

Cladistic analysis and biogeography of *Brachystethus* Laporte (Heteroptera, Pentatomidae, Edessinae)¹

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Abstract

In this paper, *Brachystethus* Laporte, 1832 is analyzed cladistically, using 21 characters and 15 taxa, including as outgroups, in a first analysis, the genera *Neotibilis* Grazia & Barcellos, 1994, *Edessa* Fabricius, 1803, *Olbia* Stål, 1862, *Peromatus* Amyot & Serville, 1843, and *Pantochlora* Stål, 1870. Further, these edessine genera were included in the ingroup, without any changes in the only resulting cladogram. The monophyly of *Brachystethus* is supported by four synapomorphies: metasternal carina partially bifurcated, pygophore with blade-like processes, anterior margin of gonocoxites 9 deeply concave medially, and a mesial thickening on gonapophyses 9. *Brachystethus* shares with *Edessa*, *Olbia*, *Pantochlora*, and *Peromatus* four synapomorphies: loss of subcallous margin on pronotum, mesosternal carina lower than metasternal carina, phallus with a short vesica, and presence of a beak-like projection on the thickening of vaginal intima. Based on the cladogram, the transferal of *Brachystethus* to Edessinae is here proposed. Biogeographical analysis has shown congruence between the distributional pattern of the clade formed by *B. rubromaculatus* Dallas, 1851, *B. signoreti* Stål, 1872, *B. cribrus* (Fabricius, 1781), and *Brachystethus* sp. nov. A, and vicariant events on Neotropical region, in the late Cretaceous.

Key words. Cladistic analysis, Edessinae, *Brachystethus*, Pentatomidae, biogeography

Introduction

Amyot & Serville (1843) established, within “Brevirostri, the group “Edessides”, including several genera, among them *Edessa* Fabricius, 1803, *Peromatus* Amyot & Serville, 1843, and *Brachystethus* Laporte, 1832. Dallas (1851) established Edessidae, including

most of the genera cited by Amyot & Serville. Stål (1860) did not change the composition of the group; Stål (1862) described *Olbia*, with two species, *O. caprina* and *O. elegans*. Kirkaldy (1909) placed *Brachystethus* within Pentatomini, proposing the tribe Edessini to include *Peromatus*, *Olbia*, and *Edessa*. After that, the only change in this exclusively neotropical group was the inclusion, by Rolston & McDonald (1979), of *Pantochlora* Stål, 1870, formerly belonging to Tessaratomidae. Since then, the status of Edessinae has been frequently modified, sometimes considered as a tribe (Gapud, 1991) other times as a sub-family (Rolston & McDonald, 1979; Schuh & Slater, 1995).

Brachystethus, an exclusively neotropical genus nowadays belonging to Pentatominae, comprises ten species. Since Kirkaldy's Catalog (1909), no other paper has included all the species, most of them described in the last century. The genus has been revised (Barcellos & Grazia, in press), with the description of a new species, and the removal of *Ochlerus discolor* Walker, 1867 from the genus.

Papers including cladistic methods in Pentatomidae have only recently become more frequent (Ahmad & Khan, 1983; Schaefer & Ahmad, 1987, Gapud, 1991; Grazia, 1997). In this paper, a cladistic analysis of *Brachystethus* is performed, and, based on the resultant cladogram, some biogeographical implications are discussed.

Material and methods

The data matrix (appendix 2) included 21 characters of genitalia and general morphology (appendix 1) for 15 taxa – including initially five outgroups. Autapomorphies were not included in the matrix, to avoid their influence in the consistency and retention indexes. The matrix was built and numerically analyzed using the softwares Tree Gardener V. 2.2 (Ramos, 1997) and Hennig 86 (Farris, 1988). The character polarizations followed the outgroup comparison method (Watrous & Wheeler, 1981). Chosen as outgroups, in a first analysis, were the genera *Neotibialis* Grazia & Barcellos, 1994, *Edessa*, *Olbia*, *Peromatus*, and *Pantochlora*; after that, the edessine genera were included in the ingroup. The criteria for choosing these taxa were the taxonomic history and a previous analysis of the morphological characters. *Brachystethus* had already been included in Edessinae, and was described as a subgenus of *Edessa*. On the other hand, several species of *Neotibialis* were originally described in *Brachystethus*, suggesting that they share homologous characters. The previous analysis of morphological structures, especially of the male genitalia, has also shown hypothesized homologies. Due to the large number of *Edessa* species (259, according to Fernandes & Doesburg, 2000a) and their interespecific variation, *Edessa elaphus* Breddin, 1905, from the type-species group (Fernandes & Doesburg, 2000b), was chosen as representative of the genus.

