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CLADISTIC ANALYSIS AND SYSTEMATICS OF THE TETRALOBINI *SENSU* STIBICK, 1979 (COLEOPTERA, ELATERIDAE, PYROPHORINAE)

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ABSTRACT

The cladistic analysis of the Tetralobini, based on the study of 47 morphological characters, resulted in the recognition of the following genera: Piezophyllus *Hope, 1842;* Paratetralobus *Laurent, 1964* (stat.n); Neotetralobus *Girard, 1987;* Pseudotetralobus *Schwarz, 1902;* Pseudalaus *Laurent, 1967;* Tetralobus *Le Peletier & A. Serville, 1825 and* Sinelater *Laurent, 1967* (stat.n). *The subtribes Piezophyllina and Tetralobina are separated by several synapomorphies. The two subgenera of* Piezophyllus *erected by Laurent, 1967 cannot be maintained and are synonimyzed.* Tetralobus, *sensu Laurent 1967, is a paraphyletic taxon and its three subgenera are elevated to the generic status; the type-material of the subgenus* Dodecamerus *Laurent, 1968 was not seen and it is not included in this analysis. The taxa are redefined and redescribed. A key to subtribes and genera is provided.*

Keywords: Cladistic Analysis; Elaterid; Systematics; Tetralobini.

INTRODUCTION

The Tetralobini is a very homogeneous group. It includes species with the integument varying from dark-brown to black and usually covered by a golden yellow, yellowish, gray or brownish gray pubescence. This tribe includes some of the biggest elaterid species.The biological data are still scanty, and were summarized by Costa *et al* (1992). The known larvae live associated with termite nests and before pupation they construct a pupal cocoon with their own secretion. According to Dr. C. Girard (Entomologie, MNHN) "les larves des *Tetralobus* ne se trouvent jamais dans "l'habitacle" des termitières de *Macrotermes*, mais toujours dans la carapace couvrant et protégeant le nid, et elles y sont très souvent nombreuses" (pers. comm.).

Up to now, this tribe included five genera and approximately 68 species: *Neotetralobus* Girard, 1987, monotypic; *Piezophyllus* (*Piezophyllus*) Hope, 1842, with two species; *Piezophyllus* (*Hopelater*) (Laurent, 1966), with three species; *Pseudalaus* Laurent, 1967, with two species; *Pseudotetralobus* Schwarz, 1902, with 15 species; *Tetralobus* (*Tetralobus*) Le Peletier & A. Serville, 1825, with 45 species; *Tetralobus* (*Paratetralobus*) Laurent, 1964, monotypic and *Tetralobus* (*Sinelater*) Laurent, 1967, monotypic.

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The cladistic analysis of the Tetralobini resulted in the recognition of seven genera: *Piezophyllus* Hope, 1842; *Paratetralobus* Laurent, 1964 (*stat.n.*); *Neotetralobus* Girard, 1987; *Pseudotetralobus* Schwarz, 1902; *Pseudalaus* Laurent, 1967; *Tetralobus* Le Peletier & A. Serville, 1825 and *Sinelater* Laurent, 1967. The taxa are redefined and redescribed. A cladogram representing the phylogenetic hypothesis of the tribe and a key to subtribes and genera are provided.

HISTORICAL REVIEW

Castelnau (1840) briefly characterized the group "Tetralobites", formed by the genus *Tetralobus* Le Peletier & A. Serville, 1825 and seven genera (*Semiotus*, *Allotrius*, *Eschscholtzia*, *Pomachilius*, *Conoderus*, *Monocrepidius* and *Synaptus*), which were later transferred to different subfamilies of Elateridae. Castelnau (*l.c.*) redescribed *Tetralobus* and included three species (*T. flabellicornis* Linnaeus, 1766, *T. cinereus* Gory, 1832 and *T. gigas* Fabricius, 1801). At a meeting of the Zoological Society of London Hope (1842) read a monograph of the family Phyllophoridae in which he presented the characters of the following genera and species: *Phyllophorus gigas*, *Tetralobus* (nine species), *Piezophyllus* (two species), *Oxynopterus* (five species), *Leptophyllus strachani* and *Pectocera* (two species).

Lacordaire (1857) renamed the group as "Tetralobides", and redescribed *Tetralobus* treating *Piezophyllus* Hope, 1842 (*pars*) as a synonym. He included 19 species in *Tetralobus* (16 African and 3 Australian), and also proposed *Charitophyllus*, *nomen novum* for *Phyllophorus* Hope, 1842 (preoccupied by an Echinodermata).

Candèze (1857, 1865) followed Lacordaire (*l.c.*) and retained the name "Tetralobides". He synonymized *Charitophyllus* with *Tetralobus* pointing out that probably *Tetralobus dufourii* Candèze, 1857, should be regarded as an intermediate between the two genera. He stated that the "Tetralobides" show an affinity with both "Oxynopterides" and the "Élatérides vrais". He redescribed *Tetralobus* and divided the 18 species into two sections according to the shape of the frons. He placed *Piezophyllus* in his "Dicrépidiidites".

Candèze (1878, 1881, 1889) employed "Tetralobites" as the group name and recorded in his catalogue (1891), 32 *Tetralobus* species of which 27 are African and 5 Australian. In 1893, he described three new species of *Tetralobus*.

Schwarz (1906) used the group name Tetralobini, defined it and erected *Pseudotetralobus* for 9 Australian species. He referred 34 species to *Tetralobus*.

Fleutiaux (1919) working only on East African species, raised the status of the group to subfamily and recorded 13 species to *Tetralobus*.

Schenkling (1925) kept the status of subfamily and referred 38 species to *Tetralobus* and the 9 original species to *Pseudotetralobus*.

Laurent (1964a, b, c, d, 1965) defined the subfamily Tetralobinae, presented comments about the geographical distribution of the species and keys to genera, subgenera and species mainly from the African Region. He also described the subgenus *Paratetralobus* to *T. hemirhipoides* Fleutiaux, 1919 from the highlands of Somalia, Ethiopia and Kenya.

Laurent (1967) revised the subfamily presenting keys to Tetralobini and Piezophyllini and to the genera of both tribes. He erected the subgenus *Sinelater* for a species from the Oriental Region and the genus *Pseudalaus* for two Central African Republic species. The Tetralobini were characterized by the lateral margin of pronotum completely carinate and stopping anteriorly near the middle of the eyes, mandibles dentate, male antennae always flabellate and wide parapleura. The Piezophyllini were characterized by the curved lateral carina of pronotum directed towards the inferior margin of the eyes, and weakening on the anterior fourth or fifth, mandibles simple, male antennae dentate and narrow episternum, wider than coxa at its external margin. The Tetralobini includes *Pseudalaus* (two species); *Tetralobus* (*Paratetralobus*) (one species); *Tetralobus* (*Sinelater*) (one species); *Tetralobus* (*Tetralobus*) (44 species) and *Pseudotetralobus* (15 species). Piezophyllini includes *Piezophyllus* (*Hopelater*) (three species) and *Piezophyllus* (*Piezoplyllus*) (two species).

Laurent (1968) added the subgenus *Dodecamerus* to *Tetralobus* for a new species from Angola. The main feature of this subgenus is the 12 segmented antennae. The description of

Tetralobus (*Dodecamerus*) *angolensis* was based on a single specimen.

Girard (1971) presented new data on the geographical distribution of *Piezophyllus spencei* Hope, 1842, *Tetralobus flabellicornis* (Linnaeus, 1767) and *T. gigas* (Fabricius, 1801). He also gave some information about the biology of the latter species, found "dans la partie épigée d'un nid de *Nasutitermes*".

Stibick (1979) treated the Tetralobini as a tribe with two subtribes, Tetralobina and Piezophyllina, within the Pyrophorinae.

Girard (1979) described two new species of *Tetralobus*, *T. rougeoti* and *T. chassaini* both from Ethiopia.

Girard (1987) described an aberrant monotypic genus *Neotetralobus*, from Cameroon, Gabon and Central African Republic.

Costa *et al.* (1992) described the mature larvae of *Pseudotetralobus* cf. *murrayi* (Candèze, 1857) and *Tetralobus cavifrons* Faimaire, 1887 and presented a set of larval features of the Tetralobini, for the first time.

MATERIAL AND METHODS

The material examined belongs to the following Institutions: AMSA - Australian Museum, Sydney (D.J. Bickel); AMNH - American Museum of Natural History, New York (L.H. Herman); BMNH - Natural History Museum, London (C.M.F. von Hayek); BPBM - Bernice P. Bishop Museum, Honolulu (G.A. Samuelson); CLBRR - Centre for Land and Biological Resources Research, Ottawa; (E.C. Becker); CSIRO - Commonwealth Scientific and Industrial Research Organization, Canberra D.C. (J.F. Lawrence and A. Calder); INSB - Institut Royal des Sciences Naturelles de Belgique (L. Baert and P. Grootaert); MAMU - Macleay Museum, The University of Sydney (D.S. Horning Jr.); MHNG - Muséum d'Histoire Naturelle, Génève (C. Besuchet); MNHN - "Muséum National d'Histoire Naturelle", Paris (C. Girard); MRAC - "Musée Royal de l'Afrique Centrale", Tervuren (J. Decelle); USNM - United State National Museum of Natural History, Washington D.C. (T. Erwin)

The type-specimens of *Piezophyllus macrocerus* (BMNH) and *Neotetralobus africanus* (MNHN) were examined. We did not see the type-specimen of *Tetralobus* (*Dodecamerus*) *angolensis* Laurent, 1968 and for that reason it was not included in the present analysis. We have studied male and female of all genera except for *Paratetralobus* of which we have seen only the males. A summary of all species seen is presented in the Table 1.

Cladistic analysis. Hemirhipini and Pyrophorini were used as combined outgroups for polarization of the character states. When necessary, Agrypnini, Conoderini and Dicrepidiinae, were also used as additional outgroups. Multi-state characters were considered ordered and unordered. The characters and transformation series are discussed below. In the matrix data, "?" represents information that is unknown, and "-" character that is inapplicable to the taxon in question.

The original data (matrix, Table 3) were analysed first by hand, and then by the implicit enumeration option of Hennig 86 (Farris, 1988). To the calculation of the consistency and retention indices (CI and RI, respectively) the autapomorphies of all terminal taxa, and the basal synapomorphies of the Tetralobini, were not considered. However, these characters are represented in the matrix to make available to future workers all information assessed (Yeates, 1992).

In the discussion of results, the symbolization of group^{+} is adopted to represent the retarded clades (Amorim, 1982).

CLADISTIC ANALYSIS OF THE TETRALOBINI GENERA

Discussion of characters (Table 2)

1. Nasal carinae

A pair of longitudinal lateral carinae occurring only in *Paratetralobus* and *Neotetralobus* is considered as apomorphic. In the Pyrophorini and Hemirhipini the nasal does not present such carinae.

2. Male antennae

In the Tetralobini, as in the Hemirhipini, the male antennae can be serrate or flabellate. In all Pyrophorini the male antennae are serrate and this condition is considered here as plesiomorphic. The flabellate antennae repre-

sent the apomorphic condition and appeared independently in some males of Tetralobini and Hemirhipini.

3. Mandibles

The falciform mandibles of *Paratetralobus* and *Neotetralobus* are interpreted here as synapomorphies of these two taxa.

4. Penicillus

The penicillus formed by short setae, occurring only in *Paratetralobus* and *Neotetralobus* was understood as an apomorphic condition.

5. Dorso-lateral pit of mandibles

The dorso-lateral region of the mandibles of the Tetralobini is setous and presents an anterior tuft of longer setae locate in a pit. In the genus *Tetralobus* this pit is very shallow and in *Pseudalaus* it is fused with a basal depression. This condition found only in the Tetralobini was considered as an apomorphy.

6. Ventral basal carina of mandibles

A ventral basal carina of the mandibles found only in *Sinelater* is understood as an apomorphy.

7. Labrum shape

In the Pyrophorini and Hemirhipini the labrum is wide, usually oval. The narrow labrum of *Pseudalaus* is considered an apomorphic condition.

8. Nasal shape (width)

A very narrow nasal of *Paratetralobus* is considered as an apomorphic condition.

9. Male antennae

In the Pyrophorini and in most of Elateridae the male antennae are 11-segmented and this condition is considered plesiomorphic. In the Hemirhipini, males with antennae 12-segmented also occur in some genera evidencing homoplasy. In the Tetralobini, the apomorphic condition is present in the genus *Pseudotetralobus*, and by the literature, according to Laurent, 1968, also in *Tetralobus* (*Dodecamerus*) *angolensis*, a species not seen by us and not considered in this study.

10. Frons

The condition of the frons with anterior margin turned upwards of *Tetralobus* is understood as an apomorphy.

11. Arrangement of mesothoracic sternites

In the Pyrophorini and Hemirhipini the mesepisternum forms part of margin of mesocoxal cavity. The mesepisternum is not part of this cavity only in *Piezophyllus benitensis*, and this condition is interpreted as an apomorphy of that species. Some Agrypnini genera also present that condition indicating independent origins.

12. Anterior margin of metasternum

The elevated, V-shaped anterior margin of metasternum of *Piezophyllus* is considered as an apomorphy.

13. Longitudinal median suture of metasternum

In the Pyrophorini the longitudinal median suture of metasternum is a simple or shallow line; in some genera of the Hemirhipini it may also be furrowed near the base or making an elliptical anterior cavity. In some species of *Pseudotetralobus* this suture is furrowed throughout its length. In *Piezophyllus* the longitudinal median suture is strongly furrowed in the posterior two thirds and this condition is treated here as an apomorphy.

14. Metacoxal plate

The tooth on internal third of metacoxal plate of *Tetralobus* and *Sinelater* is understood as an apomorphy of that group. In the majority of Pyrophorini and Hemirhipini the metacoxal plate is narrowed laterally, and without a tooth (plesiomorphic condition).

15. Metacoxal plate

In the Pyrophorini and Hemirhipini the metacoxal plate does not meet the elytral epipleura (plesiomorphic condition). In the Tetralobini the metacoxal plate meets the epipleura (apomorphic condition).

16. Metacoxal plate

The outer margin of the metacoxal plate with an elevated fold of *Pseudotetralobus* is regarded as apomorphic condition.

17. Metepisternum

In the Pyrophorini and Hemirhipini examined the outer margin of the metepisternum forms an angle near the apex (plesiomorphic condition). The character state in which outer margin tapers towards apex is considered an apomorphy of *Pseudotetralobus*.

18. Metepisternum

In the Pyrophorini, Hemirhipini and Piezophyllina the metepisternum is narrow (plesiomorphic condition). In the Tetralobini the metepisternum is much wider (apomorphic condition).

19. Prosternal spine

The prosternal spine of *Tetralobus* with an indentation near apex is interpreted as an apomorphy of that genus.

20 and 21. Lateral carina of prothorax

In the Pyrophorini, Hemirhipini and some Tetralobini there is a complete lateral prothoracic carina (plesiomorphic condition). The carina incomplete anteriorly (Piezophyllina) or incomplete posteriorly (*Neotetralobus*) are understood, respectively to each group, as apomorphic conditions, representing the states of a non linear transformation series.

