrane. Spermatheca without flanges; bulb ovoid; pump short; duct relatively elongate (fig. 5). Sperm reservoir bulb apparently of uniform thickness; wings straplike curving ventrad around bulb; no vesical coils; large membranous lobes present laterally just proximad of sperm reservoir (figs. 14, 15).

Frequently flightless, in which case hemelytra staphylinoid or micropterous,

\[3\] compound eyes much reduced, placed laterally on head, ocelli lacking or vestigial and pronotum quadrate with posterior lobe much reduced.

**TYPE GENUS:** *Lilliputocoris* Slater and Woodward

Although nothing is known of the biology of these insects other than that some live in rainforest ground litter, the wing dimorphism is distinctive in two ways. First, this is the only case known to us in the Lygaeidae where there is a sexual difference in wing development. In some other families of Hemiptera, such as the Miridae and Anthocoridae, it is not uncommon to observe species in which the males are macropterous and the females, in part or always, micropterous or brachypterous. In the Lygaeidae when wing dimorphism occurs both sexes are equally involved. Second, as noted by Slater (1977–1978), it is very unusual to find flightless Lygaeidae in lowland rainforests.

The disjunct distribution, degree of morphological isolation and the nature of the wing reduction all seem congruent with the idea that this is a very old group.

**SYSTEMATIC POSITION**

Stys (1964) has suggested that the Lygaeidae probably constitute a paraphyletic group and that the general lygaeoid-like habitus of members of the pentatomoid family Thaumastellidae is the retention of a plesiomorphic body shape.

It is true that species of *Lilliputocoris* do resemble species of *Thaumastella* and also species of the lygaeid genus *Camptocera* (Lethaeini). These three taxa are all composed of small, yellowish brown insects with convex heads, subquadrate pronota and subflattened bodies. The overall resemblance of *Lilliputocoris* to *Thaumastella* is enhanced by both taxa containing species with a similar staphylinoid morph and species with crenulate pronotal and hemelytral margins.

Therefore it is important to consider the possible relationships between *Thaumastella* and *Lilliputocoris*. Females of both taxa have a reduced ovipositor. In *Thaumastella* the ovipositor is plate-like, whereas in *Lilliputocoris*, despite the reduction, it is distinctly laciniate.

Apomorphic features found in *Lilliputocoris* and not in *Thaumastella* are the incomplete abdominal sutures (fig. 7), two-segmented tarsi (fig. 8), lack of flanges on the spermathecal bulb (fig. 5), and the uniquely shaped, forwardly directed metapleural scent gland auricle (fig. 20). The Thaumastellidae have derived features in the five-segmented antennae, a unique hemelytral corium that distally is separated into two parts with the membrane extending a short distance into this distal corial area, fusion of the eighth ventral laterotergites, trichobothria arranged in a two-plus-two pattern on sterna two through six and a one-plus-one pattern on

\[3\] Staphylinoid and micropterous used in the sense of Slater (1975, p. 53).
sternum seven. Stys (1964) and others have concluded that despite its lygaeid-like habitus *Thaumastella* should be placed as a distinct family in the superfamily Pentatomomorpha.

The ovipositor does not relate *Lilliputocoris* to any pentatomoid taxa. In the Cydnidae which is certainly a pentatomoid group (and one that has many "primitive" features) the fusion of the second valvifers is incomplete, the two structures being separated by a membrane (McDonald, 1966; Schaefer, 1968). In *Lilliputocoris* the second valvifers are fused. This is true of some Pentatomomorpha but there the second valvifers are more reduced and lack a close association with the ninth paratergites. The fusion of the second valvifers in *Lilliputocoris* also rules out a direct relationship with either the Coreoidea or Pyrrhocoridae as in these groups no midline fusion occurs in any of the paired genital structures (Schaefer, 1964, 1965). The structure of the ovipositor thus appears to be an independent reduction phenomenon and does not indicate unambiguously cladistic relationship with the pentatomoid or coreid complexes.

The incomplete, fused suture between abdominal sternum four and five is a strong synapomorphy which places *Lilliputocoris* in the lygaeid subfamily Rhyparochrominae. Sweet (in Slater, Sweet and Baranowski, 1977) discusses an important synapomorphy that is possessed by members of the rhyparochromine tribes Antillocorini and Lethaeiini. This is the presence of a double or "toughed" suture in the nymphs between abdominal terga three and four and four and five. These troughs lead from the lateral edges of the dorsal abdominal scent gland openings to the lateral margins of the abdomen where there is usually a field of spines and tubercles present. The nymph of *Lilliputocoris terraereginae* possesses just such a pair of troughed sutures and a lateral field of spines (fig. 9). We believe that this establishes *Lilliputocoris* as part of a monophyletic group with the Antillocorini and Lethaeiini.

The position of *Lilliputocoris* within the above clade is a more difficult problem. We have, in the cladogram (fig. 10), placed *Lilliputocoris* as the sister group of the Lethaeiini on the basis of the reduction or loss of the dorsal abdominal scent gland between terga five and six. We recognize that this is a reduction phenomenon and we have not been able to establish other synapomorphies. Nevertheless the reduction of the posterior abdominal scent gland is a constant feature that occurs throughout the many and varied taxa of the Lethaeiini. The Lethaeiini is certainly a monophyletic assemblage as evidenced by the unique sperm reservoir (Slater and O'Donnell, 1978), lack of a Y-chromosome, linear trichobothria on abdominal sternum five and iridescent areas at the base of the dorsal surface of the head. Unfortunately, none of these derived character states occurs in any species of *Lilliputocoris*.