Multistate characters were treated as ordered. The algorithm used in Hennig 86 was *ie**. The notation “group +” (Amorim, 1982) was used in the results and discussion.

Based on the taxa cladogram obtained, a biological area cladogram was built, in order to search for possible congruences among vicariant patterns in Central and South America for different organisms.

Results and discussion

The inclusion of edessine genera as ingroup together with *Brachystethus* did not modify the relationships among species of this genus. The cladistic analysis resulted in only one cladogram (fig. 23), with 48 steps length, consistency index = 60 and retention index = 76.

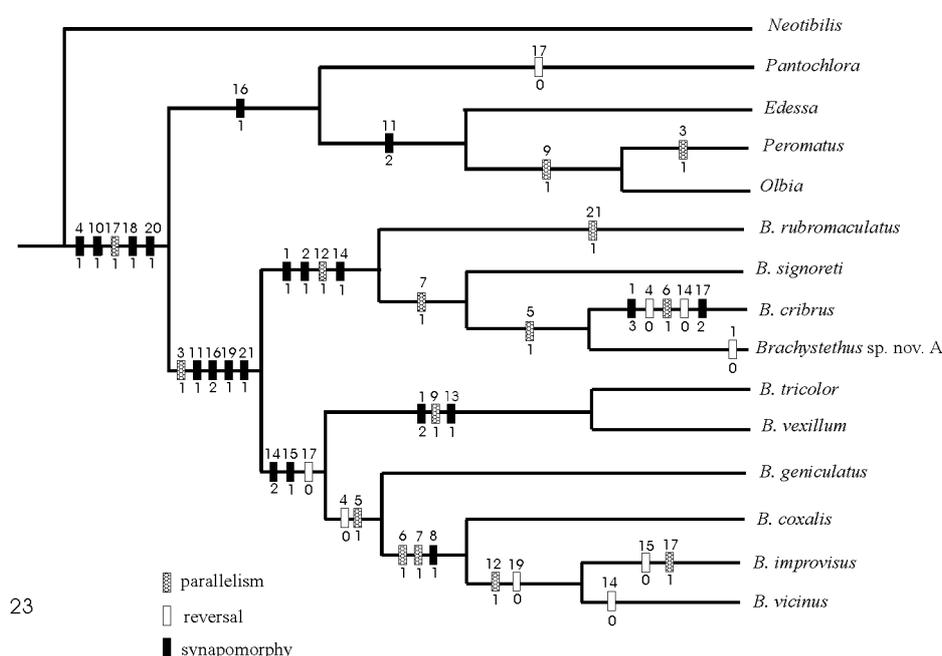


FIGURE 23. Resulting cladogram of phylogenetic analysis of *Brachystethus* (48 steps length, CI = 60, RI = 76).

Brachystethus shares with *Pantochlora*, *Edessa*, *Olbia*, and *Peromatus* the loss of yellowish subcallous margin of the pronotum; the mesosternal carina little developed, lower than metasternal carina; the short vesica; and, on female genitalia, the beak-like projection on the thickening of the vaginal intima. These synapomorphies justify the transference of *Brachystethus* to Edessinae, and support the monophyly of Edessinae with its inclusion. This study also corroborates the transference of *Pantochlora* to Pentatomidae by Kumar (1969) and its inclusion in Edessinae by Rolston & McDonald (1979).

Pantochlora, *Edessa*, *Peromatus*, and *Olbia* also constitute a monophyletic group, supported by one synapomorphy, the presence of genital cup processes with well-defined shape, ovoid to digitiform. *Pantochlora*, the most basal genus, is the sister group of the

remaining genera of the clade. *Edessa* is basal in relation to *Peromatus* and *Olbia*, sharing with them one synapomorphy, the anterior margin of the metasternal carina completely bifurcated. *Peromatus* and *Olbia* share one homoplasy, the short ostiolar rugae.

The monophyly of *Brachystethus* is supported by four synapomorphies: the anterior margin of the metasternal carina partially bifurcated, presence of blade-like processes of genital cup, anterior margin of the gonocoxites 9 deeply concave at the middle, and presence of the mesial thickening on gonapophyses 9; and also by one homoplastic character, first rostral segment surpassing bucculae in more than half of the segment's length.