22 and 23. Hind angles of pronotum

The reduced hind angles of pronotum of *Neotetralobus* is interpreted as an apomorphy of that genus. The exclusive swollen posterior angles of *Tetralobus* and *Sinelater* are considered an apomorphic condition of these genera.

24. Convexity of pronotum

The gibbous pronotum of *Neotetralobus* is considered an apomorphic condition of that genus.

25. Mesosternal cavity

The vertical mesosternal cavity of *Pseudalaus* is understood as an apomorphic condition. In the Pyrophorini and Hemirhipini examined the mesosternal cavity varies from declivous to almost horizontal (plesiomorphic condition).

26. Basal median tubercle of pronotum

In the Pyrophorini and Hemirhipini a median basal tubercle may or not be present on pronotum; the convexity of this tubercle varies a lot among the species. The tubercle turned upwards of Piezophyllina is interpreted as an apomorphy.

27. Distal area of hind wing

In *Tetralobus* and *Sinelater* the V-shaped sclerite of the distal area of hind wing reaches the lateral margin and it is understood as an apomorphic condition.

28. Punctures of elytral striae

In the Pyrophorini, Hemirhipini and Piezophyllina examined, the elytra are punctate-striate (plesiomorphic condition). In the Tetralobina the elytra may be weakly punctate-striate or the punctures are absent in some striae (apomorphic condition).

29. Elytral epipleura

In the Pyrophorini, Hemirhipini and in the most Elateridae, the epipleura forms a small carina running up to the elytral apices (plesiomorphic condition). In the Tetralobini this carina stops at different points and the epipleura is said to be open distally (apomorphic condition). In the genus *Sinelater* the epipleura is widely open distally and is understood as an apomorphy, the extreme of the transformation series.

30. Elytral humerus

In the Pyrophorini and Hemirhipini the internal region of humerus has a transverse sulcus (plesiomorphic condition). In the Tetralobini this sulcus is absent (apomorphic condition).

31. Apices of elytra

In the Pyrophorini and Hemirhipini the apices of elytra are not dehiscent (plesiomorphic condition). In the Piezophyllina the apices of elytra are dehiscent (apomorphic condition).

32. Basal tubercle of elytra

Pyrophorini and Piezophyllina have a weak basal tubercle on each elytron (plesiomorphic condition). The presence of a strong tubercle in the majority of the Tetralobini is understood to be apomorphic condition. The absence of this tubercle in *Sinelater* is interpreted as an apomorphy of this genus.

33. Tibial spurs

In the Pyrophorini, Hemirhipina and Tetralobina tibial spurs are present (plesiomorphic condition). The absence of this character in the Piezophyllina is understood as the apomorphic condition. Tibial spurs are also absent in the Chalcolepidiina and some Agrypnini genera indicating independent origins.

34. Tarsi

In the Pyrophorini, Hemirhipini and the most of Elateridae the tarsi are simple, without lobes beneath (plesiomorphic condition). The 1-4 lobed tarsi of the Tetralobini is understood as an apomorphic condition. In some other elaterid genera, mainly the Agrypnini, Conoderini and Dicrepidiinae, lobed tarsi appear in many different combinations suggesting independent origins.

35. Basal setae on tarsal claws

The 3-4 basal setae present in the genera *Tetralobus* and *Sinelater* are considered a synapomorphy of these two taxa.

36. Median lobe of aedeagus

The median lobe partially membranous like a sheath of the Tetralobini is understood as an apomorphic condition.

37. Apex of parameres

The unciform, lobed apex of the parameres found in the Pyrophorini, Hemirhipini and Piezophyllina is interpreted as the plesiomorphic condition. The elongate and straight apex found in the Tetralobina, is the apomorphic condition.

38 and 39. Distal part of parameres

The slightly narrow parameres with a ventral tooth occuring only in *Sinelater* and the abruptly narrow parameres with lateral tooth of *Pseudalaus* are understood as synapomorphics of these two taxa.

40. X Urotergite of male

In the Pyrophorini, Hemirhipini and the most of the Elateridae, the X urotergite of male is distinct and not fused to IX. The X urotergite of male, reduced and fused to IX urotergite of Tetralobini is understood as an apomorphy.

41. VIII urosternite of male

The transverse and reduced VIII urosternite of male of Tetralobini is understood as apomorphic condition.

42. IX urotergite of male

The elongate IX urotergite of male of Tetralobina is interpreted as an apomorphy.

43. Basal median longitudinal line of IX urotergite of male

The presence of a basal median longitudinal line of the IX urotergite of male of *Pseudalaus* and *Pseudotetralobus* is understood as synapomorphic condition, occurring a reversal in *Sinelater*.

44-46. Omega-like sclerite of bursa copulatrix

The presence of an omega-like sclerite of bursa copulatrix in Tetralobina is understood as apomorphic condition. The presence of omega-like central arm with two basal teeth and apex bifid is considered synapomorphic condition to *Tetralobus*, *Sinelater* and *Pseudalaus*.

47. Ovipositor: baculum

The long baculum found in Tetralobina was understood as an apomorphic condition.

RESULTS OF CLADISTIC ANALYSIS

The analysis of the 24 synapomorphies using implicit enumeration generates only one tree, 24 steps long, CI and RI of 0.96. The same topological tree, CI and RI were achieved when considering the multi-states characters ordered or unordered. In the cladogram (Fig. 1), "-" represents reversal, and the number between brackets "( )" the character states of a transformation series.

The Tetralobini are well supported by 8 synapomorphies: mandibles with dorso-lateral pits [5], metacoxal plate meeting epipleura [15], base of elytral humeri without a sulcus [30], tarsi lobed beneath [34], median lobe of aedeagus partially membranous like a sheath [36], X urotergite male reduced and fused to IX tergite [40], and VIII urotergite male transverse and reduced [41]. Another synapomorphy of the group is the elytral epipleura open distally [29(1)], narrowly in all

genera but *Sinelater*, in which it is widely open [29(2)], a character state which represents the full condition of a transformation series.

Piezophyllus is the sister group of the remaining genera. Both groups are based on many synapomorphies. Thus the already suggested division of the Tetralobini into two sub-tribes, Tetralobina and Piezophyllina, is well supported by the present analysis.

The monophyly of *Piezophyllus* is well defined by the synapomorphies of anterior margin of metasternum elevate, V-shaped near mesocoxal cavities [12], longitudinal suture of metasternum strongly furrowed on posterior two-thirds [13], lateral carina of prothorax incomplete anteriorly [20], basal median tubercle of pronotum turned upwards [26], apices of elytra dehiscent [31], and tibial spurs absent [33]. The heterobatmy for the two sub-genera of *Piezophyllus* has not been demonstrated. The sub-genus *Hopelater* can be weakly based on the autapomorphy of mesepisternum not forming part of mesocoxal cavity [11]; however, the sub-genus *Piezophyllus* cannot be defined by any apomorphy, and thus both sub-genera are considered synonymous.

The Tetralobina are defined by the synapomorphies of male antennae flabelatte [2], metepisternum wide [18], punctures of elytral striae weakly punctate-striate or punctures absent in some striae [28], basal tubercles of elytra strong [32(1)], but absent in *Sinelater* [32(2)], apex of parameres elongate, straight [37], IX urotergite male elongate [42], omega-like sclerite of bursa copulatrix present [44], to be confirmed in *Paratetralobus*, and baculum of ovipositor long [47], to be confirmed in *Neotetralobus*.

The monophyly of the group *Paratetralobus* is based on the synapomorphies of nasal carina present [1], mandibles falciform [3] and penicillus of mandibles long [4]. *Paratetralobus* is distinguished only by the autapomorphy of the nasal narrower than the scape width [8]. The monophyly of *Neotetralobus* is well supported by the autapomorphies of lateral carina of prothorax incomplete posteriorly [21], posterior angle of pronotum reduced [22], and pronotum gibbous [24].

The group *Pseudotetralobus* is only supported by the synapomorphy of the basal median longitudinal line on the IX urotergite male [43]. This character is subject to a reversal in *Tetralobus* [43]. *Pseudotetralobus* is well defined by the autapomorphies of male antennae 12-segmented [9], outer margin of metacoxal plate with an elevate fold [16], and outer margin of metepisternum tapering towards apex [17]. The group *Pseudalaus* is supported by the synapomorphies of omega-like sclerite of bursa copulatrix with two basal teeth [45], and the same sclerite with central arm bifid at apex [46]. *Pseudalaus* is well distinguished by the autapomorphies of labrum narrow [7], mesosternal cavity vertical [25], and distal part of parameres abruptly narrow, with lateral tooth [39]. The group *Tetralobus* is well characterized by the synapomorphies of metacoxal plate with one tooth on internal third [14], posterior angle of pronotum swollen [23], sclerite of distal area of hind wing reaching lateral margin [27], and 3 or 4 basal setae on tarsal claws [35]. The monophyly of *Tetralobus* is well supported by the synapomorphies of anterior margin of frons turned upwards [10], and outer margin of prosternal spine bearing an indentation near apex [19]; the absence of the basal median longitudinal line on IX urotergite male is considered a reversal [43]. *Sinelater* is well characterized by the autapomorphies of ventro-basal carina of mandibles [6], elytral epipleura widely open distally [29(2)], absence of basal tubercle of elytra [32(2)], and distal part of parameres slightly narrow, with ventral tooth [38].

The three sub-genera of *Tetralobus* (*Tetralobus*, *Paratetralobus* and *Sinelater*) are well characterized by synapomorphies, but they are not monophyletic and they are elevated to the generic status.

GEOGRAPHICAL DISTRIBUTION

The Tribe Tetralobini seems to be a very old group originated before the break up of Gondwana. Its distribution is typically Pan-Tropical, although nowadays there are no representatives in the Neotropical Region, probably due to past extinctions (Fig. 2).

Piezophyllus presents two species in the tropical plateau zone and tropical lowlands of Senegal, Guinea, Ivory Coast, Ghana, Cameroon, Congo, Central African Republic and Sudan; two species in Madagascar and one species in Borneo

and Sumatra (Malay Region). *Paratetralobus* occurs in the highlands of Ethiopia, Somalia and Kenya. *Neotetralobus* is found in the forest of the tropical plateau zone of Central African Republic, Cameroon, and Gabon. *Pseudotetralobus* occurs in the zone of the temperate forest and in the tropical semi-arid zone of Australia; one species is found in the Territory of Papua and New Guinea; we have seen also one female labelled "China" from the Australian Museum. *Pseudalaus* is found in the tropical plateau zone and tropical lowlands zone of Ghana, Central African Republic and tropical semi-arid zones of Kenya. *Tetralobus* is widespread all over the African territory except for the desertic areas. According to Girard (1979) the species of *Tetralobus* "peuplent des milieux variés et se rencontrent aussi bien dans les zones de Savanes que dans les grandes régions forestières"; one species is cited from Singapore (Malay Region) and four species from Madagascar. *Sinelater* is found in China and North and South Vietnam.

The two sub-tribes show basically the same distributional patterns. It seems that Piezophyllina (Fig. 3) is restricted to the forested regions and that Tetralobina (Fig. 4) is more widespread and could be found in forested and savanah regions (at least in Africa). The occurrence of Tetralobina in China, Malay Region, Australia and Papua-New Guinea could be explained by dispersion from elements of the Australian and Malaysian regions to China or vice-versa.

Species of the two sub-tribes should be found both in the highlands (800-4000m) as in the lowlands. According to the available data some species in Africa and Australia are adaptated to live in association with termites nests of *Nasutitermes* sp., *Macrotermes* sp. (both Termitidae) and *Coptotermes lacteus* (Rhinotermitidae). It is worthwhile mentioning that these termites have a Gondwanic distribution.

SYSTEMATICS

Tetralobini Castelnau, 1840

Tetralobites Castelnau, 1840:230 (*pars*); Candèze, 1878:10; 1881:25; 1889:16; 1891:47; 1892:17; 1896:20.
Phyllophoridae Hope, 1842:73 (*pars*); Tetralobides; Lacordaire, 1857:137, 163; Candèze, 1857: 16,366; 1865:20.
Tetralobini; Schwarz, 1906:57; Stibick, 1979:160; Costa *et al.*, 1992:879.
Tetralobitae; Fleutiaux, 1940:106.
Tetralobinae; Fleutiaux, 1919:5, 32; Schenkling, 1925:70; Fleutiaux, 1947:238, 294; Laurent, 1964a: 214; 1964b: 354;1964c:495; 1964d:857; 1965:37; 1967:83; 1968:328.

Diagnosis. The tribe Tetralobini is characterized by the following synapomorphies: mandibles with a tuft of setae located in a dorso-lateral pit; metacoxal plate meeting the epipleura; base of epipleura without a sulcus to receive the hind angles of prothorax; tarsi 1-4 lobed beneath; median lobe of aedeagus partially membranous like a sheath; tenth urotergite of male reduced and fused to ninth urotergite; eigth urosternite of male transverse and reduced.

Comments. Lacordaire (1857) was the first to restrict the concept of this group; his diagnostic characters had been repeated by subsequent authors, from these only the tarsi 1-4 lobed beneath proved to be an actual synapomorphy. The others are of difficult polarization or occur also in other elaterid taxa. However one of his characters was misinterpreted and should be commented. He pointed out that the mandibles are "dentées avant leur extremité", and this condition was stressed by several authors since Candèze (1857) to Laurent (1967). However, we have not found toothed mandibles in the dissected specimens of all the genera studied.

Piezophyllina Laurent, 1967

Piezophyllini; Laurent, 1967:85,96.
Piezophyllina; Stibick, 1979:160.

Diagnosis. The sub-tribe Tetralobina is characterized by the following synapomorphies: anterior margin of metasternum elevate and V-shaped near mesocoxal cavities; longitudinal median suture of metasternum strongly furrowed; lateral carina of prothorax incomplete anteriorly; basal median tubercle of pronotum turned upwards; apices of elytra dehiscent; tibial spurs absent.

Comments. Most of the characters in Laurent's (1967:85) key are simplesiomorphies, except for the lateral carina of prothorax incomplete anteriorly.

Tetralobina Castelnau, 1840

Tetralobina; Stibick, 1979:160.
Tetralobina; Laurent, 1967:85.

Diagnosis. The sub-tribe Tetralobina is characterized by the following synapomorphies: male antennae flabellate; metepisternum wide; elytral striae weakly punctate-striate or punctures absent in some striae; apex of parameres of aedeagus elongate and straight; ninth urotergite of male elongate; baculum of the female ovipositor long.

Another probable synapomorphy to this group is the presence of an omega-like sclerite of bursa copulatrix in all genera studied but that needs to be confirmed to *Paratetralobus*.

Comments. Laurent (1967) gave as characteristic of this group: lateral carina of pronotum complete; mandibles dentate; male antennae flabellate and metepisternum, "parapleures", wide. However, as discussed above, the mandibles are not toothed. Moreover, should be noted that the lateral carina of pronotum is complete anteriorly.

KEY TO SUB-TRIBES AND GENERA OF TETRALOBINI

1. Male antennae serrate; lateral carina of prothorax incomplete anteriorly; basal median tubercle of pronotum turned upwards; tibial spurs absent ....(Piezophyllina, Africa, Madagascar, Borneo and Sumatra)..... ..... *Piezophyllus* Hope.