Our original decision to place *Lilliputocoris* in the tribe Antillocorini, as noted above, was a tentative one. Ashlock (1964) originally defined the Antillocorini as having as synapomorphies linear trichobothria on abdominal sternum five and a concave apical corial margin. As more and more Antillocorini are being discovered with the trichobothria of abdominal segment five in the plesiomorphic position (and some species with straight apical corial margins) (Slater, 1980, and in prep.),
it is becoming evident that the Antillocorini may well be a paraphyletic group. While recognition of such a taxon may or may not be warranted, depending on one's systematic philosophy, it is evident that *Lilliputocoris* is not closely related to any of the known taxa in the Antillocorini. The various species of *Lilliputocoris* in fact form a closely related monophyletic group held together by several synapomorphies such as the absence of a dorsal abdominal scent gland between terga five and six, the clavate second and third antennal segments, the reduced and modified ovipositor, the two-segmented tarsi, the uniquely formed metapleural scent gland auricle and adjacent evaporative area, and by the loss of abdominal inner laterotergites.

Inner laterotergites are present in the Lethaeini. Thus *Lilliputocoris* cannot be considered a member of the Lethaeini. We therefore conclude that the most appropriate taxonomic procedure is to treat the genus as a distinct tribe and tentatively as the sister group of the Lethaeini. We recognize that such action necessitates the evolution of the linear arrangement of the trichobothria on abdominal sternum five independently in the Antillocorini and in the Lethaeini. This does not seem unreasonable as it certainly has arisen independently in the Targaremini (see discussion below).

**SYSTEMATIC RELATIONSHIPS WITHIN THE RHYPAROCHROMINAE**

When this manuscript was originally submitted Dr. Randall Schuh suggested that it might not be inappropriate to include a preliminary cladogram and a discussion of the cladistic relationships of the tribes currently recognized in the subfamily Rhyparochrominae. To do so might further clarify the reasons for our decision to recognize *Lilliputocoris* as a distinct tribe as well as place current views on the relationships of the tribes into the form of a testable hypothesis. The following discussion is a working hypothesis. We wish it to be viewed as exactly that. Much more evidence is needed to firmly establish (or refute) several of the suggested sister group relationships. The analysis does reveal where major cladistic character strengths and weaknesses lie and suggests which tribes may be paraphyletic.

**Paraphyly:** Unlike many cladists we are not necessarily opposed to the use of paraphyletic taxa in a classification. We see considerable merit in the views of Gauld and Mound (1982) on this subject. We do believe that if such groups are included that they be clearly recognized as such so that they are not used in biogeographic analyses in the same way that monophyletic groups are. An example of the value of an analysis of this kind and of the functional limitations of probable paraphyletic groups is the status of the tribe Stygnocorini. This taxon as currently understood is an assemblage whose limits Slater and Sweet (1970) considerably restricted from a former polyphyletic assemblage recognized by Scudder (1957). As the cladogram (fig. 10) illustrates the Stygnocorini belong to a clade that contains most of the tribes of the Rhyparochrominae. However, genera at present placed in the Stygnocorini do not have a single synapomorphy that segregates them from the other tribes.

Slater and Sweet (1970) discuss the Stygnocorini as a group of “primitive” rhyparochromines within the “Y-suture” assemblage. The present cladistic analysis therefore is important in emphasizing that at present the distribution of the Stygnocorini cannot be considered of zoogeographic significance as the taxon may be paraphyletic. That this may indeed be so is at least suggested by the similarity in habitats of some Stygnocorini to some Ozophorini. Indeed the loss of the inner laterotergites alone would place some taxa in the Ozophorini rather than the Stygnocorini. (Note that the cladogram suggests three independent losses of the inner laterotergites.)

Other suggested cases of paraphyly are revealed by the cladogram. The Antillocorini which were erected by Ashlock (1964) to include taxa without a nymphal Y-suture, but with linear trichobothria on abdominal sternum five and a deep concavity on the inner portion of the apical corial margin, are now known to contain a number of taxa with straight apical corial margins and non-linear trichobothria. There thus does not appear to be a synapomorphy for this tribe.

Sweet (1967) erected the Udeocorini for a number of chiefly Australian genera and separated it from the Myodochini by the presence of inner laterotergites in the Udeocorini.
and their absence in the Myodochini. Presence of inner laterotergites is a plesiomorphic condition in the Rhyparochrominae and thus the Udeocorini, like the Antillocorini and the Stygnocorini, do not at present possess a single definitive synapomorphic feature and again may well represent a paraphyletic group.

For a cladistic analysis of this type to be valuable for future workers it seems desirable to include a short discussion of what we consider to be "strong" and "weak" characters in the cladogram. Once again we recognize that this is a matter of philosophical controversy, some cladists believing that the distribution of characters without consideration of their relative importance is necessary. We do not believe this is the place to enter such a debate but we do believe that some char-
acters are much more important than others as the following discussion indicates.

The presence of a fused suture between abdominal terga four and five is the single character that appears to be a strong synapomorphy holding the Rhyparochrominae together as a monophyletic group. Two points should be made. The Plinthisini, which are usually included in the Rhyparochrominae, do not have this suture fused. Sweet (1967) retained the Plinthisini in the subfamily on the basis of overall habitus, similar feeding habits, and the possession of head trichobothria. The last feature is surely plesiomorphic. The general habitus and feeding habits are suggestive but not useful cladistically. Putshkov (1958) has already suggested that the Plinthisini (which possess a number of autapomorphies) might better be recognized as a subfamily.