B. rubromaculatus Dallas, 1851 constitutes a monophyletic group with *B. signoreti* Stål, 1872, *B. cribrus* (Fabricius, 1781), and *Brachystethus* sp. nov. A, sharing with them three synapomorphies – abdominal venter with red spots, fourth antennal segment medially swollen, and dorsal rim of pygophore with low, triangular lobes. They also share one homoplasy – metasternal carina strongly elevated anteriorly.

The clade comprised of *B. signoreti*, *B. cribrus*, and *Brachystethus* sp. nov. A is supported by one homoplasy: yellowish color of apex of femora and base of tibiae; the clade *B. cribrus* + *Brachystethus* sp. nov. A, shares the homoplasy presence of yellowish calli on corium.

Brachystethus tricolor Bolívar, 1879, *B. vexillum* Breddin, 1903, *B. geniculatus* (Fabricius, 1787), *B. coxalis* Breddin, 1904, *B. improvisus* Breddin, 1905, and *B. vicinus* Signoret, 1851 constitute a monophyletic group, corroborated by two synapomorphies: lobes of dorsal rim conspicuous, parameres with acute apex; and one homoplasy, genital cup processes not or scarcely visible in dorsal view.

Brachystethus tricolor and *B. vexillum* also form a monophyletic group, supported by two synapomorphies: abdominal venter predominantly red, and presence of a transversal sulcus on metasternal carina; they also share one homoplasy, short ostiolar rugae. In fact, these species present only small differences, particularly in male genitalia and dorsal color pattern. Examination of more specimens will prove the validity of these species.

The clade *B. geniculatus* + is supported by two homoplasies, subcallous yellowish margin of the pronotum, and yellowish calli on corium.

Brachystethus coxalis, *B. improvisus*, and *B. vicinus* share one synapomorphy, yellowish tarsi, and two homoplasies: yellowish coxae and yellowish color of apex of femora and base of tibiae.

Brachystethus improvisus and *B. vicinus* share two homoplasies: metasternal carina anteriorly elevated and anterior margin of gonocoxites 9 sinuated, little excavated. These species are cryptic, being distinguished only by genital characters.

Biogeography

Brachystethus is an exclusively Neotropical genus, widespread in this region, ranging from Mexico to Argentina (fig. 24).



FIGURE 24. Distribution of *Brachystethus* and biological area cladogram for *B. rubromaculatus*, *B. signoreti*, *B. cribrus* and *Brachystethus* sp. nov. A.

A comparison between the taxa cladogram and distributional data shows that the monophyletic group *B. rubromaculatus* + *B. signoreti* + *B. cribrus* + *Brachystethus* sp. nov. A presents three totally disjunct areas of endemism. *B. rubromaculatus*, the most basal species of the group, is restricted to Central America. *B. signoreti* is distributed over a narrow strip in northwestern South America, in Venezuela and Ecuador. This species is the sister group of the clade formed by *B. cribrus* and *Brachystethus* sp. nov. A. *Brachystethus cribrus* is distributed over an extensive area in the Amazon Basin; and *Brachystethus* sp. nov. A, known so far only by its holotype, has its distributional area inside that of *B. cribrus*.

According to Amorim & Pires (1996), the first disjunction in the continental areas of the Neotropics clearly shows a northwestern track versus a southeastern track, the first one including tropical Central America and northwestern South America and the second com-

posed of southeastern Amazonia, the Atlantic Forest, northern Argentina, Paraguay, and Uruguay. This disjunction might be related to the division of Amazonia by a lake along the Amazonas/Madeira/Mamoré Rivers, in the Late Cretaceous. The strictly northwestern distribution of *B. rubromaculatus*, *B. signoreti*, *B. cribrus*, and *Brachystethus* sp. nov. A suggests that they probably speciated after this vicariant event, not considering the possibilities of dispersion, extinction, or even lack of collection. Because other species of *Brachystethus* have been collected in southern and southeastern Brazil, a lack of collecting does not seem a plausible explanation.

The first division of the Northwest component occurred with the formation of an epicontinental sea in the Maracaibo region, after the Late Cretaceous. This event separated an area in Mesoamerica from typically Amazonian elements. The Mesoamerican component extends southward into South America west from the Andean mountain chain into Colombia, Ecuador, and Peru (Amorim & Pires, 1996) This division is mostly congruent with the distributions of *B. rubromaculatus* (exclusively Mesoamerican) and *B. signoreti* (along the northwest coast of South America), separating these species from the Amazonian clade *B. cribrus* + *Brachystethus* sp. nov. A. Despite two records for *B. cribrus*, from central and northeastern Brazil, which are incongruent with the northwestern X southeastern Amazonian pattern, the distribution of the monophyletic clade *B. rubromaculatus*, *B. cribrus*, *B. signoreti*, and *Brachystethus* sp. nov. A agrees with former studies on *Evoplilus* group (Hemiptera, Pentatomidae) by Grazia (1997), and also on *Rhynchosciara* (Diptera, Sciaridae), the *Rhipidita* genera group (Diptera, Ditomidae), some Melliponinae (Hymenoptera, Apidae), and the Neotropical Callitrichidae marmosets (Primates) (Amorim & Pires, 1996).