Male antennae flabellate; lateral carina of prothorax complete anteriorly;basal median tubercle of pronotum not turned upwards; tibial spurs present .... (Tetralobina, Africa, Madagascar, Australia, Singapore, New Guinea and Vietnam) 2

2(1). Longitudinal nasal carina present; mandibles slender, falciform 3

Longitudinal nasal carina absent; mandibles stout, triangular 4

3(2). Nasal narrower than the scape width; lateral carina of prothorax complete; posterior angles of pronotum projected and flat ..... (Africa) ..... *Paratetralobus* Laurent

Nasal wider than the scape width; lateral carina of prothorax incomplete posteriorly; posterior angles of pronotum reduced and swollen ..... (Africa) ..... *Neotetralobus* Girard

4(2). Male antennae 12-segmented; outer margin of metacoxal plate with an elevate fold; outer margin of metepisternum tapering towards apex ..... (Australia and New Guinea) .... *Pseudotetralobus* Schwarz

Male antennae ll-segmented; outer margin of metacoxal plate without an elevate fold; outer margin of metepisternum forming an angle near apex 5

5(4). Labrum narrow; mesosternal pit vertical; metacoxal plate not toothed; posterior angles of pronotum flat..... (Africa) ..... *Pseudalaus* Laurent

Labrum wide; mesosternal pit declive; metacoxal plate with one tooth on internal third; posterior angles of pronotum swollen 6

6(5). Anterior margin of frons turned upwards; outer margin of prosternal spine with an indentation near apex; epipleura narrowly open distally .... (Africa, Madagascar, Singapore) .....*Tetralobus* Le Peletier

Anterior margin of frons not turned upwards; outer margin of prosternal spine without

an indentation near apex; epipleura widely open distally..... (China, Vietnam) ..... *Sinelater* Laurent

Piezophyllus

Piezophyllus Hope, 1842:76.
Piezophyllus (*Hopelater*); Laurent, 1967:99, *syn.n.*

Type species of *Piezophyllus* : *Tetralobus robustus* Hope, 1842:76, original designation, synonymy of *Piezophyllus macrocerus* Castelnau, 1836:12; of *Hopelater* :*Piezophyllus spencei* Hope, 1842, Laurent designation, 1967:99.

Piezophyllus benitensis Fleutiaux, 1902
(Figs. 6, 22-36)

Piezophyllus benitensis Fleutiaux, 1902:225; Basilewsky, 1958:358.
Piezophyllus (*Hopelater*) *benitensis*; Laurent, 1967:102.

Length: 29-30mm (Fig. 6).

Integument from dark-brown to black with legs and antennae reddish-brown. Pubescence thin, short and golden yellow, longer on metasternum.

Frons not carinate, concave on anterior median region, forming a pit near anterior margin; a longitudinal impunctate ridge from the pit to base; anterior margin rounded, forming a small edge; punctation moderately coarse, dense and heterogeneous. Nasal plate (Fig. 25) subquadrangular, densely punctate; lateral punctation smaller. Left antenna of male surpassing the hind angle of pronotum in approximately two segments; right antenna shorter; 11-segmented and serrate; 2nd and 3rd segments transverse; 3rd segment with a small spiniform appendix. Mandibles (Figs. 22-24) stout, 1.3-1.4 times longer than wide, with a dorsolateral elevation forming a carina; setous laterally, forming a tuft inside a small anterior depression; penicillus fringe-like.

Pronotum 1.1 times longer than wide, strongly convex; anterior margin slightly prominent at middle; lateral margins marginate, not visible from above; lateral carina incomplete anteriorly; hind angles divergent with a carina near the lateral margins and a shorter one innerly; median basal tubercle elongate, flattened, with apex directed upwards; punctation coarse and dense giving a rugous appearance. Prosternum (Fig. 29) wide distad, with punctation very coarse, smaller between the procoxae; procoxal cavities marginate, with a smaller tubercle; prosternal spine almost straight with rounded apex; prosternal lobe emarginate laterally forming a tooth-like projection; anterior margin almost straight; punctation smaller than prosternum. Prosternal sutures (Fig. 29) accompained by a high and impunctate band reaching the anterior margin of hypomera. Hypomeron (Fig. 29) with a furrowed line near the prosternal sutures; punctation coarse and dense, smaller near the base; basal region smooth. Mesepisternum not forming part of margin of mesocoxal cavity (Fig. 29); elevate latero-anteriorly. Metepisternum narrow. Metasternum elevate between the mesocoxae; mesocoxae marginate (Fig. 29) by an elevate area Y-shaped joined at middle, accompained by a depression; punctation coarse and dense on lateroanterior half and smaller on the other parts; metasternal median suture strongly furrowed on posterior two thirds. Metacoxal plate (Fig. 29) slightly narrowed near the middle and slightly widened laterally. Scutellum elongate, triangular, declivous and furrowed longitudinal medially; posterior margin rounded. Hind wing (Fig. 26) with open anal cell; distal area with an upsilon-shaped sclerotization. Elytra wider than pronotum, convex, slightly tapered apicad on distal third; individually tapered to apex with a very small prominence tooth-like; apices dehiscent; punctate-striate; striae marked by a punctuated line, interstices flattened and micropunctate; a weak basal tubercle present. Epipleura open distally. Tibial spurs absent (Figs. 27-28); tarsal lamellae decreasing in length from segments I to IV; claws with one long basal seta.

Male genitalia. Urotergite VIII (Fig. 30) elongate, with basal region membranous; densely covered by short setae. Urosternite VIII (Fig. 33) transverse and partially membranous; distal margin bilobate; setae concentrate near inner margin of each lobe. Urotergite IX (Fig. 31) partially membranous, setous on distal half, except median region; urotergite X reduced and fused to urosternite IX, but lateral sutures present at distal area. Urosternite IX (Fig. 32) elongate with apex emar-

ginate; setae moderately long disposed on distal half. Aedeagus (Figs. 34-36): basal piece 0.6 times as long as parameres with two distal spiniform prominences. Parameres separate with rounded apex; subapical region membranous with sensorial points and a lateral dentiform prominence. Median lobe partially membranous, like a sheath, slightly tapered to apex; apex rounded.

Material examined. Cameroon, 30 km E Nanga-Eboko (at black light), 16-19.II.1972, J.A. Gruwell col., 1♂ (USNM). Ghana. Tafo, IV.1968, E.O. Boafo col, 1♂ (MZSP). Sudan. Sourses Yubo. Equatoria inside rest-house, 08.V.1948, 1♂ (USNM).

Piezophyllus borneensis Fleutiaux, 1902
(Figs. 37-42)

Piezophyllus borneensis Fleutiaux, 1902:226.
Piezophyllus (*Hopelater*) *borneensis*; Laurent, 1967:102.

Male genitalia. Urotergite VIII (Fig. 37) sub-rectangular with distal margin slightly bilobate. Urosternite VIII (Fig. 40) transverse, partially membranous, bilobate distally with moderately long setae in each lobe; sclerotized area larger than in *P. benitensis*. Urotergite IX (Fig. 38) slightly rounded distally with setae near the lateroanterior margin; lateral sutures of X urotergite present only in a very small distal area. Urosternite IX (Fig. 39) partially membranous, bilobate distally with setae on distal third. Aedeagus (Figs. 41-43): parameres almost the same length dorsal- and ventrally; laterodistal prominence rounded.

Material examined: Indonesia. North Sumatra. Subulussalam, R. de 14-15.VI.1990, 1♂, Keyser & G. Clark cols. (MAMU).

Comments: This species shares with *P. benitensis* Fleutiaux, 1902 the apomorphic condition of the mesepisternum not forming part of margin of mesocoxal cavity.

Piezophyllus macrocerus (Castelnau, 1836)
(Figs. 5, 7-21)

Tetralobus macrocerus Castelnau, 1836:12.
Tetralobus robustus Hope, 1842:75.
Piezophyllus macrocerus; Candèze, 1859:12.
Piezophyllus (*Piezophyllus*) *macrocerus*; Laurent, 1967:98.

Length: 38-46 mm. (Fig. 5).

Integument from dark-brown to black. Pubescence golden yellow and dense, covering the integument color, longer on metasternum of male.

Frons not carinate, with a V-shaped impression, not reaching the anterior margin; anterior margin rounded forming a small edge; punctation dense, small and heterogeneous; fore angles smooth. Nasal plate (Fig. 8) densely punctate with a median prominence near the base. Antennae longer than hind angles of pronotum, 11-segmented and serrate in both sexes, shorter in females; 1st segment black, the others brownish; 2nd and 3rd segments transverse and subequal. Mandible (Figs. 9-11) stout, 1.4-1.5 times longer than wide, elevate laterodorsally forming a carina-like; setous laterally, forming a tuft inside an anterior pit; penicillus fringe-like.

Pronotum 0.9 times as long as wide, subtrapezoidal, strongly convex (Fig. 12); convexity decreasing basad; anterior margin almost straight; lateral margins marginate on basal two-thirds; lateral carina not visible from above, absent on anterior fourth; hind angles wide, divergent, with a long carina near lateral margin and a shorter one innerly; median basal tubercle well developed, elongate, flattened with rounded apex turned upwards; two rounded cavities near the middle and a longitudinal median furrow not reaching the margins; punctation dense, small, coalescent on disc, coarser on fore angles and discal region. Prosternum (Fig. 12) elongate, coarsely rugous; procoxal cavities strongly marginate, each one with two rounded tubercles; prosternal spine almost straight, slightly tapered apicad; prosternal lobe emarginate and marginate laterally, anterior margin truncate with fore angles rounded; punctation small, sparse and weak. Prosternal sutures (Fig. 12) accompained by a higher impunctate band reaching the lateroanterior margin of hypomeron; open frontally forming a

channel. Hypomera with a moderately wide furrow near the prosternal sutures, marginate by an irregular impunctate area; punctation coarser than that of pronotum, dense and heterogeneous; coarser and sparser near prosternal sutures; basal region smooth. Mesepimeron and mesepisternum form part of margin of mesocoxal cavity; metepisternum narrow strongly tapered apicad; mesepimeron elevate latero-anteriorly. Metasternum prominent between the mesocoxae; mesocoxal cavities marginate by a V-shaped higher band, punctation dense, coarse at lateral half and smaller near the median suture; metasternal median suture incomplete, strongly furrowed on posterior two thirds. Metacoxal plate widened laterally. Scutellum elongate, triangular and declivous, longitudinally impressed; posterior margin truncate. Elytra wider than pronotum and strongly convex; distal third tapered apicad; each elytron tapered apicad and with distal spine only in male; apices dehiscent; striae marked by coarse and sparse punctures; interstices flattened and densely micropunctate, slightly convex at base, forming a weak basal tubercle. Epipleura open distally. Hind wing (Fig. 7) with open anal cell; distal area with two elongate sclerotizations, joined by a lighter area. Tibial spurs absent; tarsal lamellae (Fig. 21) decreasing from segments I to IV. Claws with one long basal setae (Fig. 20).

Male genitalia (allotype) (Figs 13, 14). Genital segments partially damaged. Urotergite VIII the best preserved, elongate, basal region membranous, recovered by thin and short pubescence. Urosternite VIII lost. Urosternite IX elongate, partially membranous, distal area broken, densely setous on distal half. Urotergite IX, distal half destroyed; proximal half with a dense and long pubescence; urotergite X destroyed. Basal piece as long as parameres; parameres tapered apicad, each with a lateral unciform tooth. Median lobe partially membranous, like a microspined sheath, apex rounded.

Female genitalia. Urotergite VIII (Fig. 16) membranous basally, gradually tapered apicad, covered by short setae; long setae disposed on distal half. Urosternite VIII (Fig. 15) tapered apicad, partially membranous; distal region covered by short setae; long setae on anterior margin, basal sclerite 1.3 times longer than distal area. Ovipositor (Fig. 17) with styli, baculus wide, 3 times longer than coxites; coxites with scattered long pedunculate setae and numerous microsetae; distal region of stylus (Figs. 18, 19) covered by numerous, pedunculate, long and short setae.

Material examined. Madagascar. ex-coll. Janson, ex-coll. Dejean, 1 ♂ (BMNH); 1 ♀ (BMNH); 1 ♂ (allotype) (BMNH); 1 ♀ (Neotype) (BMNH); ex-coll. Gorham, 1 ♂ (USNM).

Paratetralobus *stat. n.*

Tetralobus (*Paratetralobus*) Laurent, 1964:220. Type-specie: *Tetralobus hemirhipoides* Fleutiaux, 1919:36, by monotypy.

Paratetralobus hemirhipoides (Fleutiaux, 1919)
(Figs 44, 46-59)

Tetralobus hemirhipoides Fleutiaux, 1919:36; Schenkling, 1925:71.
Tetralobus (*Paratetralobus*) *hemirhipoides*; Laurent, 1964:220; 1967:105.

Length: 27-36mm. (Fig. 44).

Integument reddish-brown. Pubescence short, moderately dense and golden yellow, longer on metasternum and metacoxal plates.

Frons pentagonal; anterior margin weakly carinate, carina incomplete at middle; strongly concave medially near anterior margin; concavity decreases basad; punctation coarse, dense and heterogenous. Nasal plate (Fig. 49) narrower than the scape width; punctate with two longitudinal lateral carinae convergent distally. Antennae of male (Fig. 44) 11-segmented and strongly flabellate; 2nd and 3rd segments very short, transverse; 3rd one prominent laterally. Mandible (Figs. 46-48) falciform, 1.7-1.9 times longer than wide; elevate dorso-medially forming a sinuous carina, setous, dorsolaterally, forming an anterior tuft of longer setae locate in a pit; penicillus fringe-like of short setae.

Pronotum trapezoidal; anterior margin almost straight; lateral margins marginate; lateral carina seen from above; hind angles wide, slightly divergent with parallel carina to the lateral margins, shorter in the smaller specimen; discal region with a slight longitudinal median concavity

and one rounded pit each side; punctation dense and heterogeneous, stronger near anterior and lateral margins; a median sub-basal small tubercle present. Prosternum (Fig. 51) wide, convex, with coarse, dense and heterogeneous punctation, procoxal cavities marginate; margins of procoxal cavities partially punctate; prosternal spine (Figs. 51, 52) punctate, tapered apicad; prosternal lobe slightly concave with anterior margin directed downward, marginate anteriorly; punctation denser than the prosternum. Prosternal sutures (Figs. 51, 52) accompained by an elevate band, punctate distally, reaching the lateral margins of pronotum, and a narrow furrow on hypomera accompaining this band. Hypomera punctate only on 2/3 anterior; punctation coarse and dense anteriorly decreasing in density basad. Mesosternal cavity (Fig. 52) rounded; borders wide at basal third, declivous anteriorly. Mesepimeron and mesepisternum forming part of margin of mesocoxal cavities (Fig. 52). Metepisternum large. Metasternum with small and dense punctation; mesocoxal cavities marginate. Metacoxal plate (Fig.52) narrowed near the middle. Scutellum cordiform and declivous; anterior margin straight. Hind wing (Fig. 50) with open anal cell; distal area with three sclerotizations. Elytra wider than pronotum, slightly narrow at apex; punctate-striate; interstices slightly convex basally and almost indistinguishable basad; basal region of 3rd and 4th interstices elevate forming a tuberculiform prominence. Epipleura open distally. Legs short; tibial spurs (Figs. 57) present; lamellae increasing in size from I-IV tarsal segments; claws with a long and a short basal seta.