The fused and incomplete suture between abdominal sterna four and five is also possessed by several species of Largidae. Whether this is evidence that they form part of a monophyletic assemblage with the Rhyparochrominae or that this apomorphic condition has developed independently is beyond the scope of this paper and must await the results of a phylogenetic analysis of the Largidae and Pyrrhocoridae currently underway by Stehlik and Stys.

We have placed the taxa with "troughed sutures" on the nymphal tergum together by considering this a true synapomorphy. (See character 2.) This is a parsimonious hypothesis but there are reasonable alternative possibilities. The hypothesis assumes that the troughed suture between terga three and four developed first and subsequently two monophyletic assemblages "diverged." The first retained the troughed suture between terga three and four and developed a similar troughed suture between terga four and five. This is represented by the present clade which contains the Antillocorini, Lilliputocorini, and Lethaeini. The hypothesis also assumes that another ancestral type elaborated the troughed suture between terga three and four into the Y-sutured condition. It is of course possible that these two events occurred independently in which case the monophyly of the two groups would not be destroyed but it would necessitate the recognition of a trichotomy near the base of the cladogram (elimination of character 2).

Recognition of the troughed suture (character 2) as a synapomorphy requires the recognition of the secondary loss of the Y-suture in the ancestor of the Gonianotini and Megalontini while at the same time rejecting the secondary loss of the suture in the Cleradini. That secondary loss of the Y-suture in the Gonianotini and Megalontini is probably correct is supported by the dorsalization of some of the anterior abdominal spiracles and the development of a strongly sclerotized spermathecal pump, both conditions occur in tribes with a Y-suture present (characters 5, 7, 19).

The position of the Cleradini on the cladogram is arbitrary. We have placed them near the base of the cladogram to emphasize their anomalous position and the large number of autapomorphies present in the tribe. The overall habitus of many Cleradini suggests a possible relationship with the Drymini. The fact that the species of Cleradini whose feeding habits are known are blood suckers living in the nests of vertebrates, and that at least one drymine also lives in nests and is at least in part predaceous (Slater and Carayon, 1963), and that several drymines are arboreal (Gas
trodes, Apollonius) suggests the possibility that the cleradines may have once had a common ancestor with the Drymini. However, we have not found a synapomorphy for the two groups. The cleradine complex is currently under study by both Malapatil and Harrington and we should have a more sophisticated analysis available within a few years.

We have previously discussed the clade containing the Antillocorini, Lilliputocorini, and Lethaeini and here only wish to reemphasize that the double-troughed sutures (character 4) appear to be a very strong synapomorphic feature that establishes a monophyletic group. The presumed synapomorphy (character 10) that unites the Lilliputocorini and Lethaeini is a loss feature and therefore the evidence for monophyly is much less compelling.

The polyphotomy that includes the Stygnocorini, Phasmosomini, Ozophorini, Targaremini, and Drymini will, we believe, require a great deal of work before it can be resolved. We have noted above the possible
paraphyletic nature of the Stygnocorini. The presumed synapomorphies used in the cladogram to group the Phasmosomini with the Ozophorini and the Targaremini with the Drymini are not compelling. In particular the forward movement of the trichobothria used to group the Targaremini and Drymini (character 16) can at least equally well be considered to be two independent developments. Our decision to accept it as a working hypothesis is partly because many species of the two tribes have a similar habitus and the biogeography is intriguing although beyond the scope of this paper to discuss.

LIST OF APOMORPHIC CONDITIONS USED IN THE ANALYSIS OF CLADISTIC RELATIONSHIPS IN THE RHYPAROCHROMINAE

1. Fusion of sutures between abdominal sterna four and five.
2. Development of a scent conducting trough between abdominal terga three and four in the nymphs.
3. Elaboration and bifurcation of the above trough laterally between abdominal terga three and four into a "Y-suture."
4. Development of a trough in the nymphs between abdominal terga four and five.
5. Movement of abdominal spiracle four from a ventral to a dorsal position on the abdomen.

Dorsally placed spiracles on anterior abdominal segments is considered to be a derived condition. The polarity appears to have been from a dorsal spiral only on segment four, to dorsal spiracles on segments three and four and finally to dorsal spiracles on segments two, three, and four. Both the Megalonotini and Rhyparochromini have dorsal spiracles on segments three and four. Either the dorsalization of spiracle three has developed independently twice or the Y-suture has been lost twice. The cladogram (fig. 10) indicates an independent development of a dorsal spiral on segment three. The heavy sclerotization of most nymphs of Gonianotini and Megalonotini (as well as a similar distribution) suggests a close relationship between these two tribes.

Ventral spiracles are the plesiomorphic condition in the Heteroptera. However, this is not necessarily true of the Lygaeidae. Sweet (1981) has introduced the interesting possibility that the abdominal sclerotization of the Lygaeidae is close to the plesiomorphic condition but with the connexivum shifted dorsally. This would result in primitive dorsal spiracles in the family. Sweet himself, however, believes that dorsalization is secondary in the Rhyparochrominae. We have accepted this conclusion as it seems to be consistent with other evidence.

7. Movement of spiracle three from a ventral to a dorsal position.
8. Movement of spiracle two from a ventral to a dorsal position.
9. Loss of the abdominal inner laterotergites.