The distribution of the remaining species of the genus, which also form a monophyletic group, is not totally congruent with the vicariant events in the Neotropical region. *Brachystethus tricolor* and *B. vexillum* have partially overlapping distributions, in Peru, but as we mentioned above they could be conspecific. The sister group of this clade, *B. geniculatus*+, presents incongruent distributional patterns. *B. geniculatus* is distributed in eastern Brazil, Bolivia, Paraguay, Argentina, and Uruguay, and is the most common species of the genus, well represented in collections. The northern limit of this species seems to be Bahia state, in spite of the citation of “Cayenne” as its type-locality. The analysis of biogeographical patterns of southeastern South America suggests that specimens of *B. geniculatus* from Bahia and from southern Brazil may not constitute a historical unity. In fact, despite having the same genital pattern, there are small differences on size and general color; however, these differences do not yet justify the description of a new species. *B. coxalis* is recorded from Panama, southern Venezuela, and Peru, but this species is rarely collected. *Brachystethus vicinus* occupies an area partially overlapping *B. geniculatus*' area, but extends to Amazonia, whereas its sister species, *B. improvisus*, occurs mostly in the northwestern component of the Neotropical region, and was also recorded in the Amazonian basin. As this clade is weakly supported (two homoplasies), further studies are nec-

essary to corroborate this phylogenetic hypothesis. Indeed, the incongruent biogeographical patterns presented by *B. tricolor* + may merely constitute replications of the same pattern shown by the clade comprised of *B. rubromaculatus*, *B. signoreti*, *B. cribrus*, and *Brachystethus* sp. nov. A, which would not be visible due to possible undescribed or even extinct species. In this case, *B. tricolor* +, as presently known, would be an incomplete clade, for which it is impossible to make any biogeographical assumptions.

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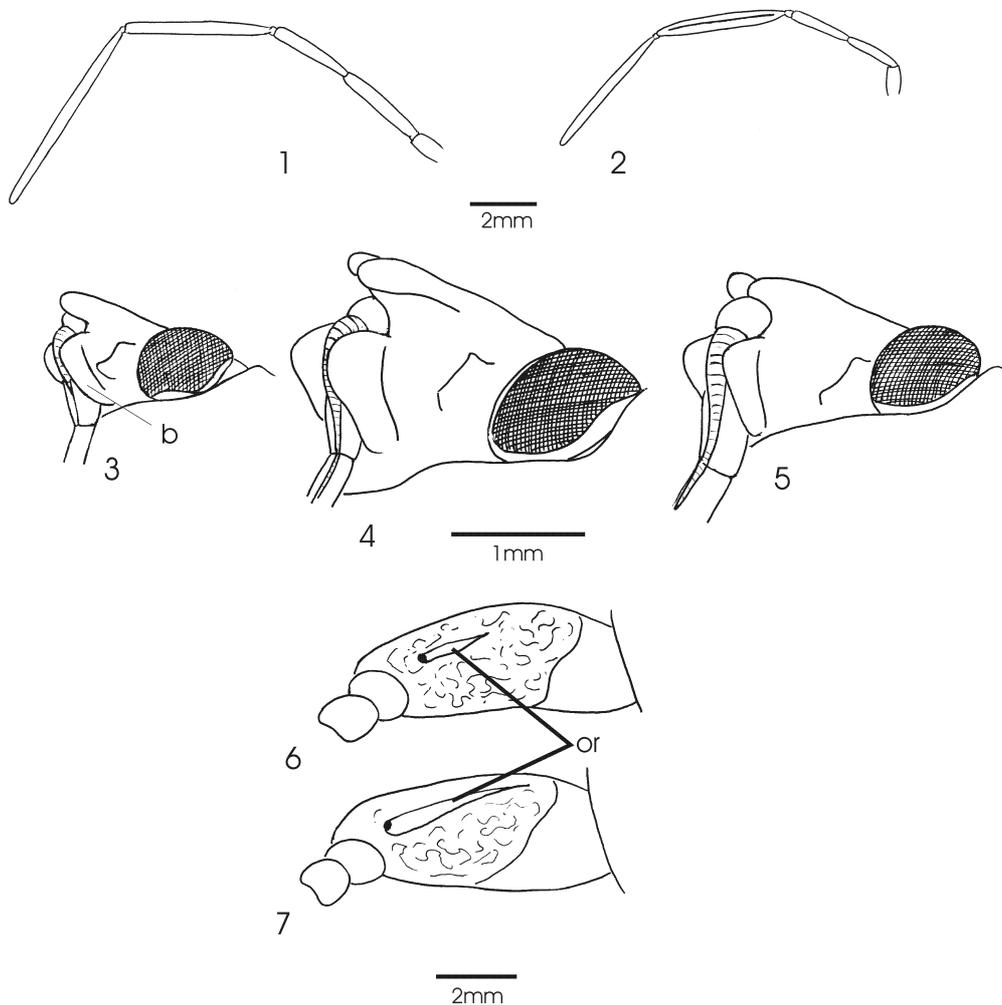
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GENERAL COLOR