Male genitalia. Urotergite VIII (Fig. 53) partially membranous, elongate, rounded distally, densely covered by short setae; setae longer on anterior margin. Urosternite VIII (Fig. 54) transverse, bilobate distally; partially membranous with short setae near distal margin of each lobe. Urotergite IX (Fig. 55) elongate, slightly tapered and bilobate apicad; setae near laterodistal and distal margins; the distal setae are longer; urotergite X reduced, fused to IX. Urosternite IX (Fig. 56) elongate, partially membranous; two lateral long setae near the apex; distal region covered by short setae. Aedeagus (Figs. 58, 59): parameres separate, 1.6 times longer than basal piece, slightly tapered apicad; lateral margins declivous basally; median lobe wide, dorsal area membranous, like a sheath and without longitudinal median sclerite, slightly narrow near the base and at apex; furcae longer than parameres.

Material examined. Kenya. Maktau 1236, MacArthur, (Kenya Nath. Mus. exchange), 2 ♂ (USNM).

Neotetralobus

Neotetralobus Girard, 1987:49.
Type-species: *Neotetralobus africanus* Girard, 1987:51, by monotypy.

Neotetralobus africanus Girard, 1987

(Figs. 45, 60-74)

Neotetralobus africanus Girard, 1987: 49-52, 7 figs.
Length: 27 - 32 mm (Fig. 45).

Integument reddish-brown. Pubescence very short, thin, erect and yellowish, longer on metasternum of male. Female larger than male.

Frons narrowed at distal fourth; not carinate; anterior margin rounded forming a small edge near antennae insertions; a deep longitudinal pit near anterior margin continuing as a longitudinal small ridge reaching the base; punctation small, dense and heterogeneous. Nasal plate (Fig. 63) trapezoidal, continuous with the frons with one small longitudinal lateral carina each side, punctation small, dense and heterogeneous. Antennae short, not reaching the hind angles of pronotum, 11-segmented in both sexes; pectinate in female and flabellate in male; 2nd and 3rd segments transverse; 3rd segment with a small sharpened spiniform appendix. Mandibles (Figs. 60-62) falciform, 1.7-1.8 times longer than wide, a dorsolateral elevation forming a carina; several dorsolateral setae with a tuft of longer setae in a dorsolateral pit; penicillus short, fringe-like.

Pronotum gibbous, about 1.5 times wider than long; lateral and anterior margins not visible from above; anterior margin marginate; lateral carina present only on anterior two thirds; strongly convex near the middle and abruptly inclined foreward; longitudinal median furrow not reaching the base, giving to pronotum a bilobated appearence; hind angles reduced, rounded with a small, spine-like process at the base; median basal tubercle short, flattened and marginate distally;

punctation very small and dense, base wrinkly. Prosternum wide, convex, with punctation small and dense; procoxal cavities smooth, slightly marginate, with a transversal furrow near anterior margin; prosternal lobe marginate, sinuous, short, anterior margin strongly rounded; prosternal spine slightly tapered apicad; apex rounded; prosternal sutures accompained by a higher impunctate band reaching the fore angles of hypomera. Hypomera marginate, micropunctate; basal region smooth, without sulcus near prosternal sutures. Mesosternal cavity wide and rounded; borders elevate and marginate basally and declivous foreward. Mesepimeron and mesepisternum forming part of margin of mesocoxal cavity; mesepisternum almost flat, elevate near the mesepimeron. Metasternum not elevate between mesocoxae, densely micropunctate with a weak, median longitudinal furrow, marginate around mesocoxal cavity. Metepisternum large. Metacoxal plate slightly narrowed medially. Scutellum cordiform and declivous. Elytra about 3.5 times longer than pronotum, slightly wider than pronotum, parallel, apex rounded; striae marked by a punctuated line; interstices flattened in female and slightly convex in male; 5th interstice concave basally, basal tubercle present. Epipleura open distally. Hind wing (Fig. 74) with anal cell open; distal area with a sclerotization U-shaped. Tibial spurs present; tarsal lamellae short, decreasing in length from segments I to IV; claws with basal setae.

Male genitalia. Urotergite VIII (Fig. 69) slightly elongate, membranous basally with proximal margin rounded and densely covered by short setae. Urosternite VIII (Fig. 68) transverse, partially membranous, distal margin trilobate and with short setae. Urosternite IX (Fig. 70) elongate; distal margin emarginate; setae disposed near distal margin and medially on anterior half. Urotergite IX (Fig. 71) elongate, narrowed at apex; proximal margin bilobate; a band of setae each side, the distal longer; urotergite X reduced and fused to urotergite IX. Aedeagus (Figs. 72, 73): basal piece 1.3 times shorter than parameres; parameres separate, almost straight and narrowed at basal third, slightly tapered apicad. Median lobe with lateral areas membranous and covered by microsetae; apex rounded.

Female genitalia. Urotergite VIII (Fig. 67) sub-hexagonal, densely covered by short setae; basal region membranous and glabrous. Urosternite VIII (Fig. 66) partially membranous, slightly tapered apicad; several short setae near the apex; basal sclerite 3 times longer than distal area. Ovipositor broken. Omega-like sclerite of anterior bursa copulatrix (Figs. 64-65) with lateral arms slightly curved and central arm stout and pointed acute apex, margins irregular, lateral teeth absent. A pair of a very developed colleterial glands with a basal diverticulum each and with the opening of oviduct (Fig. 64). Posterior bursa copulatrix very elongate with the opening of one spermathecal duct and one opening of the acessory gland duct.

Material examined. Cameroon. Eseka, 1 ♂ (paratype) (MHNP). Central African Republic. La Maboké, 18.II.1968, P. Teocchi col., 1 ♀ (allotype) (MHNP).

Pseudotetralobus

Pseudotetralobus Schwarz, 1902:210.
Type-species: *Pseudotetralobus dohrni* Schwarz, 1902:210, by monotypy.

Pseudotetralobus dohrni Schwarz, 1902
(Figs. 75, 77-93)

Pseudotetralobus dohrni Schwarz, 1902:210; 1906:57-58; Elston, 1928:182; Neboiss, 1956:17; van Zwaluwenburg, 1959:347; Laurent, 1967:95.

Length: 32-39 mm (Fig. 75).

Integument brown, legs and antennae sometimes lighter; first three segments of antennae shiny, the remainder ones dull, in both sexes; antennae of male luteous from 4th to 12th segments. Dorsal pubescence yellowish and dense, almost recovering the integument; in the ventral region, slightly longer. Female larger than male.

Frons narrow, not carinate, strongly concave at median anterior region forming a longitudinal furrow; anterior margin rounded forming a small edge only near antennae insertions; punctation dense and heterogeneous, coarser anteriorly. Nasal plate (Fig. 82) continuous with frons, densely punctate without longitudinal carina. Antennae reaching the hind angles of pronotum only in male; 12-segmented in both sexes; strongly

flabellate in male and pectinate in female; 2nd and 3rd segments transverse and approximately equal in male and 3rd longer than 2nd in female. Mandible (Figs. 77-79) stout, 1.2-1.3 times longer than wide; dorsal region setous and elevate laterally forming a carina; a tuft in a small pit on dorsal lateral anterior third; penicillus fringe-like.

Pronotum 1.1 times longer than wide, lateral carina visible from above; anterior margin prominent medially; fore angles rounded, marginate anteriorly; strongly convex on anterior median region; hind angles flat, divergent with a long lateral carina running very near the lateral margins, more developed in males; punctation coarse, dense and heterogeneous, sparser on longitudinal median region; basal tubercle well developed. Prosternum (Figs. 89, 90) with punctation heterogeneous, sparse, coarser than that of pronotum. Prosternal lobe (Figs 89-90) emarginate, 3-lobate, the median lobe the largest; punctation denser and smaller than that of prosternum; prosternal spine widened near the middle third and tapered apicad. Prosternal sutures (Figs. 89, 90) accompained by an impunctate band and a small sulcus not reaching the fore angles of hypomera; procoxal cavities marginate and smooth; hypomera densely and heterogenously punctate except on basal region; punctation larger than that of pronotum. Mesosternal cavity (Fig. 89) rounded basally with borders slightly declivous. Mesepimeron and mesepisternum forming part of mesocoxal cavity (Fig. 89). Punctation of metasternum small and dense, smaller basad; metasternum marginate but not elevate around mesocoxal cavities and with longitudinal shallow median line. Metepisternum large, with outer margin tapering towards apex. Metacoxal plate (Fig. 89) slightly narrowed near the middle, outer margin with an elevate fold. Scutellum triangular and declivous, slightly sulcate longitudinal-medially. Elytra parallel, with rounded basal tubercle 3rd and 4th striae; slightly narrowed at apex; weakly punctate-striate; interstices densely micropunctate; apex emarginate with a sutural spine. Hind wing (Figs. 80, 81) with anal cell open; distal area with a sclerotization upsilon-shaped; a row of approximately 37 spines near the costal margin, not surpassing the wing border. Epipleura open distally. Tibial spurs present; tarsal lamellae increasing in size from segments I to IV. Claws setous with a basal setae.

Male genitalia. Urotergite VIII (Fig. 86) slightly elongate and membranous basally; setae more concentrate near anterior and lateral margins. Urosternite VIII (Fig. 84) transverse, partially membranous; distal margin bilobate and with short setae near the lobe margins. Urosternite IX (Fig. 83) elongate, slightly tapered to apex; distal region with setae of variable size. Urotergite IX (Fig. 85) elongate, tapered apicad, bilobate at the apical fifth, lobes slightly convergent distally; longitudinal median line interrupted at middle; each distal lobe with a pair of small setae on lateral internal margin and several others on lateral external margin; urotergite X reduced and fused to urotergite XI. Aedeagus (Figs. 87-88): parameres separate, narrowed and rounded near the apex, 1.3 longer than basal piece; median lobe partially membranous; abruptly narrowed to apex, membranous area densely setous near apex.

Female genitalia. Urotergite VIII (Fig. 91) membranous basally, covered by short setae and marginate by long setae. Urosternite VIII (Fig. 92) partially membranous, strongly tapered to distal third; setae of variable size near margins of anterior half; basal sclerite 1.7 times longer than distal area. Ovipositor (Fig. 93) with very elongate baculi (6.5 times longer than coxites); coxites small with one articulate stylus each; stylus (Fig. 94) with distal long setae and several ventral microsetae. Omega-like sclerite of anterior bursa copulatrix (Fig. 95) with lateral arms slightly curved and central arm strongly sharpened, apex obliquely truncate; lateral teeth absent; a pair of a very developed colleterial glands (Fig. 93) with a basal diverticulum each, and with the opening of the oviduct. Posterior bursa copulatrix elongate, with the openings of a pair of spermathecal ducts and one opening of the accessory gland duct.

Material examined. Papua New Guinea. Ex. coll. Merton C. Lane, coll. 1975, 1 ♂ (USNM); (= New Guinea), Pratt, 1 ♂ (BISHOP), Aru Island, coll. 721, 1910-168, 1 ♀ (BMNH).

Pseudotetralobus australasiae (Gory, 1836)
(Figs. 96-99)

Tetralobus australasiae Gory, 1836:513; Candèze,

1857:381.
Pseudotetralobus australasiae Schwarz, 1902:210; Laurent, 1967:107.

Female genitalia. Baculi (Fig. 98) 4.5 times longer than coxites. Coxites (Figs. 96-98) setous with a dorsal longitudinal lateral row of microsetae and a laterodistal articulate stylus each; styli with several dorsal long setae and ventrodistal microsetae. Omega-like sclerite of anterior bursa copulatrix with distal region of median arm serrulate.

Material examined. Australia, New South Wales, Black Mts. A.C.T., light trap, 3.II.57, P.B. Carne col., 1♂ (CSIRO); idem, 21.I.47, 1 ♀ (CSIRO); Blue Mts, 1 ♀ (USNM).

Comments: The omega-like sclerite (Fig. 99) of anterior bursa copulatrix is typical of the genus but with lateral margins of central arm, serrate.

Pseudalaus

Pseudalaus Laurent, 1967:92.
Type-species: *Tetralobus dohrni* Candèze, 1821:26, by original designation.

Pseudalaus dohrni (Candèze, 1881:26)
(Figs. 76, 100-120)

Tetralobus dohrni Candèze, 1881:26; 1882:26; 1890:48; Schwarz, 1906:58; Laurent, 1964:222, 225.
Pseudalaus dohrni; Laurent, 1967:93; Girard, 1987:50.

Length: 20-22 mm (Fig. 76).

Integument black and bright. Glabrous appearance; pubescence very thin and sparse, almost translucent, longer and denser on meso- and metasternum of male.

Frons not carinate, concave at anterior median region; anterior margin rounded forming a small edge; punctation coarse, umbilicate, dense and heterogeneous; basal region with a median and a lateral impunctate areas. Nasal plate (Fig. 105) without carina; punctation smaller than the frontal one. Labrum narrow (Fig. 105). Antennae not reaching the hind angles of pronotum; 11-segmented in both sexes; pectinate in female (Fig. 100) and flabellate in male; 2nd and 3rd segments transverse; 3rd segment subequal in length to the 2nd, with a spiniform appendix in male; 4th segment of female triangular and longer than the two anterior together; segments 4-11 of male with an irregular row of coarse punctures. Mandible (Figs. 101-103) 1.1.-1.2 times longer than wide, elevate dorso-laterally forming a carina, and a narrow longitudinal furrow; several setae on dorsolateral and lateral regions inserted in large punctures; penicillus fringe-like. Ventral region with two rounded shallow depressions.

Pronotum 1.1 times longer than wide; lateral carina not seen from above; regularly convex; anterior margin almost straight; fore angles short and rounded; hind angles flat, slightly divergent, stout, not carinate; median basal tubercle slightly flattened and rounded; punctation umbilicate, coarse and dense near lateral margins, decreasing in thickness and density towards the middle. Prosternum elongate, convex; punctation small and sparse, coarser and denser near the prosternal sutures; procoxal cavities marginate and smooth; prosternal lobe prominent, marginate and sinuous; punctation smaller than prosternum. Prosternal sutures straight, accompained by a higher impunctate band and sulcus. Prosternal spine straight and rounded. Hypomera with punctation umbilicate, coarse and dense, smaller near the base; basal and laterobasal regions smooth. Mesosternal cavity rounded with borders vertical at basal region, due the elevate position of metasternum, and horizontal foreward. Mesepimeron and mesepisternum forming part of margin of mesocoxal cavity (Fig. 104). Metasternum (Fig. 104) elevate and prominent between the mesocoxae; metasternum with median longitudinal line; metasternum marginate around the mesocoxal cavities, running parallel the internal suture of metepisternum up to middle; punctation small and dense. Metepisternum large. Metacoxal plate slightly narrowed medially. Scutellum subpentagonal and declivous; posterior margin rounded. Elytra as wide as pronotum, tapered apicad; apex rounded; punctate; feeble striae present only basally, striae flat on disc; a rounded basal tubercle-like prominence between the 3rd and 4th striae. Epipleura open distally. Hind wing (Fig. 106) with open anal cell; distal area with a

V-shaped sclerotization; rr vein weakly marked. Tibial spurs present; tarsal lamellae (Fig. 119) decreasing in size from segments I to IV. Claws (Fig. 120) setous and with one basal seta.