Sweet (1967) has used the loss of inner laterotergites as an important feature to establish the tribes Ozophorini and Udeocorini. We have used it but have considerable reservations about its value in phylogenetic analysis. It is after all a loss character. Also in taxa where it is present its degree of development is extremely diverse ranging from wide very heavily sclerotized plates to slender lightly sclerotized strips that in some cases can scarcely be seen unless the abdomen is cleared and stained. Therefore, the Ozophorini and Myodochini which are separated from the Stygnocorini and Udeocorini chiefly by this feature will certainly benefit from a further analysis of relationships.

10. Reduction and loss of the dorsal abdominal scent gland between terga five and six.
11. Loss of the dorsal abdominal scent gland between abdominal terga three and four.
12. Loss of secondary veins in the cubital sector of the metathoracic wing.
13. Loss of the cubital furrow in the metathoracic wing.
14. Fusion of veins R and M in the metathoracic wing for a considerable distance distad of their juncture.
15. Linear placement of trichobothria on abdominal sternum five.
16. Forward movement of the posterior pair
of trichobothria on abdominal sternum five.

This character state is tentatively considered to establish a synapomorphy for the Drymini and Targaremini. Since the trichobothria are linear in the latter and the two posterior trichobothria are more or less dorsoventrally situated in the former this may not be a true relationship. The habitus is often very similar in the two taxa. This is a relationship worthy of a detailed analysis.

17. Development of "pores" anteriorly on the abdominal sternum.
18. Anterior movement of both posterior trichobothria of sternum five.

Scudder (1957) used this character state as the most important synapomorphy for an inclusive tribe which included all of the rhyparochromine taxa with dorsal spiracles. Sweet (1967) notes that transverse ridging can be seen to be weakly developed in other taxa when viewed under a high power of a light microscope. Nevertheless, the condition in the taxa with dorsal spiracles is in our opinion a strong indication of a close cladistic relationship.

21. Development of "corrugated" head grooves.

Sweet (1967) uses the presence of "corrugated head grooves" as a synapomorphy useful for recognition of the tribe Ozophorini. However, very similar grooves are present in some Stygnocorini (Slater and Sweet, 1970). What appear to be at least analogous head surfaces are present in some Myodochini as well.

22. Development of a pseudoperculum on the egg.
24. Utilization of vertebrate blood.
25. Lateral placement of ocelli.
26. An expanded connexival membrane.
27. Loss of the Y-chromosome.
28. Extreme modification of the sperm reservoir.
29. Development of "iridescent" head areas.
30. Modification of the scent gland auricle and evaporative area.
31. Reduction of the ovipositor.
32. Concavity of the apical corial margin.
33. Loss of a tarsal segment.
34. Development of a secondary longitudinal abdominal suture.

LILLIPUTOCORIS SLATER AND WOODWARD
Lilliputocoris Slater and Woodward, 1979, p. 16.

TYPE SPECIES: Lilliputocoris exigus Slater and Woodward. Monobasic.
DIAGNOSIS: Same as for tribe.

KEY TO SPECIES OF LILLIPUTOCORIS
1. Length of first antennal segment considerably greater than width of head across eyes (Borneo) (macropters only known) ............... gossocerata, new species
   1a. Length of first antennal segment less than (rarely nearly subequal to) width of head across eyes .......................... 2
   2. Macropterous ............ 3
   2a. Micropterous or staphylinoid 7
   3. First antennal segment relatively elongate, much more than three-fourths as long as width of head across eyes .......................... 4
   3a. First antennal segment relatively short, at most only slightly more than two-thirds and always much less than three-fourths as long as width of head across eyes .......................... 5
   4. Basal one-half of lateral corial margins bearing a series of conspicuous crenulate teeth (fig. 17); antennae nearly unicolorous, chiefly yellowish brown (Australia) ............... terraeleginae, new species
   4a. Basal one-half of lateral corial margins smooth or nearly so, lacking a series of conspicuous crenulate teeth; antennae chiefly dark chocolate brown; distal ends of antennal segments two and three contrastingly pale (Ghana) ............ ghanaensis, new species
   5. Punctures of pronotal lobe fine and inconspicuous, not remotely approaching diameter of claval punctures (fig. 12) (Brazil) ............... neotropicalis, new species
   5a. Punctures of posterior pronotal lobe relatively coarse and conspicuous, nearly of same diameter as those of clavus ........................ 6
   6. Head and pronotal calli smooth and polished, former with only a few scattered punctures present (fig. 11) (Sri Lanka) ............... exigus Slater and Woodward
   6a. Head finely but thickly punctate over entire surface; calli granulose or minutely punctate
7a. Staphylinoid, hemelytra covering third abdominal tergum, broadly in contact at midline (fig. 18) ................. 8

8. First antennal segment short not exceeding tylys by as much as one-half its length (fig. 13) (Papua New Guinea; Australia) ........ punctatus (Woodward)

8a. First antennal segment relatively elongate exceeding tylys by much more than one-half its length ......................... 9

9. Suture between abdominal terga four-five and six smooth, lacking a series of ridges and furrows; lateral margins of hemelytra nearly smooth, lacking well-developed crenulate teeth (Seychelles) ......................... seychellensis, new species

9a. Suture between abdominal terga four-five bearing a series of ridges and furrows (fig. 24); lateral margins of hemelytra with prominent outwardly directed teeth (fig. 18) (Australia) .... terraereginae, new species

**Lilliputocoris exiguis** Slater and Woodward

**Lilliputocoris exiguis** Slater and Woodward, 1979, pp. 17–18.

**Diagnosis:** Recognized by the smooth polished head and pronotal calli and the relatively short first antennal segment which is only two-thirds as long as the width of the head across the eyes.