1. Color pattern of the abdominal venter: [0] uniform [1] with red spots [2] predominantly red [3] with longitudinal series of yellow spots.

HEAD

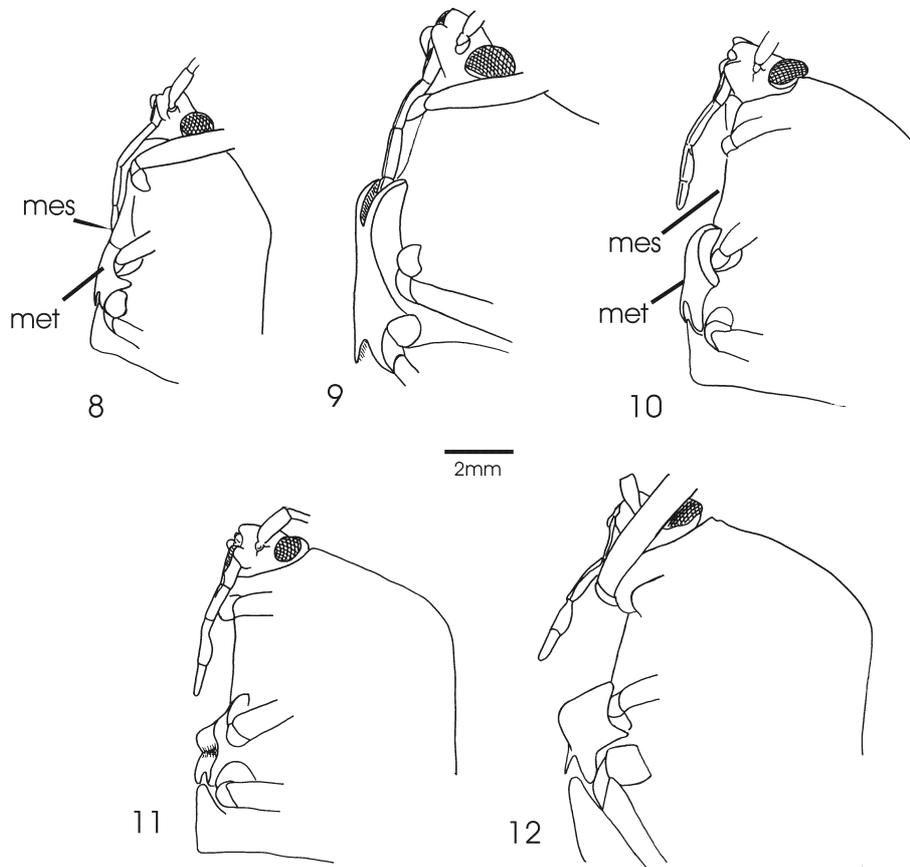
2. Shape of fourth antennal segment: [0] cylindrical (fig. 1) [1] mesially swollen (fig. 2).
3. First rostral segment: [0] not or barely surpassing bucculae (figs. 3, 4) [1] clearly surpassing bucculae, in more than half of segment length (fig. 5).



FIGURES 1-7. 1-2, Antennae of *B. vicinus* and *B. cribrus*. 3-5, Head, lateral view; 3, *Neotibilis fulvicornis*, 4, *Edessa elaphus*, 5, *Brachystethus geniculatus* (b = buccula); 6-7, metapleura, ventral view: 6, *B. tricolor*, 7, *B. cribrus* (or = ostiolar rugae).