Male genitalia. Urotergite VIII (Fig. 112) slightly elongate with anterior margin rounded; densely covered by short setae. Urosternite VIII (Fig. 109) transverse, partially membranous; anterior margin bilobate, marginate by short setae. Urosternite IX (Fig. 111) elongate with anterior margin rounded; setae disposed on distal third; some lateral setae longer. Urotergite IX (Fig. 110) slightly elongate, narrowed at apex; bilobate at the apical third, lobes slightly convergent distally; longitudinal median line interrupted at basal third; a longitudinal band of setae each lobe, the distal ones are longer; urotergite X reduced and fused to urotergite IX. Aedeagus (Figs. 107, 108): basal piece 1.1 times longer than parameres; lateral margins of parameres abruptly narrowed on basal fourth and tapering from the median lateral spine to apex. Median lobe wide, partially membranous, slightly tapered apicad; apex rounded.

Female genitalia. Urotergite VIII (Fig. 116) slightly elongate, membranous basally, densely covered by short setae and marginate by longer ones; distal third tapered apicad. Urosternite VIII (Fig. 113) elongate, partially membranous, covered by short setae, the median anterior setae longer; basal sclerite 4 times longer than distal area. Ovipositor (Fig. 114) with very elongate baculi (8 times longer than coxites); coxites (Fig. 117) small, with one articulate stylus each; a row of microsetae begining on dorsobasal fourth and continuing up to ventrolateral margin near the styli articulations; several long setae on laterodorsal and ventral margins; stylus (Fig. 118) with distal long setae and several ventral, pedunculate, short setae. Omega-like sclerite of anterior bursa copulatrix (Fig. 115) with lateral arms curved and a sharp central arm with one small tooth on each side and a bifid apex, with lobes subequal, acute.

Material examined. Zaire. Lokandu, III. 1939, Capt. Marée, coll. Mus. Congo, 1 ♂, 1 ♀ (MRAC). Localities not found: Akropong, C.E. Tottenham coll., B.M. 1963-414, 421, 1 ♂ (BMNH); idem, 424, 1 ♀ (BMNH); Achantis Pl, ex-coll. E. Candèze, 1 ♂ (INSB).

Tetralobus

Tetralobus Le Peletier de St. Fargeau & A. Serville, 1825:594.
Type-species: *Elater flabellicornis* Linnaeus 1767:651, designated by Lacordaire, 1857:164.
Tetralobus (*Dodecamerus*) Laurent, 1968:328, type-species: *Tetralobus* (*Dodecamerus*) *angolensis* Laurent, 1968:328-329.
Comments: *Dodecamerus* was described based on a single male from Angola by Laurent. We were unable to locate this specimen supposed to be in the BMNH. By the short original description, it is impossible to discuss the status of this taxon.

Tetralobus flabellicornis (Linnaeus, 1767)
(Figs. 121, 123-143)

Elater flabellicornis Linnaeus, 1767:651.
Tetralobus flabellicornis; Le Peletier de St. Fargeau et Audinet, 1825:594; Boheman, 1851; 377; Candèze, 1857;567, 569; Fleutiaux, 1919:32.
Tetralobus (*Tetralobus*) *flabellicornis*; Laurent, 1964:222 and 358; Laurent, 1967:105.

Length: ♂ : 40-64mm; ♀ : 46-80mm (Fig. 121)

Integument from brownish to black; antennae from dark-brown to reddish-brown. Pubescence from gray to yellowish or to brownish gray; dorsal pubescence thin, dense and short; longer on basal third of pronotum, scutellum and basal region of elytra; hypomera, meso-and metasternum with pubescence longer than dorsal region.

Frons carinate concave on anterior median region, forming a pit near anterior margin; a small longitudinal median ridge at basal half; anterior margin turned upwards with prominent median region, strongly sharpened in some specimens; punctation small, dense and heterogeneous. Nasal plate (Fig. 130) narrowed near the middle, small and heterogeneously punctate. Antennae almost reaching the hind angles of pronotum in both sexes; 11-segmented; flabellate in male and pectinate in female (Fig. 127); three first segments brighter; 2nd and 3rd segments transverse, shorter in male. Mandibles (Figs. 123-125) 1.4-1.7 times longer than wide elevate dorso-medially forming a sinuous carina; dorsolateral setae short; longer setae in a shallow pit; penicillus with long

setae, fringe-like.

Pronotum wider than long, more convex on longitudinal median region; lateral carina seen from above; anterior margin almost straight; fore angles short and round; hind angles slightly divergent, swollen and stout with convergent apex; punctation small, dense and heterogeneous, coarser on lateral margins; a median sub-basal small tubercle present. Prosternum wide, slightly convex, with coarse, and heterogeneous punctation, procoxal cavities marginate, outer margin of prosternal spine with an indentation near apex; prosternal lobe emarginate laterally; anterior margin almost straight; punctation smaller than prosternum. Prosternal sutures short, accompained by a high and impunctate band almost reaching the lateral margins of pronotum and a narrow furrow on hypomera accompaining this band. Hypomera punctation thin and dense; basal region smooth. Mesosternal cavity wide; borders stout and almost horizontal distally and declivous proximally. Mesepimeron and mesepisternum forming part of margin of mesocoxal cavity. Metepisternum large. Metasternum with thin and dense punctation; mesocoxal cavities marginate by a higher band, V-shaped. Metacoxal plate forming a tooth on internal third. Scutellum subpentagonal and declivous. Hind wing (Fig. 126) with open anal cell; distal area with a large sclerotized region reaching the lateral margin and one smaller distal median. Elytra slightly wider than hind angles of pronotum; punctate-striate; striae weakly marked; interstices slightly costiform; basal tubercle present; apices with a small sutural spine in some specimens. Epipleura open distally. Legs short; femur stout; tibial spurs present; lamellae (Fig. 128) increasing in size from I-IV tarsal segments; claws (Fig. 129) setous with two long basal setae and one long sub-basal setae.

Male genitalia. Urotergite VIII (Fig. 140) partially membranous, almost as long as wide, round distally, densely covered by short setae; setae longer on distal margin. Urosternite VIII (Fig. 139), transverse bilobate distally, partially membranous with short setae near distal margin of each lobe. Urotergite IX (Fig. 138) wide basally, narrowed distad, partially membranous, bilobate apicad; setae near latero distal and distal margins; the distal setae are longer; urotergite X reduced, fused to IX. Urosternite IX (Fig. 141) elongate, partially membranous; distal region covered by short setae. Aedeagus (Figs. 142-143): parameres separate, slightly tapered apicad, almost of the same length of basal piece; lateral margins medially emarginate ventrally. Median lobe wide; slightly tapering to apex, dorsal region membranous like a sheath; with a large longitudinal median sclerite; furcae longer than parameres.

Female genitalia. Urotergite VIII (Fig. 134) membranous basally, wide, round distally; distal third with sparse short setae; long setae like a fringe on distal margin; membranous area with microsetae. Urosternite VIII (Fig. 135) elongate, partially membranous covered by short setae, the marginal setae longer; basal sclerite 3.2 times longer than distal area. Ovipositor (Figs. 131, 132) with styli; baculus 6.8 times longer than coxites; coxite with long simple setae; distal region of stylus (Fig. 136) covered by numerous pedunculate long and short setae (Fig. 137). Omega-like sclerite (Fig. 133) of anterior bursa copulatrix with lateral arms slightly curved and sharpened central arm with one small tooth each side and a bifid apex with lobes unequal, rounded; a pair of a very developed colleterial glands (Fig. 131) with a large basal diverticulum each and with an opening of oviduct; posterior bursa copulatrix elongate with basal microspined region innerly, with the openings of a pair of spermathecal ducts.

Material examined. Cameroon. *Cameroon Oriental*: Nanga-Eboko, Dr. Lenczy, 1959, 1 ♂ (MZSP). Zaire. *Haut Zaire* Niangara, XI.1910, Lang & Chapin cols, 2 ♀ (AMNH); Faradge, XI.1911, Lang & Chapin cols, 1 ♀ (AMNH). Kenya. Nairobi, Nairobi Museum, Kenya Nat. Mus. Exchange, 1 ♀ (USNM); Masi, colony Africa, 1938, 1 ♂ (AMNH) Tanzania. *Tanga*: Usambara, C. Holgis, 1921-253 1 ♂ (BMNH); Tanga, Allde, 1 ♀ (BMNH). *Coast*: Dar-es-Salaam, 17.VI.1948, Central African Exp. J.L. Clark, 1 ♀ (AMNH). South West Africa. *Equateur*: Karawa, Ubangi dist. Belg. Congo, 1937, T.B. Wallin Acc. 36255, 1 ♀ (AMNH); Kalidona, F. Gaerds, 1 ♂ (USNM). South Africa. *Transvaal*: Moketsi, 14-18.II.1968, Kronbein & Spangler, 1 ♀ (USNM); Kruger Nat'l. Park Petroriuskop, 20-21.II.1968, Kronbein & Spangler cols., 1 ♂, 1 ♀ (USNM). *Natal*: Durban, Durban Museum, Ac.4247, 1 ♀ (AMNH); 1917, 2 ♀ (AMNH); 4903, 3 ♀, 1 ♂ (AMNH). Locality

not found: C.E.S. Suakoko, 29.X.1953, 3 citrus lives plot, nr. 5 yard, 1 ♂, 1 ♀ (USNM).

Sinelater *stat n.*

Tetralobus (*Sinelater*) Laurent, 1967:94.
Type-specie: *Tetralobus perroti* Fleutiaux, 1940:107, by monotypy.
(Monotypic)

Sinelater perroti (Fleutiaux, 1940)
(Figs. 122, 147-163)

Tetralobus perroti Fleutiaux, 1940:107; 1947:294; Laurent, 1964:356.
Tetralobus (*Sinelater*) *perroti*; Laurent, 1967:94.

Length. ♂, ♀ : 60mm (Fig. 122).

Integument black; antennae and tarsal lamellae reddish-brown. Pubescence thin, dense and golden- yellow only on elytra; humeral region with shorter pubescence. Head and prothorax glabrous. Metasternum with long, thin and sparse pubescence; tergites and legs with very thin pubescence giving a glabrous appearance.

Frons slightly concave on anterior region; anterior margin slightly prominent, rounded, not carinate; punctation fine and dense, mat-like. Nasal plate (Fig. 157) narrowed near the middle, small, dense and heterogeneously punctate. Antennae not reaching the hind angles of pronotum and 11-segmented in both sexes; flabellate in male and pectinate in female (Fig. 147); three first segments black and sparsely setous; the others reddish-brown and densely microsetous; 2nd and 3rd segments transverse; 3rd segment slightly prominent foreward in male. Mandible (Figs. 144-146): stout, basal two thirds almost straight laterally; dorso median region forming a sinuous carina; ventral region with a basal carina; setous dorsolaterally; longer setae in a sub-apical pit; penicillus with long setae, fringe-like.

Pronotum subtrapezoidal, wider than long, more convex on longitudinal median region; rounded lateral carina seen from above; anterior margin almost straight; fore angles short and rounded; hind angles swollen, divergent with convergent apex; small, dense, heterogeneous and mat punctation; a median basal flattened tubercle present. Prosternum convex, small and heterogeneous mat punctation, coarser than hypomeron; procoxal cavities marginate; prosternal spine abruptly narrowed to apex, forming a round prominence near the apex; prosternal lobe slightly emarginate laterally; anterior margin rounded; a longitudinal median furrow on basal region of prosternum and prosternal spine; thin, heterogeneous and mat punctation. Prosternal sutures accompained by a high and impunctate band almost reaching the lateral margins of pronotum and a narrow furrow on hypomera accompaining this band. Hypomera punctation dense, thin and mat; basal region smooth. Mesosternal cavity wide; borders stout and almost horizontal distally and declivous proximally. Mesepimeron and mesepisternum forming part of margin of mesocoxal cavity. Metepisternum large. Metasternum punctation thin, dense and homogeneous; mesocoxal cavity marginate by a higher band; metasternal median suture furrowed. Metacoxal plate forming a tooth on internal third. Scutellum subpentagonal and declivous anteriorly, sparsely punctate medially, other regions smooth, pubescence longer than that of elytra. Hind wing (Fig. 148) with open anal cell; distal area with a large sclerotized region reaching the lateral margin. Elytra slightly wider than hind angles of pronotum; striae weakly marked; densely micropunctate; interstices flat; basal tubercle absent; apices rounded. Epipleura largely open distally. Legs (Fig. 149) short; femur stout; lamellae increasing in size from I-IV tarsal segments; tibial spurs present; claws setous with two longer basal setae.

Male genitalia. Urotergite VIII (Fig. 150) partially membranous, almost as long as wide, densely covered by short setae. Urosternite VIII (Fig. 153) transverse, partially membranous, strongly bilobate distally with short setae near distal margin of each lobe; the marginal setae longer. Urotergite IX (Fig. 152) wide, bilobate at the apical third, lobes slightly convergent distally, a longitudinal median line interrupted at basal fourth; a lateral band of short setae almost reaching the base; distal setae longer; urotergite X reduced and fused to IX. Urosternite IX (Fig. 151) elongate, partially membranous, distal region with scattered short setae. Aedeagus (Figs. 154-155): parameres separated, tapered apicad; 1.6 times longer than basal piece; lateral margin emarginate ventrally forming a small subapical tooth.