**Discussion:** This is a very small (1.62 mm.) nearly uniformly bright brown species. The hemelytra and legs are pale yellow. The lateral margins of the pronotum and hemelytra lack conspicuous crenulations.

**Lilliputocoris exiguis** was described from a single female from Sri Lanka and remains known only from the holotype.

**Etymology:** The name refers to the small size of the insect.

**Lilliputocoris ghanaensis**, new species

**Diagnosis:** Recognized by its elongate, dark chocolate brown first antennal segments, the bicolored second and third antennal segments which have the proximal two-thirds dark and the distal one-third ochraceous and by the lack of crenulate teeth on the basal portions of the lateral corial margins.

**Description:** General color testaceous. Scutellum and a macula at apex of corium dark red-brown to chocolate brown. Pleural and ventral surfaces red-brown. Abdomen becoming pale yellow laterally. Antennal segment one ochraceous; proximal two-thirds of antennal segments two and three dark chocolate brown contrasting strikingly with ochraceous coloration of distal one-third of each segment; fourth antennal segment testaceous, infuscated with dark brown proximally. Head, pronotum, and scutellum thickly and coarsely punctate. Dorsal surface clothed with numerous, conspicuous, elongate, silvery, upstanding hairs.

Head only slightly declivent anteriorly; vertex strongly convex. Tylus extending only to proximal one-third of first antennal segment. Ocelli very prominent, located as close to midline as to compound eyes. Length head 0.26, width 0.34, interocular space 0.27. Pronotum with lateral margins deeply sinuate, weakly crenulate; meson broadly and deeply impressed, this impressed area narrowing posteriorly; transverse impression incomplete; anterior collar area well delimited; calli widely separated, nearly impunctate. Length pronotum 0.28, width 0.56. Scutellum somewhat elevated mesally but lacking a distinct median carina. Length scutellum 0.14, width 0.36. Hemelytra with clavus very broad; three more or less anastomosing rows of coarse punctures present, claval commissure noticeably longer than scutellum. Length claval commissure 0.20. Corium with lateral margins deeply concave or sinuate lacking conspicuous crenulations; midline distance apex clavus–apex corium 0.34, midline distance apex corium–apex membrane 0.36. Labium reaching metacoxae. Length labial segments I 0.20, II 0.20, III, and IV obscured. Antennae stout, segments two and three moderately clavate, segment four broadly fusiform. Length antennal segments I 0.29, II 0.30, III 0.20, IV 0.30. Total body length 1.62.

**Etymology:** Named for Ghana, West

*In the following descriptions all measurements are in millimeters.*
Fig. 11. *Lilliputocoris exiguo* Slater and Woodward, dorsal view.
Africa, the country from which the holotype was collected.

**Holotype**: Female, GHANA: Tafo November 6, 1965, Dennis Leston collector; deposited in the American Museum of Natural History.

**Lilliputocoris grossocerata**, new species

**Diagnosis**: Recognized by the extremely elongate, uniformly dark chocolate brown antennae that contrast strongly with the honey yellow coloration of the remainder of the body and by the crenulate lateral pronotal margins.

**Description**: General coloration of body including legs bright yellow. Membrane of forewing bicolored, a dark fumose irregular band running transversely across membrane from distal ends of apical corial margins, this dark band very much broadened mesally; a second fumose area present on distal end of membrane and extending anteriorly to middle of membrane, remainder of membrane translucent. Distal portion of apical corial margin dark brown. All femora with dark brown spots. Entire antennae a very strongly contrasting dark chocolate brown. Head nearly smooth. Pronotum, scutellum, clavus, and corium coarsely punctate. Dorsal surface appearing nearly glabrous but with a few scattered semideclivent hairs.

Head only slightly declivent anteriorly. Tylus extending to basal one-fourth of first antennal segment. Eyes well removed from anterior margin of pronotum by a short thick straight sided "neck." Ocelli present slightly behind eyes, the latter small and extending only slightly above bases of antenniferous tubercles. Length head 0.32, width 0.32, interocular space 0.23. Pronotum with a distinct anterior collar; lateral margins of pronotum deeply sinuate with posterior lobe much expanded and conspicuously crenulate; transverse impression complete; posterior margin slightly convex between swollen humeral angles. Length pronotum 0.27, width pronotum 0.50. Scutellum lacking a median elevation. Length scutellum 0.16, width 0.20.

Lateral corial margins sinuate, narrowest at level of middle of claval commissure. Length claval commissure 0.16. Midline distance apex clavus–apex corium 0.30, midline distance apex corium–apex membrane 0.38. Abdominal tergum with scent gland openings present on sutures between terga three and four and four and five, a groove extending along suture part way to lateral margin from edge of each gland opening. Labium extending almost to metacoxae. Length labial segments I 0.16, II 0.18, III 0.14, IV 0.19. Antennae very conspicuous, all segments clothed with elongate upstanding hairs, segments two, three, and four fusiform. Length antennal segments I 0.36, II 0.31, III 0.20, IV 0.28. Total body length 1.50.