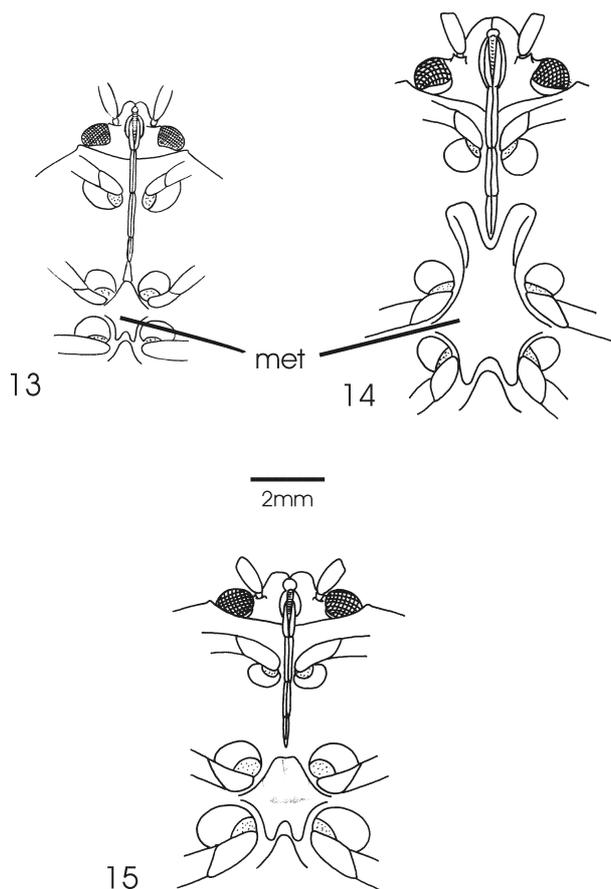
THORAX

4. Subcallous, yellowish border on pronotum: [0] present [1] absent.
5. Yellowish calli on corium: [0] absent [1] present.
6. Color of coxae: [0] castaneous to black [1] yellowish.
7. Color pattern of femora and tibiae: [0] uniform [1] apex of femora and base of tibiae yellowish.
8. Color of tarsi: [0] concolorous with the remaining segments [1] yellowish.
9. Length of ostiolar rugae: [0] long (fig.7) [1] short (fig. 6).
10. Mesosternal carina, in profile: [0] continuous with metasternal carina (fig. 8) [1] lower than metasternal carina (figs. 9-12).



FIGURES 8-12. Head and thorax, lateral view: **8**, *Neotibilis fulvicornis*; **9**, *Edessa elaphus*; **10**, *Brachystethus geniculatus*; **11**, *Brachystethus tricolor*; **12**, *Brachystethus cribrus* (mes = mesosternum, met = metasternum).

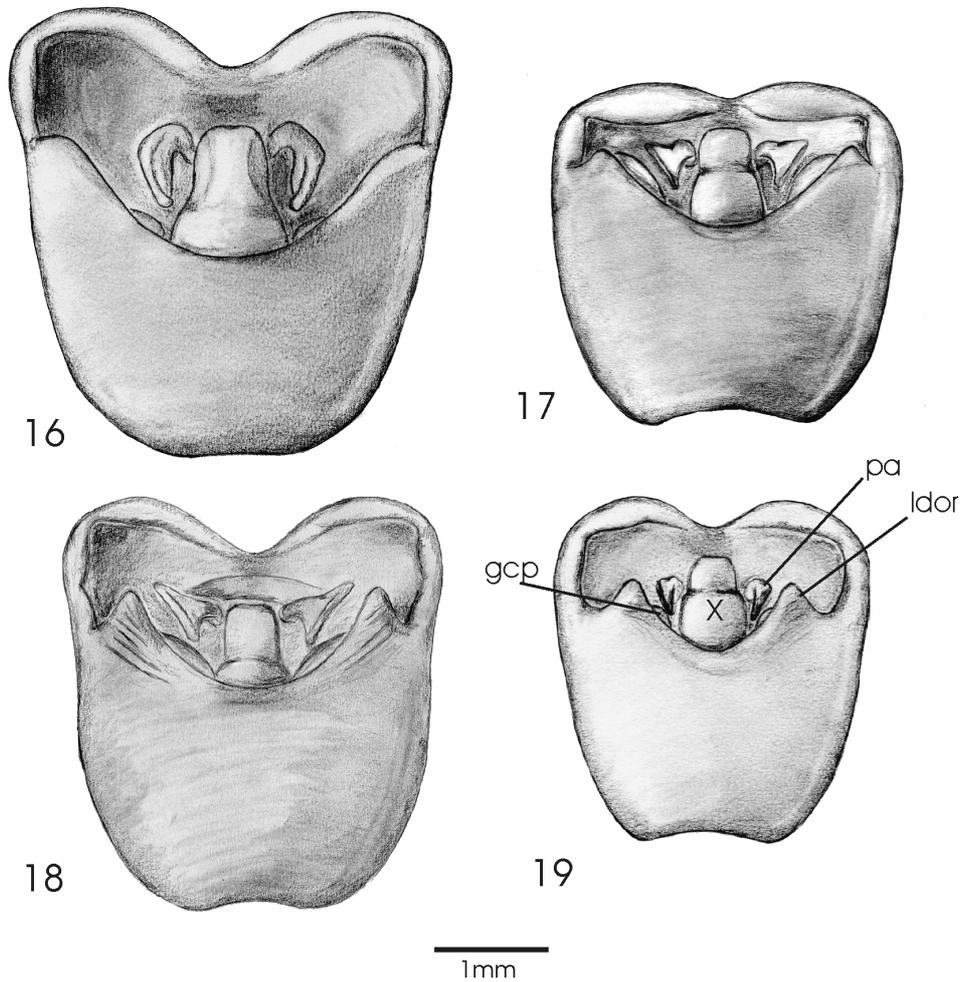
11. Anterior margin of metasternal carina: [0] entire (fig. 13) [1] partially bifurcated (fig. 15) [2] completely bifurcated (fig. 14).
12. Shape of anterior region of metasternal carina, in profile: [0] flat or only slightly elevated (figs. 8-11) [1] strongly elevated (fig. 12).
13. Transversal sulcus on metasternal carina: [0] absent [1] present (fig. 11).