Table 1. Number of species of Tetralobini, type-species examined and depository Institutions

Genera	Nr. of species	Type-species	Examined species	Nr. of specimens examined
Piezophyllus	05	Tetralobus robustus Hope, 1842 syn. of Tetralobus macrocerus Castelnau, 1836	P.benitensis Fleutiaux, 1902	2♂ (USNM); 1♂ (MZSP)
			P.borneensis Fleutiaux, 1902	1♂ (MAMJ)
			P.macrocerus (Castelnau, 1836)	2♂, 2♀ (BMNH); 1♂ (USNM)
Paratetralobus	01	Tetralobus hemirhipoides Fleutiaux, 1919	P.hemirhipoides (Fleutiaux, 1919)	2♂ (USNM)
Neotetralobus	01	N.africanus Girard, 1987	N.africanus Girard, 1987	1♂, 1♀ (MNHN)
Pseudotetralobus	15	Pseudotetralobus dohrni Schwarz, 1902	P.albertisi (Candèze, 1878)	1♂ (CSIRO)
			P.australasiae (Gory, 1836)	1♂, 1♀ (CSIRO); 1♀ (USNM)
			P.capucinus (Candèze, 1882)	1♂, 1♀ (CSIRO)
			P.corrosus (Candèze, 1878)	1♂, 1♀ (CSIRO); 2♂ (CLBRR)
			P.dohrni Schwarz, 1902	1♂ (BPBM); 1♂ (USNM); 1♀ (BMNH)
			P.fortnumi (Hope, 1842)	1♂ (USNM); 1♂ (MZSP); 2♂ (CLBRR)
			P.murrayi (Candèze, 1857)	1♂, 1♀ (MNHG); 2♀ (USNM); 1♀ (CLBRR); 1♂, 2 larvae (CSIRO)
			P.quadrifoveatus (Mcleay, 1888)	9♂ (BPBM); 1♂ (CSIRO)
			Pseudotetralobus sp	1♀ (AMSA)
Pseudalaus	02	Tetralobus dohrni Candèze, 1881	P.dohrni (Candèze, 1881)	1♂, 1♀ (MRAC); 1♂, 1♀ (BMNH); 1♂ (ISNB)
Tetralobus	43	Elater flabellicornis, L., 1767	T.auratilis Schwarz, 1903	2♂ (USNM)
			T.auricomus Hope, 1842	1♂, 3♀ (USNM)
			T.bifoveolatus Boheman, 1851	1♂ (BPBM)
			T.cavifrons Fairmaire, 1887	1♂ (AMNH); 1♀ (USNM); 1♀ 1 larva (BMNH)
			T.flabellicornis (Linné, 1767)	2♂, 11♀ (AMNH); 3♂, 4♀ (USNM); 1♂, 1♀ (BMNH); 1♂ (MZSP)
			T.gigas (Fabricius, 1801)	3♀ (AMNH)
			T.mystacinus Candèze, 1857	3♂ (MZSP); 1♂ (USNM)
			T.natalensis Candèze, 1857	2♂, 1♀ (BPBM)
			T. rotundifrons Guérin, 1847	3♂, 1♀ (USNM)
			T.subsulcatus Guérin, 1847	1♂, 1♀ (USNM)
			T.tuberculatus Laurent, 1964	3♂, 1♀ (AMNH)
			Tetralobus spp	5♂, 4♀ (AMNH); 6♂, 2♀ (BPBM); 9♂, 2♀ (USNM)
Sinelater	01	Tetralobus perroti Fleutiaux, 1940	S.perroti (Fleutiaux, 1940)	1♂, 1♀ (MNHN)
TOTAL	68		26	135 adults and 3 larvae

Table 2. Plesiomorphic (0) and apomorphic (1) character states. Transformation series (0) plesiomorphic: (1) apomorphic intermediate; (2) fully apomorphic.

1. Nasal carinae
   0. absent
   1. present

2. Male antennae
   0. serrate
   1. flabellate

3. Mandibles
   0. stout
   1. falciform

4. Penicillus of mandibles
   0. long
   1. short

5. Dorso-lateral pit of mandibles
   0. absent
   1. present

6. Ventral basal carina of mandibles
   0. absent
   1. present

7. Labrum shape
   0. wide
   1. narrow

8. Nasal shape (width)
   0. Nasal wider than the scape width
   1. nasal narrower than the scape width

9. Male Antennae
   0. 11-segmented
   1. 12-segmented

10. Frons
   0. anterior margin not turned upwards
   1. anterior margin turned upwards

11. Mesothoracic sternites arrangements
   0. mesepisternum forms part of margin of mesocoxal cavity
   1. mesepisternum does not form part of margin of mesocoxal cavity

12. Anterior margin of metasternum
   0. not elevate and simple marginate
   1. elevate, V-shaped near mesocoxal cavities

13. Longitudinal median suture of metasternum
   0. shallow line
   1. strongly furrowed on posterior two thirds

14. Metacoxal plate
   0. simple
   1. with one tooth on internal third

15. Metacoxal plate
   0. not reaching epipleura
   1. reaching epipleura

16. Outer margin of metacoxal plate
   0. without an elevate fold
   1. with an elevate fold

17. Outer margin of metepisternum
   0. forming an angle near apex
   1. tapering towards apex

18. Metepisternum
   0. narrow
   1. wide

19. Outer margin prosternal spine
   0. without an indentation near apex
   1. with an indentation near apex

20. Lateral carina of prothorax
   0. complete
   1. incomplete anteriorly

21. Lateral carina of prothorax
   0. complete
   1. incomplete posteriorly

22. Posterior angle of pronotum
   0. projected
   1. reduced

23. Posterior angle of pronotum
   0. flat
   1. swollen

24. Convexity of pronotum

0. normal
1. gibbous

25. Mesosternal cavity
0. declive
1. vertical

26. Basal median tubercle of pronotum
0. normal
1. turned upwards

27. Distal area of hind wing
0. sclerite not reaching lateral margin
1. sclerite reaching lateral margin

28. Elytral striae
0. punctate-striate
1. weakly punctate-striate or punctures absent in some striae

29. Epipleura
0. closed
1. narrowly open distally
2. widely open distally

30. Elytral humeri
0. base with a sulcus
1. base without a sulcus

31. Apices of elytra
0. not dehiscent
1. dehiscent

32. Basal tubercle of elytra
0. weak
1. strong
2. absent

33. Tibial spurs
0. present
1. absent

34. Tarsi
0. simple
1. lobed beneath

35. Basal setae on tarsal claws
0. 1 seta present
1. 3-4 setae present

36. Median lobe of aedeagus
0. not partially membranous like a sheath
1. partially membranous like a sheath

37. Apex of parameres of aedeagus
0. unciform, lobed
1. elongate, straight

38. Distal part of parameres of aedeagus
0. not slightly narrow with ventral tooth
1. slightly narrow with ventral tooth

39. Distal part of parameres of aedeagus
0. without lateral tooth
1. abruptly narrow, with lateral tooth

40. X urotergite male
0. normal not fused
1. reduced and fused to IX urotergite

41. VIII urosternite male
0. normal
1. transverse and reduced

42. IX urotergite male
0. transverse
1. elongate

43. Basal median longitudinal line of IX urotergite male
0. absent
1. present

44. Omega-like sclerite of bursa copulatrix
0. absent
1. present

45. Omega-like sclerite of bursa copulatrix
0. without basal teeth
1. with two basal teeth

46. Omega-like sclerite of bursa copulatrix
0. apex of central arm simple
1. apex of central arm bifid

47. Baculum of ovipositor
0. short
1. long

Table 3. Distribution of characters in the Tetralobini genera. Plesiomorphic (0), apomorphic (1), (2) fully apomorphic, "?" information unknown, "-" character inapplicable to the taxon in question. Characters listed in table 2.

character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
genera																								
Piezophyllus (Hopelater)	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	0	0
Piezophyllus (Piezophyllus)	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0
Paratetralobus	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Neotetralobus	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1
Pseudotetralobus	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
Pseudalaus	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Tetralobus	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	1	0
Sinelater	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0

character	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
genera																							
Piezophyllus (Hopelater)	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	?	?	?	?
Piezophyllus (Piezophyllus)	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	-	-	0
Paratetralobus	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	0	?	?	?	?
Neotetralobus	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	0	?
Pseudotetralobus	0	0	0	1	1	1	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	0	1
Pseudalaus	1	0	0	1	1	1	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1
Tetralobus	0	0	1	1	1	1	0	1	0	1	1	1	1	0	0	1	1	1	0	1	1	1	1
Sinelater	0	0	1	1	2	1	0	2	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1

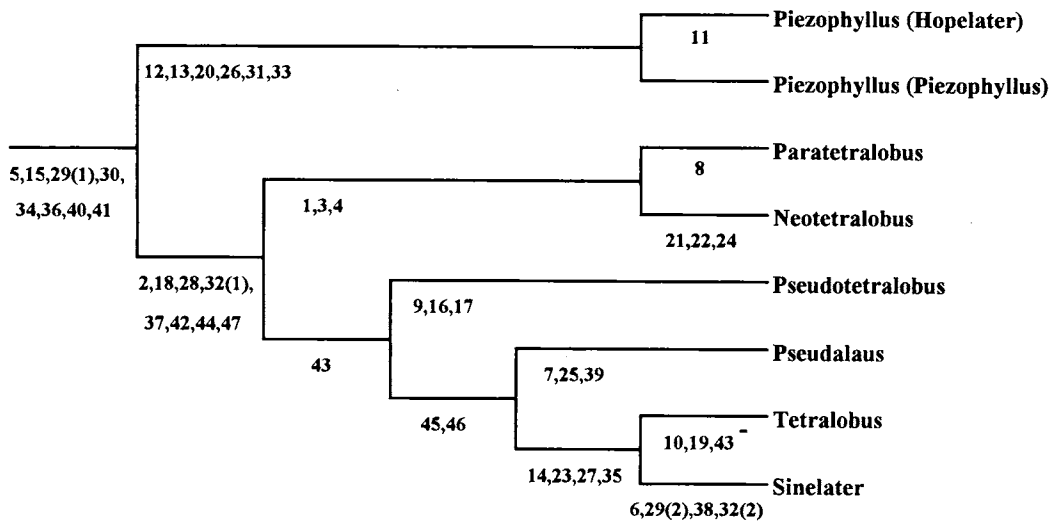


Fig. 1, cladogram of Tetralobini genera. Numbers indicating the apomorphies. The symbol (-) indicates a reversal; multi-state characters are indicate by (1), (2).

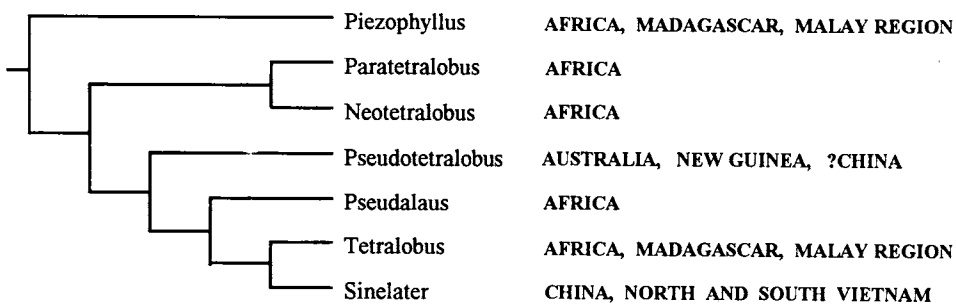


Fig. 2, cladogram of area of Tetralobini genera.

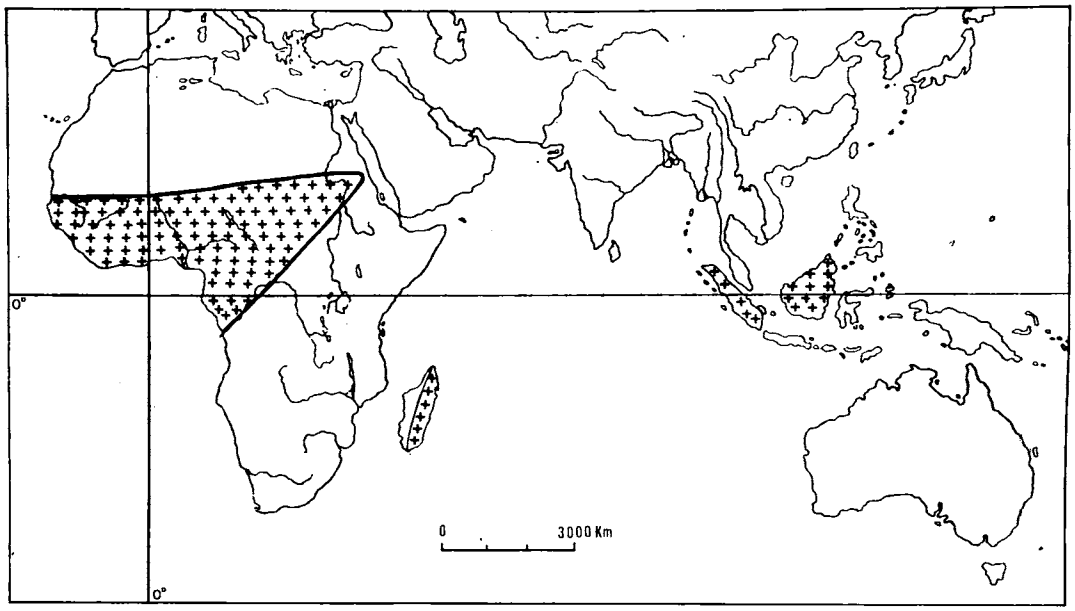


Fig. 3, geographical distribution of Piezophyllina.

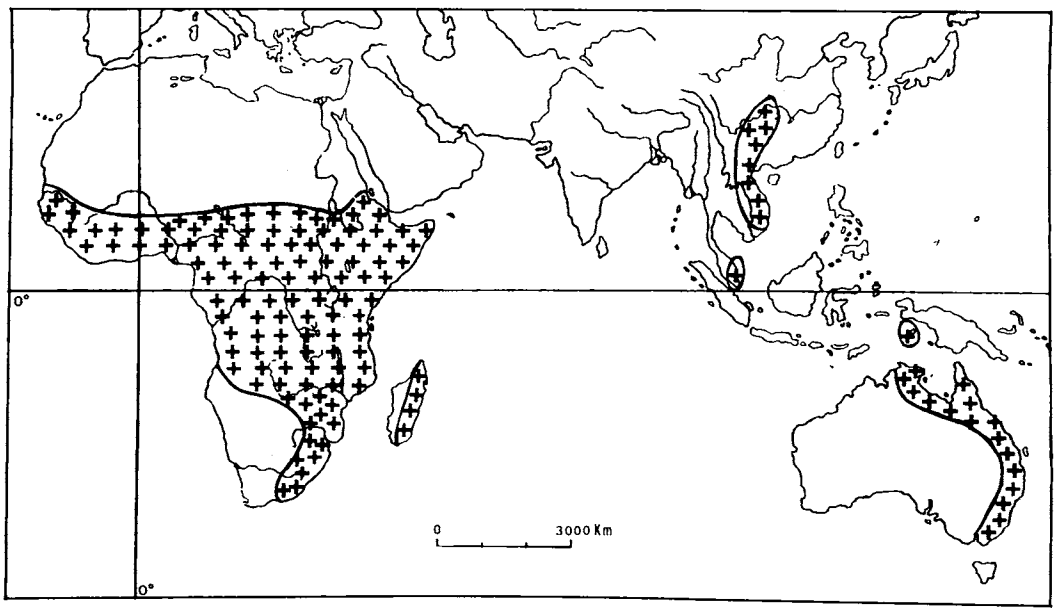


Fig. 4, geographical distribution of Tetralobina.