**Etymology**: Named for the very large elongate conspicuous "horns" or antennae.

**Holotype**: Female, BORNEO: Sarawak, Baco National Park near Kuching, SL (=soil litter) rainforest July 1, 1968, berlesate, accession number 68.767 (Robert W. Taylor collector); deposited in The Australian National Insect Collection number 9446.

**Paratype**: One female, BORNEO: Sarawak, East Malaysia, Semongk Forest Reserve January 3, 1978, from litter in primary rainforest (Thomas E. Woodward collector); deposited in The University of Queensland Insect Collection.

**Lilliputocoris neotropicalis**, new species

**Figure 12**

**Diagnosis**: Recognized by its minute inconspicuous pronotal punctures and short first antennal segment.

**Description**: General coloration pale testaceous. Distal one-half of apical corial margin narrowly dark brown. Membrane marked with pale brown very much as in *terraeigna*. First antennal segment pale basally, becoming fuscous on distal two-thirds. Antennal segments two and three chiefly dark chocolate brown with strongly contrasting pale distal ends. Head shining and polished, almost impunctate across convex vertex. Pronotal punctures large and coarse, anteriorly delimiting a "collar-like" area; coarse punctures also present transversely along the incomplete transverse impression and on posterior pronotal lobe immediately behind it, remainder of posterior lobe nearly impunctate, at most with small, shallow widely separate inconspicuous punctures.
Scutellum with large punctures but these widely separated from one another, never giving surface an anastomosing appearance. Dorsal surface clothed with numerous elongate upstanding pale hairs.

General body shape including head convexity, medially depressed and laterally sinuate pronotum and noncarinate scutellum very similar to *ghanaensis*. Tylus elongate extending well beyond basal one-third of first antennal segment. Length head 0.26, width 0.32, interocular space 0.19. Lateral margins of anterior pronotal lobe very feebly crenulate. Length pronotum 0.26, width 0.53. Scutellum nearly smooth, not noticeably elevated mesally. Length scutellum 0.18, width 0.32. Clavus with punctures very much reduced, these conspicuous only along margins of scutellum and along claval suture, greater part of claval surface essentially
impunctate. Length claval commissure 0.18. Central area of corium hyaline, lateral margins only shallowly sinuate, lacking crenulations; midline distance apex clavus–apex corium 0.34, midline distance apex corium–apex membrane 0.30. Labium partially obscured, probably reaching metacoxae. Length labial segments I 0.25, II 0.14, III and IV obscured. Antennae relatively slender. Length antennal segments I 0.20, II 0.20, III 0.14, IV—missing. Total body length 1.38.

**Etymology:** Named for the Neotropical faunal region, from which the holotype was collected.

**Holotype:** Female, BRAZIL: Para, Jacareacanga June 1970, F. R. Barbosa collector; deposited in the American Museum of Natural History. (Note: this locality is at 6°09'S, 58°15'W.)

*Lilliputocoris punctatus* (Woodward)

Figures 13–15


**Diagnosis:** Recognized by the thickly punctate dorsal surface and by the short first antennal segment which is never more than three-fourths the width of the head across the eyes.

**Discussion:** This species was originally described from a single staphylinoid specimen from near Port Moresby, Papua New Guinea. Macropterous forms now available for study differ from the sympatric terraereginae by the much shorter first antennal segment, the almost completely dark color of the antennae, the lack of a median brown area on the hemelytral membrane, a less prominently mesally depressed pronotum, and the finer pronotal, scutellar and hemelytral punctures. Staphylinoids differ as noted in the preceding key and by the finer dorsal punctures. The crenulations along the lateral margins of the hemelytra are usually less prominently developed than they are in terraereginae.

The 34 specimens available for study show striking sexual differences in wing development. All 15 males are macropterous, 17 of 19 females are staphylinoid.

The following corrections should be made to the original description: (1.) pp. 51–52 “male” should read “female”; (2.) p. 52, line 5 “0.33” should read “0.20.”

**Measurements:** *Macropterous form—*

Length head male 0.25, female 0.22; width head male 0.30, female 0.31; interocular space male 0.18, female 0.20. Length pronotum male and female 0.24, width male 0.48, female 0.50. Length scutellum male 0.14, female 0.16; width male 0.23, female 0.26. Length claval commissure male 0.16, female 0.19. Midline distance apex clavus–apex corium male 0.35, female 0.30. Midline distance apex corium–apex membrane male and female 0.30. Length labial segments I male and female 0.18; II male 0.17, female 0.15; III male 0.10, female 0.08; IV male 0.22, female 0.20. Length antennal segments I male 0.23, female 0.20; II male 0.23, female 0.20; III male 0.17, female 0.15; IV male and female 0.25. Width across hemelytra male 0.51, female 0.50. Total body length male and female 1.43.

**Staphylinoid form** (measurements indicate range): Length head 0.26–0.28, width...
0.29–0.30, interocular space 0.22–0.23. Length pronotum 0.20, width 0.37–0.39. Length scutellum 0.13–0.16, width 0.22–0.26. Length forewing (to mesal margin) 0.13–0.16. Length labial segments I 0.17–0.19, II 0.17–0.19, III 0.10, IV 0.22. Length antennal segments I 0.18–0.21, II 0.19–0.20, III 0.13–0.14, IV 0.17–0.20. Width across abdomen 0.49–0.57. Total body length 1.30–1.34.


Lilliputocoris seychellensis, new species

Figures 4–8, 16

Diagnosis: Recognized by its strongly punctate staphylinoid hemelytra, lack of ridges and furrows on sutures between abdominal terga four and five and six and lack of the posterior pair of trichobothria on sternum five.