FIGURES 13-15. Head and thorax, ventral view: **13**, *Neotibilis fulvicornis*; **14**, *Edessa elaphus*; **15**, *B. cribrus* (mes = mesosternum, met = metasternum).

MALE GENITALIA

14. Dorsal rim of pygophore: [0] without lobes (fig. 16) [1] with low, wide lobes (fig. 17) [2] with conspicuous lobes (figs. 18,19).
15. Apex of parameres: [0] wide (figs. 17, 18) [1] acute (figs. 16,19).
16. Genital cup processes: [0] absent [1] ovoid to finger-like [2] blade-like (figs. 16-19).
17. Genital cup processes, in dorsal view: [0] not or scarcely visible (figs. 16,19) [1] moderately visible (fig. 18) [2] almost totally visible (fig. 17).

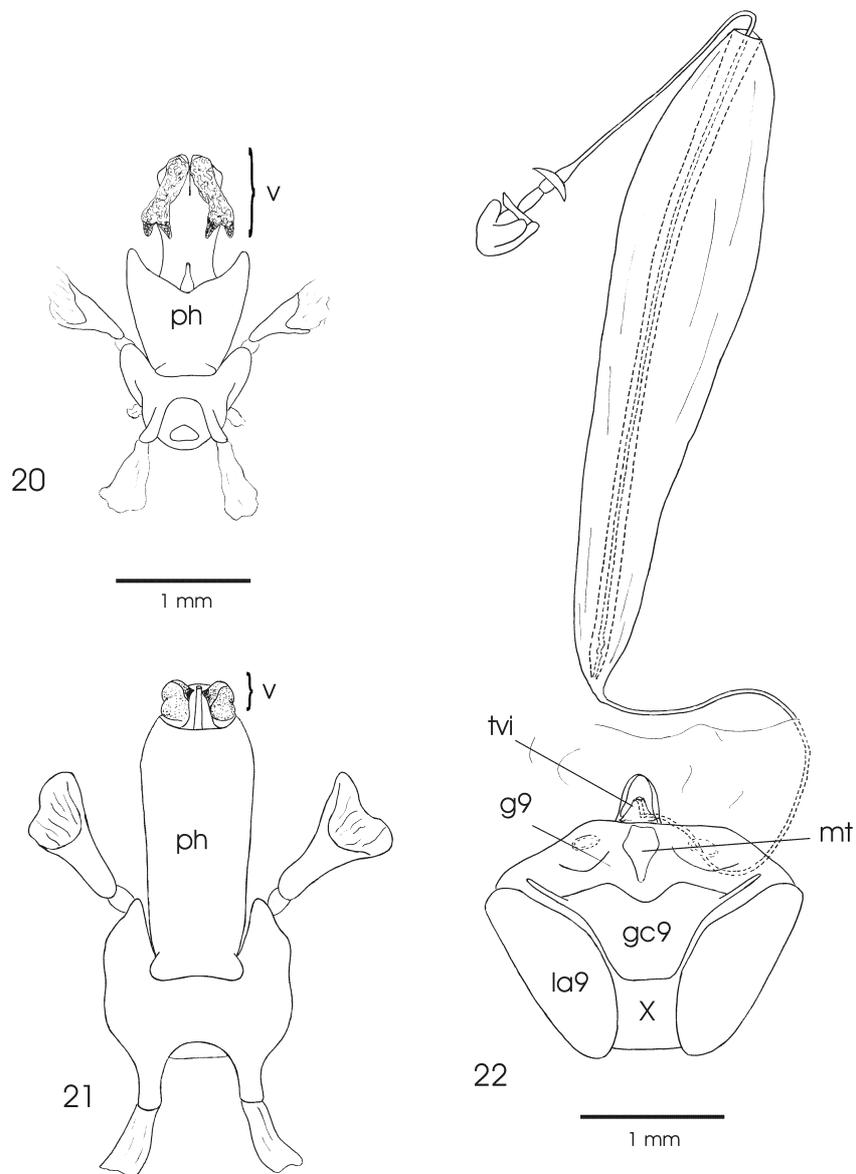


FIGURES 16-19. Pygophore, ventral view: **16**, *Brachystethus vicinus*; **17**, *Brachystethus signoreti*; **18**, *Brachystethus improvisus*; **19**, *Brachystethus geniculatus* (gcp = genital capsule process, ldor = lobe of dorsal rim, pa = paramere, X = tenth segment).

18. Vesica: [0] well developed, about half as long as total length of *phallus* (fig. 20) [1] vesica reduced, $\frac{1}{4}$ or less of total length of *phallus* (fig. 21).

FEMALE GENITALIA (fig. 22)

19. Anterior margin of gonocoxites 9: [0] sinuate, little excavated [1] deeply concave in the middle
- 20 Thickening of vaginal intima: [0] without beak-like projection [1] with a beak-like projection, visible in profile.
21. Medial thickening of gonapophyses 9: [0] absent [1] present.