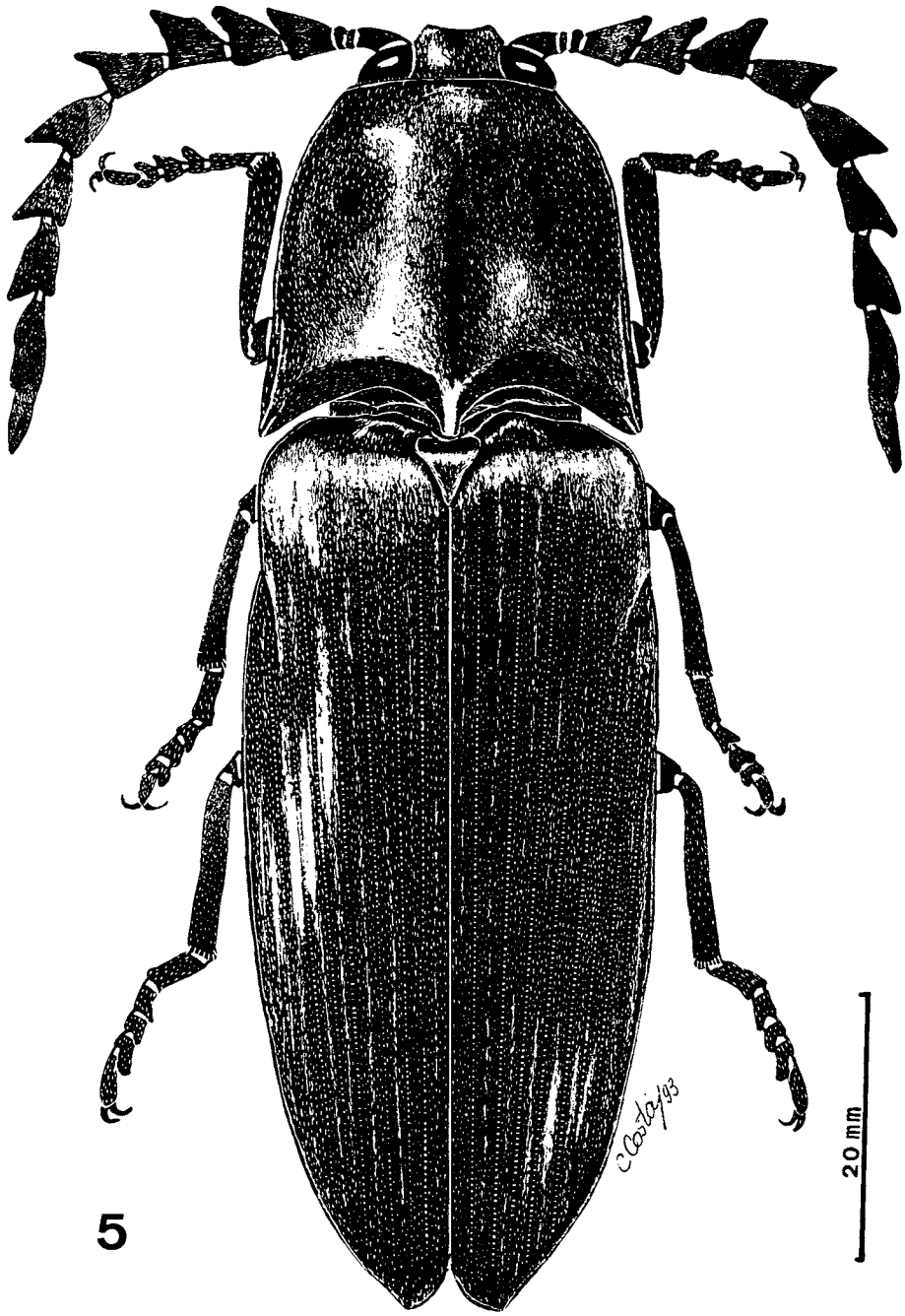


Fig. 5, habitus: *Piezophyllus macrocerus*.

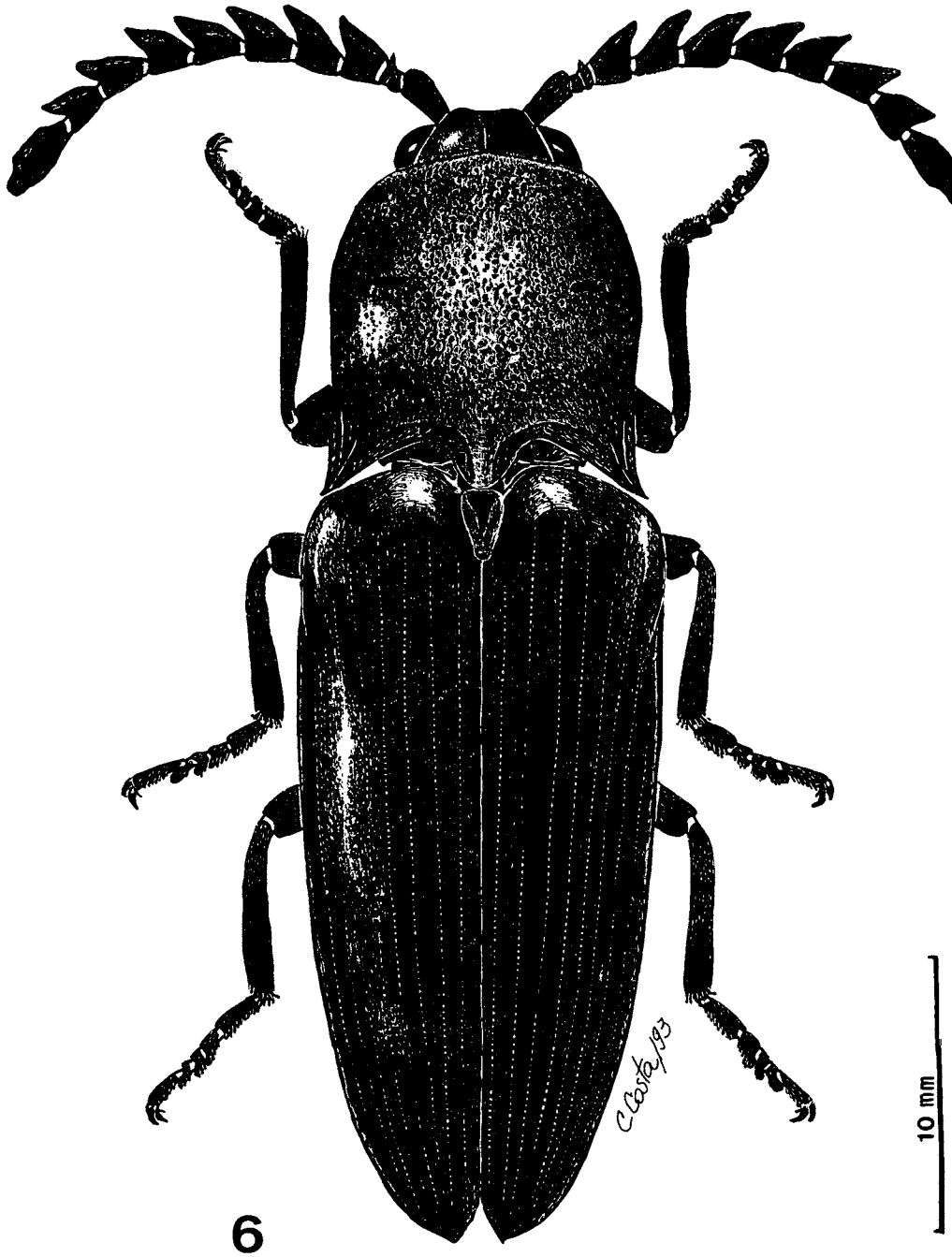
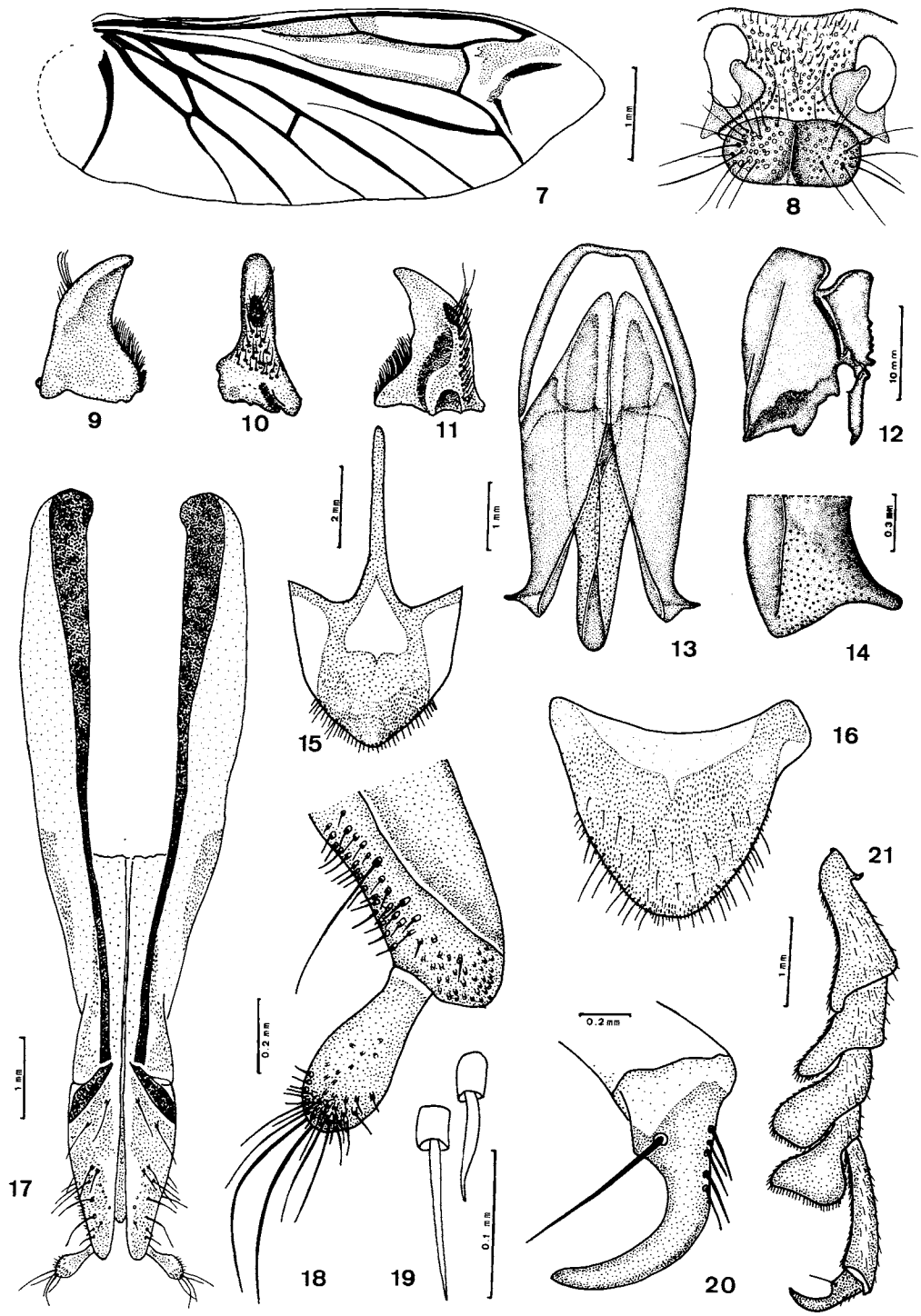
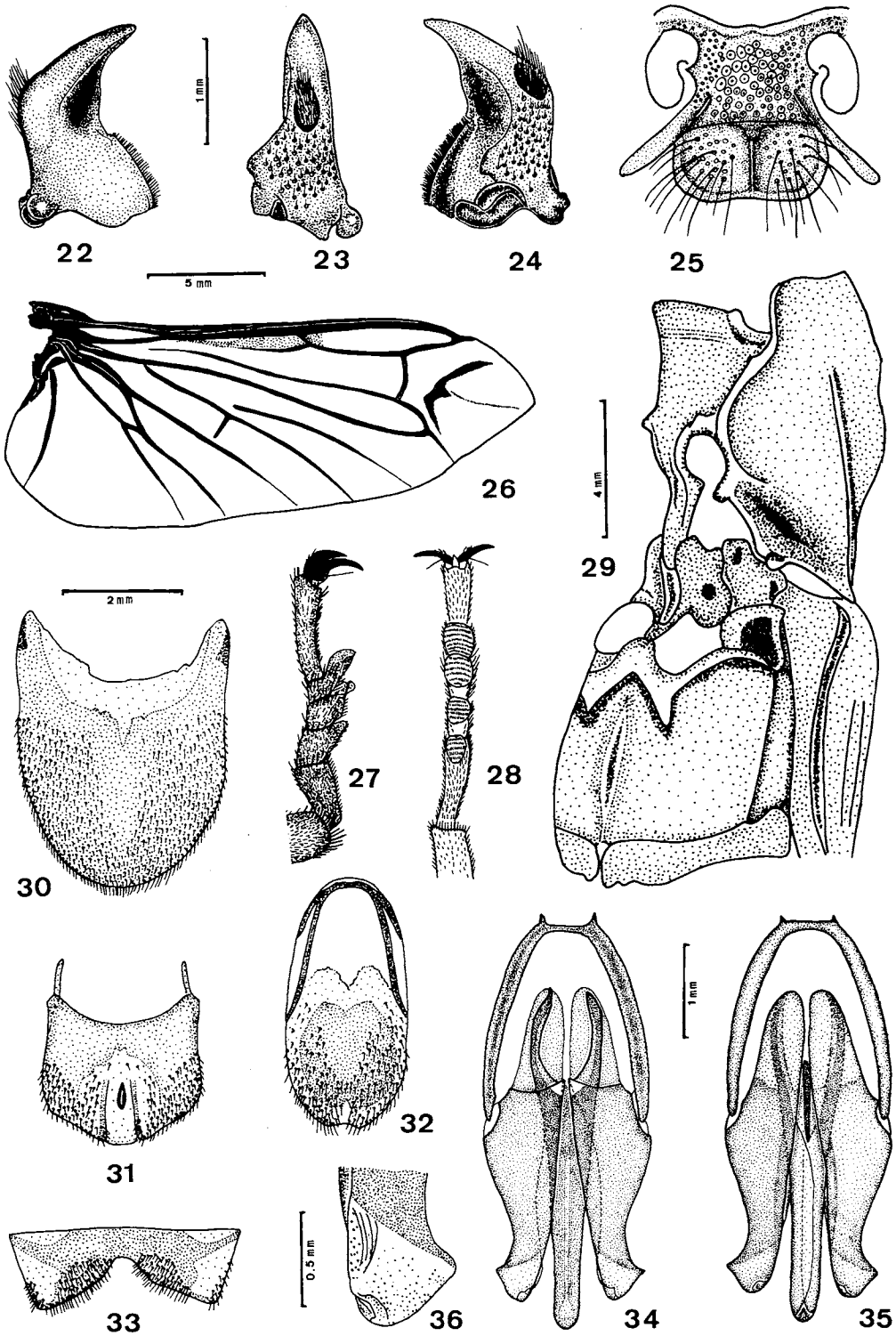