Description: General coloration reddish brown. Legs and distal one-half to two-thirds of antennal segments two and three testaceous.

Shape, punctuation, pubescence, and structure very similar to staphylinoids of L. terraereginae. Lateral margins of pronotum at most very feebly crenulate. Lateral margins of hemelytra lacking spinelike crenulations, appearing smooth. Tylus extending to proximal one-third of first antennal segment. Sutures between abdominal terga three and four and four and five fine and narrow, lacking a series of ridges and grooves. Length head 0.29, width 0.32, interocular space 0.26.
Fig. 16. *Lilliputocoris seychellensis*, new species, dorsal view.

Length pronotum 0.24, width 0.43. Length scutellum 0.17, width 0.27. Maximum length wing pad 0.38, width wing pad 0.52. Maximum width abdomen 0.56. Length labial seg-
ments I 0.20, II 0.20, III 0.10, IV obscured. Length antennal segments I 0.28, II 0.22, III 0.16, IV missing (Paratype 0.24). Total body length 1.46.

**ETYMOLOGY:** Named for the Seychelle Islands from which the species was collected.


**PARATYPE:** One female: same data as holotype deposited in James A. Slater Collection.

**Lilliputocoris taylori**, new species

Figures 1–3

**DIAGNOSIS:** Recognized by the minute wing pads that are only narrowly in contact mesally and do not extend posteriorly over tergum three, by the scent scars on the abdominal dorsum appearing to be placed intersegmentally and the lack of the posterior pair of trichobothria on sternum five.

**DESCRIPTION:** General coloration bright reddish brown becoming almost orange-yellow on head and femora. Antennae chocolate brown on proximal two-thirds of segment two and proximal one-half of segment three; fourth segment pale yellow, slightly darkened at proximal end. Conspicuous upstanding hairs present on dorsal surface. Head impunctate across vertex, weakly punctate anteriorly, a single row of coarse punctures present at anterior end where “neck” inserts into prothorax. Pronotum coarsely punctate anteriorly and behind calli, latter and posterior portion of pronotum impunctate. Scutellum and wing pads coarsely punctate.

Head moderately declivent anteriorly, tyline reaching only basal one-third of first antennal segment. Compound eyes very much reduced, only a few ommatidia present. Ocelli absent. Vertex strongly convex. Length head 0.26, width 0.32, interocular space 0.28. Pronotum quadrate, anterolateral margins even rounded, lateral margins parallel-sided, coarsely crenulate. Calli very large, convex, and impunctate. Pronotal surface slightly impressed mesally behind calli, posterior lobe greatly reduced, maximum width of pronotum at level of calli. Length pronotum 0.22, maximum width 0.37. Scutellum depressed posteriorly lacking any indication of a median elevation. Length scutellum 0.14, width 0.31. Micropterous hemelytra reduced to short broad posteriorly truncate pads that barely reach base of abdomen and narrowly meet at midline; posterior margin slightly angled anteriorly from caudolateral angles; lateral margins strongly convex and strongly crenulate. Width across wing pads 0.50, length wing pad 0.20. Abdomen elliptical, dorsal surface convex, anterior margin of tergum three thickened and tilted upward as a sharp rim. Maximum width across abdomen 0.62. Dorsal abdominal scent gland scars present between terga three and four and four and five, but intersegmental sutures curving caudomesad so that gland scars are placed behind suture lines. Labium exceeding metacoxae. Length labial segments I 0.22, II 0.22, III 0.12, IV 0.24. Length antennal segments I 0.30, II 0.22, III 0.16, IV 0.22. Total body length 1.54.

**ETYMOLOGY:** Named for Dr. R. W. Taylor of the Australian National Insect Collection who collected a large part of the type series.

**HOLOTYPE:** Female, BORNEO: Sarawak, Semengok Forest Reserve. 11 miles southwest of Kuching, June 30, 1963, rainforest, berlesate accession number 68.778, Robert W. Taylor collector; deposited in the Australian National Insect Collection number 9445.

**PARATYPES:** One female same data as holotype; one female same except 2–3.VII.1968 (berlesate number 68.784); one female same as above except (berlesate number 68.781); one female same except 28–31.V.1968 (leaf mold, berlesate number 68.197 rainforest); two females same as above except (berlesate number 68.201); one female same as above except (berlesate number 68.196); one female same except 1–4.VI.1968 (berlesate number 68.259); three females same except (berlesate number 68.261). Two females Baco National Park near Kuching SL [=soil litter] rainforest 1–VI.1968 (berlesate number 68.757). One female Borneo: Sabah, mile 45 Labok Road from Sandakan (Lungmanis) 12–13.VI.1968 (rainforest, berlesate number 68.502); deposited in the Australian National Insect Collection, Queensland Museum, American
Fig. 17. *Lilliputocoris terraereginae*, new species, dorsal view, macropter.
Fig. 18. *Lilliputocoris terraereginae*, new species, dorsal view, staphylinoid.

Museum of Natural History, University of Queensland, Agricultural Research Institute Semongok Sarawak, and James A. Slater Collection.

*Lilliputocoris terraereginae*, new species Figures 9, 17–24

**Diagnosis:** Recognized by the relatively long first antennal segment, the nearly pale yellowish brown color of the antennae and the conspicuous crenulate teeth on the lateral margins of the pronotum and basal half of the corium.