FIGURES 20-22. *Phallus*, dorsal view: 20, *Neotibilis fulvicornis*, 21, *Brachystethus rubromaculatus* (ph = *phallosome*, v = *vesica*). Fig. 22. Laterotergites, gonocoxites and gonapophyses of ninth segment, and ectodermal genital ducts of *Brachystethus cribrus*, ventral view (g9, gonapophyses 9; gc9, gonocoxites 9; la9, laterotergites 9; mt, medial thickening of gonapophyses 9; tvi, thickening of vaginal intima; X, tenth segment).

APPENDIX 2. Character matrix (0= plesiomorphic, 1,2,3= apomorphic states; ? = not comparable)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>Neotibilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
<i>Pantochlora</i>	0	0	0	1	0	0	0	0	0	1	0	?	0	0	?	1	0	1	0	1	0
<i>Edessa</i>	0	0	0	1	0	?	0	0	0	1	2	0	0	0	0	1	1	1	0	1	0
<i>Peromatus</i>	0	0	1	1	0	?	0	0	1	1	2	0	0	0	0	1	1	1	0	1	0
<i>Olbia</i>	0	0	0	1	0	?	0	0	1	1	2	0	0	0	0	1	1	1	?	1	0
<i>B.rubromaculatus</i>	1	1	1	1	0	0	0	0	0	1	1	1	0	1	0	2	1	1	1	1	1
<i>B.signoreti</i>	1	1	1	1	0	0	1	0	0	1	1	1	0	1	0	2	1	1	1	1	1
<i>B.cribrus</i>	3	1	1	0	1	1	1	0	0	1	1	1	0	0	0	2	2	1	1	1	1
<i>B.sp. nov A</i>	0	?	1	1	1	0	1	0	0	1	1	1	0	1	0	2	1	1	?	?	?
<i>B.tricolor</i>	2	0	1	?	?	0	0	0	1	1	1	0	1	2	1	2	0	1	?	?	?
<i>B.vexillum</i>	2	0	1	1	0	0	0	0	1	1	1	0	1	2	1	2	0	1	1	1	1
<i>B.geniculatus</i>	0	0	1	0	1	0	0	0	0	1	1	0	0	2	1	2	0	1	1	1	1
<i>B.coxalis</i>	0	0	1	0	1	1	1	1	0	1	1	0	0	2	1	2	0	1	?	?	?
<i>B.improvisus</i>	0	0	1	0	1	1	1	1	0	1	1	1	0	2	0	2	1	1	0	1	1
<i>B.vicinus</i>	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	2	0	1	0	1	1