**Description:** Coloration nearly uniformly pale yellowish-testaceous. Base of scutellum, apical corial macula and pleural and ventral areas of thorax brown. Membrane of forewing with extensive brown to fuscous areas, one across base, one median and broadening to apex. Vertex finely punctate with a row of coarser punctures behind ocelli and a transverse impunctate area between each eye and ocellus. Dorsal surface with elongate upstanding hairs.

Shape of head, pronotum and hemelytra as in *ghanaensis*. Lateral corial margins with distinct prominent crenulate-like teeth. Labium reaching metacoxae.

Length head 0.34, width 0.36, interocular space 0.24. Length pronotum 0.30, width 0.61. Length scutellum 0.17, width 0.25. Length claval commissure 0.23. Midline distance apex clavus–apex corium 0.43; midline distance apex corium–apex membrane 0.40. Length labial segments I 0.23, II 0.22, III 0.14, IV 0.28. Length antennal segments I 0.35, II 0.34, III 0.23, IV 0.27. Total body length 1.80.

Staphylinoid females differ from macropterous males as follows: yellowish brown; antennal segment four and tyulus usually paler brownish yellow; abdomen shining brown or yellowish brown; ventral surface of head, thorax, and base of abdomen yellowish brown to dark brown. Length head 0.30–0.35; width across eyes 0.35–0.37; interocular space 0.28–0.32 (*ca* 8–10X width of eye; ocelli vestigial. Length antennal segments I 0.28–0.31, II 0.24–0.28, III 0.17–0.19, IV 0.24–0.25. Length labial segments I 0.23–0.26, II 0.23–0.25, III 0.11–0.14, IV 0.25–0.28. Length pronotum 0.25–0.28; posterior width 0.45–0.51. Length scutellum 0.15–0.18; width 0.28–0.34. Forewings leaving abdomen exposed from tergum IV to apex; entire surface of hemelytra with large, deep, mostly contiguous punctures, interspaces raised, giving surface a coarsely granulate appearance; apical margins broadly and shallowly concave, posterolateral angles acutely or subacutely produced posteriorly; length mesal margin 0.18–0.20. Total body length 1.61–1.71; width across abdomen 0.67–0.74.

**Etymology:** Named for Queensland, the Australian State from which the species was collected.

**Holotype:** Male (macropterous), AUSTRALIA: Queensland 730 m. Mount Tiptree, June 29, 1971, Taylor and Feehan collectors, berlese Australian National Insect Collection 345, rainforest, 17°03'S, 145°37'E;
deposited in the Australian National Insect Collection number 9444.

Paratypes: Queensland, two macropterous males, nine staphylinoid females same data as for holotype; two macropterous males (one dissected), seven staphylinoid females, data as above except berlesate Australian National Insect Collection (=ANIC Below) number 346; one staphylinoid female, data as above except 840 m. berlesate ANIC number 347, 17°04'S, 145°37'E; one macropterous male, two staphylinoid females (one with abdomen separated and aluminium coated), data as above except 900 m. berlesate ANIC 348, 17°04'S, 145°37'E; one staphylinoid female, 1140 m. near Mt. Haig, 30.VI.1971, Taylor and Feehan, berlesate ANIC 349, rainforest, 17°06'S, 145°37'E; one staphylinoid female, data as above except 750 m., berlesate ANIC 350, 17°10'S, 145°36'E; one macropterous male, 20 km. south of Ravenshoe, 800 m., 3.VII.1971, Taylor and Feehan, berlesate ANIC 358, rainforest, 17°49'S, 145°32'E; two staphylinoid females (aluminium coated), Beatrice River, Palmerston Highway, 30.VII.1956, from leaf litter, rainforest, about 700 m., T. E. Woodward; one staphylinoid female, Black Mountain Road, 30 km. north of Kuranda, 4.XI.1969, ANIC berlesate number 165, leaf mold, rainforest, J. G. Brooks, deposited in Australian National Insect Collection, Queensland Museum, American Museum of Natural History, University of Queensland and J. A. Slater Collections.

Discussion: Lilliputocoris terraereginae differs from L. punctatus the other Queensland species as follows: both macropters and staphylinoids larger; antennae proportionately longer, segment I extending farther beyond apex of head and with length subequal to head width in macropters and subequal to interocular space in staphylinoids (less in each instance in punctatus); antennal segment four of staphylinoids without a large dorsal concavity; pronotum, scutellum, and forewings more coarsely and deeply punctate; hairs along lateral margins of pronotum and corium arising from conspicuous acute tubercles; macropters with an extensive dark median area on hemelytral membrane; forewings of staphylinoids with apical margins shallowly concave and posterolateral angles acutely or subacutely produced backward.

Whereas all specimens of L. terraereginae were collected at altitudes of over 600 m. in northeast Queensland, punctatus was collected only at or near sea level in coastal or subcoastal areas in Papua New Guinea and northeast Queensland, in some instances geographically very close to the sites of occurrence of terraereginae.

In most morphological features whereby terraereginae differs from punctatus, the former appears to be the more apomorphic. The longer first antennal segment, proportionately more reduced eyes in the staphylinoids, the coarser and deeper punctation, the prominent setiferous tubercles along the lateral pronotal and corial margins, and the backwardly produced caudolateral angles of the forewings of staphylinoids all appear to be derived features. This indicates the probability of terraereginae and related species being derived from a punctatus-like ancestor and at least in this case becoming secondarily adapted to higher altitude conditions.

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