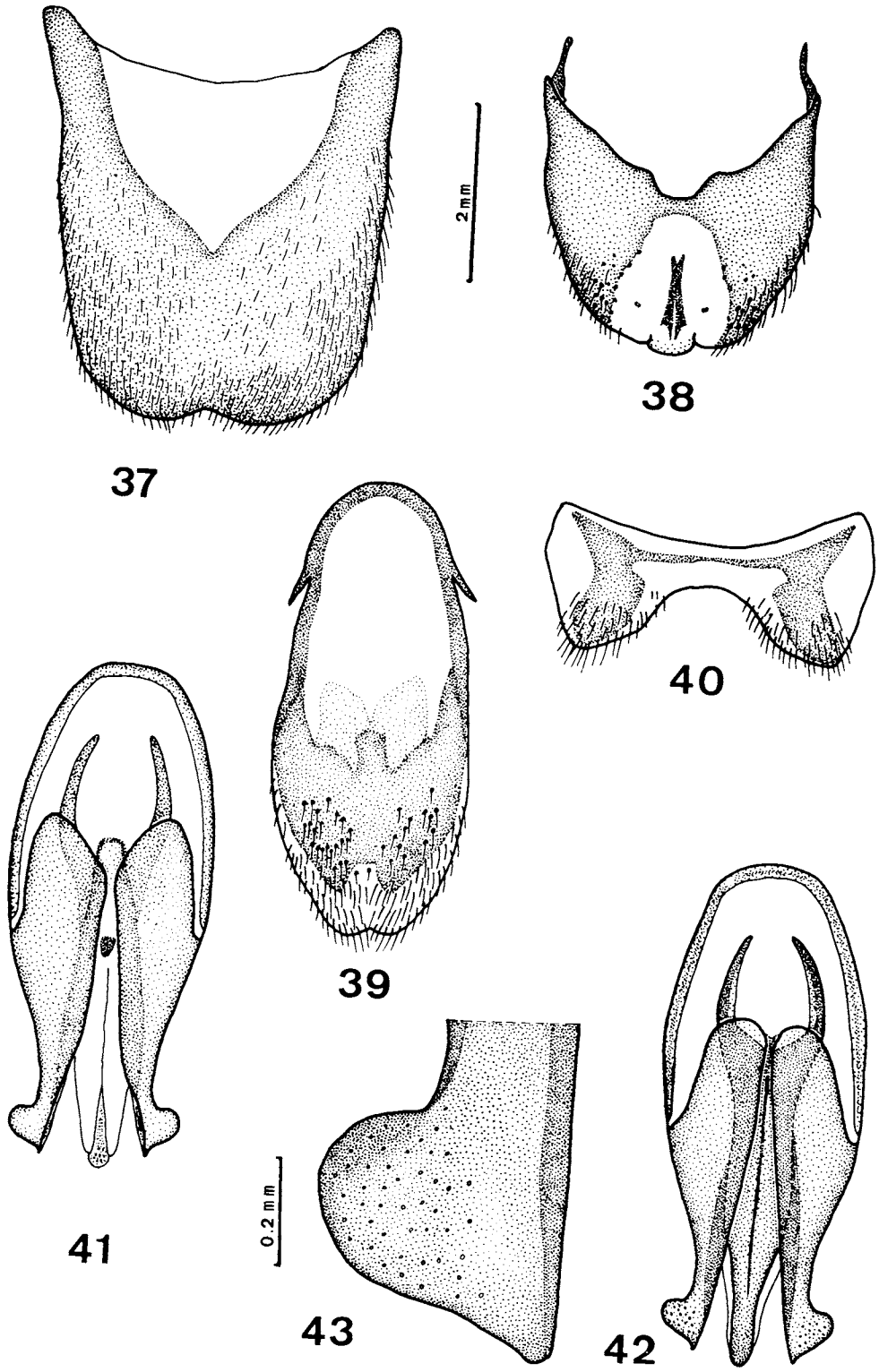
Fig. 6, habitus: *P. benitensis*.



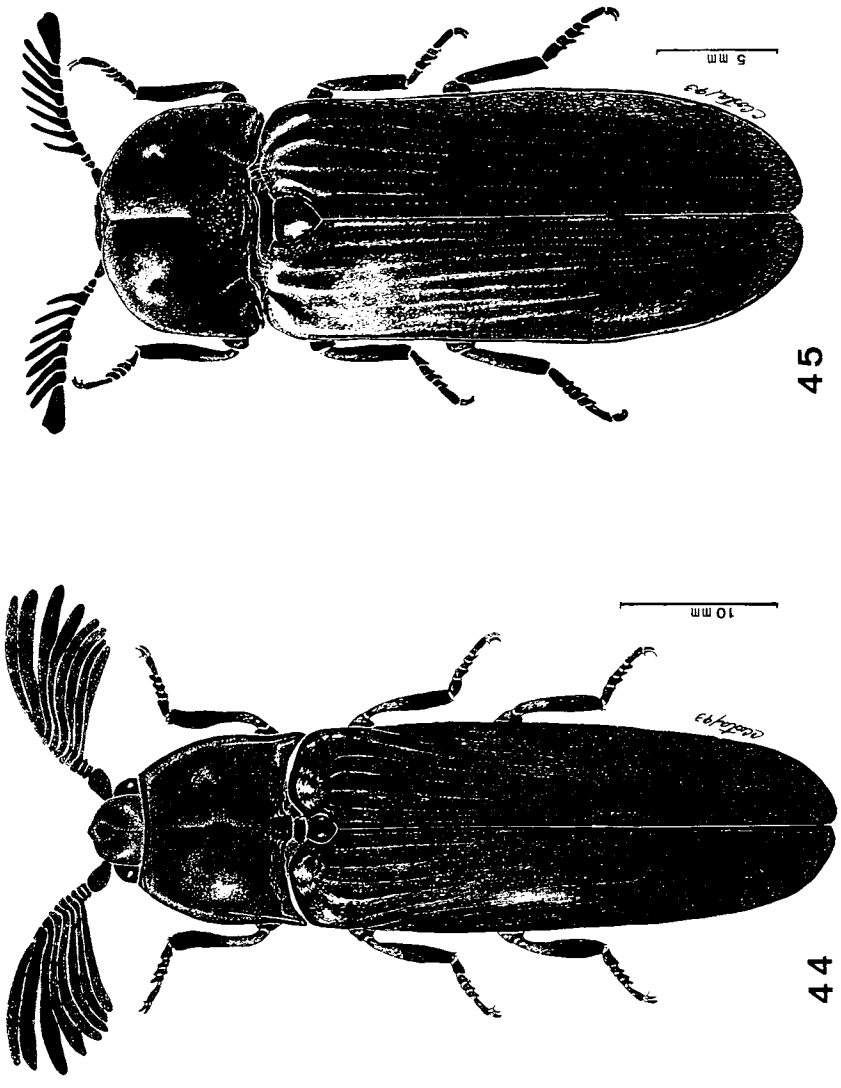
Figs. 7-21; *Piezophyllus macrocerus*. ♂ : 7, hind wing; 8, labrum and nasal plate; 9-11, mandible (ventral, lateral, dorsal); 12, prothorax (lateral); 13, aedeagus (dorsal); 14, parameres apex. ♀ : 15, urosternite VIII; 16, urotergite VIII; 17, ovipositor and baculi; 18, stylus and coxite apex; 19, setae of stylus; 20, claw; 21, tarsal segments. Figs. 7, 12; 8-11; 15, 16, respectively to the same scale.



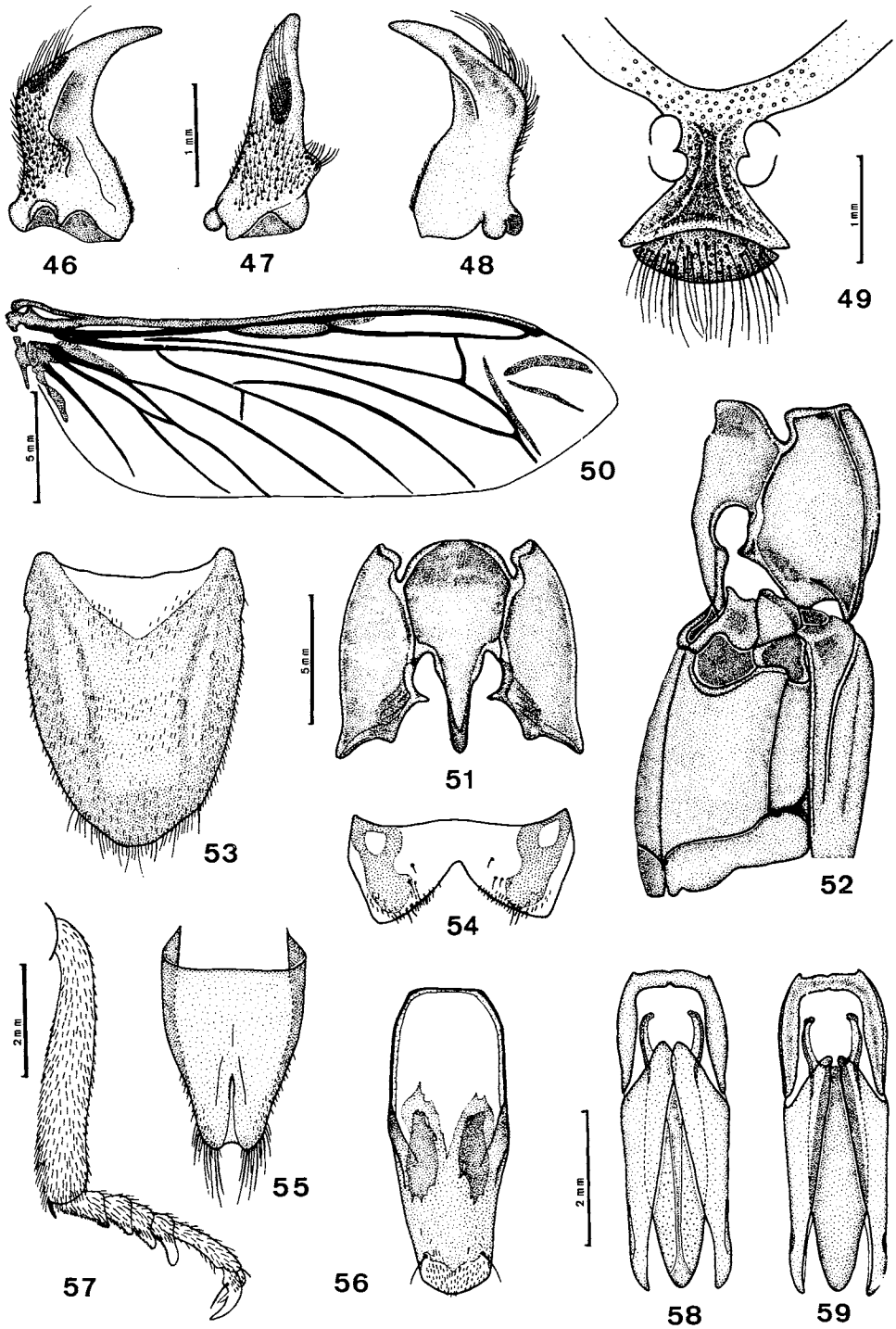
Figs. 22-36; *Piezophyllus benitensis*. ♂ : 22-24, mandible (ventral, lateral, dorsal); 25, labrum and nasal plate; 26, hind wing; 27, 28, tarsal segments (lateral, ventral); 29, pro-, meso- and metathorax (ventrolateral); 30, urotergite VIII; 31, urotergites IX, X; 32, urosternite IX; 33, urosternite VIII; 34, 35, aedeagus (ventral, dorsal); 36, paramere apex. The figs 22-24; 25, 34, 35; 27, 28, 30-33, respectively to the same scale.



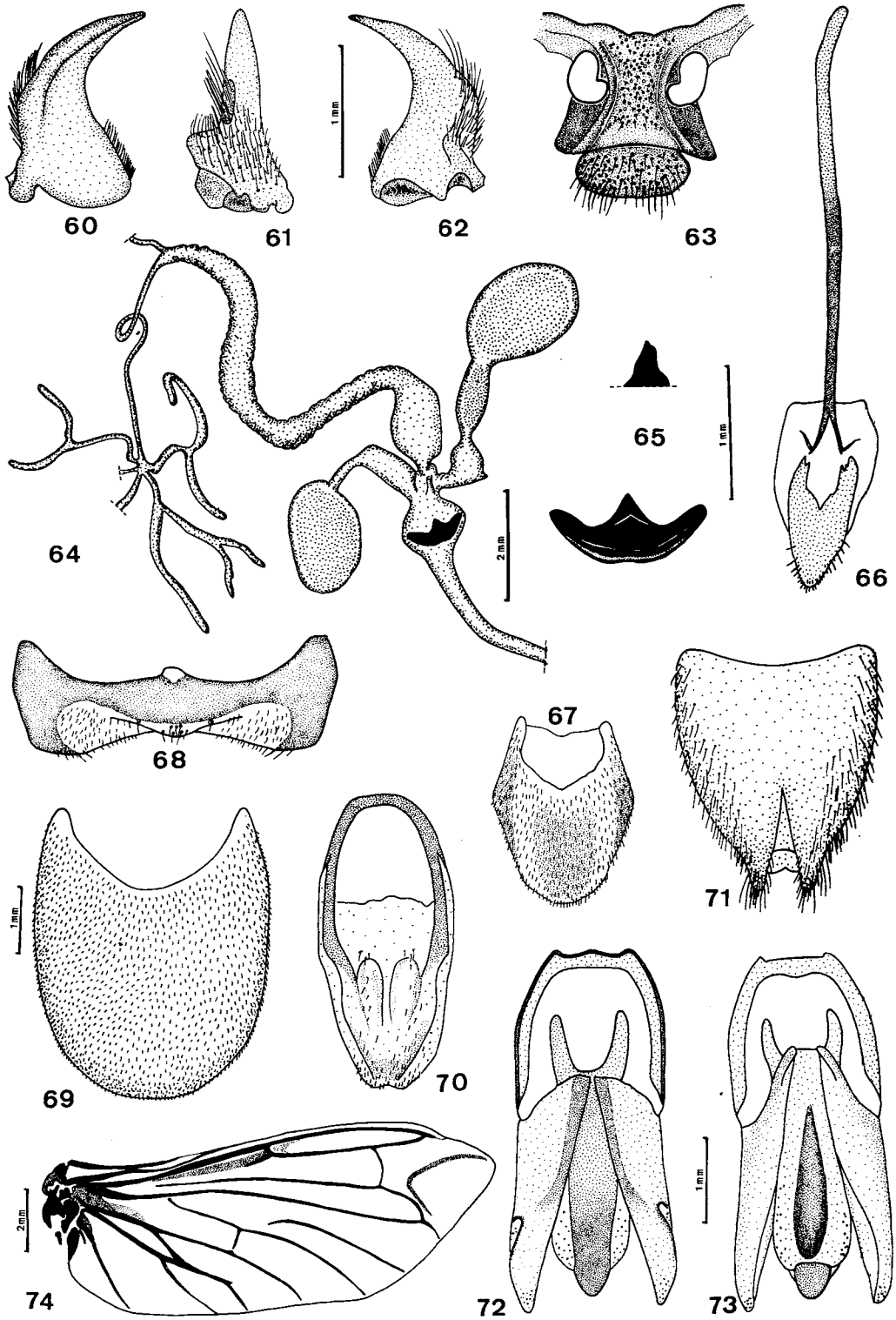
Figs. 37-43; *Piezophylkis borneensis*. ♂ : 37, urotergite VIII; 38, urotergites IX, X; 39, urosternite IX; 40, urosternite VIII; 41, 42, aedeagus (dorsal, ventral); 43, paramere apex. Figs. 37-42 to the same scale.



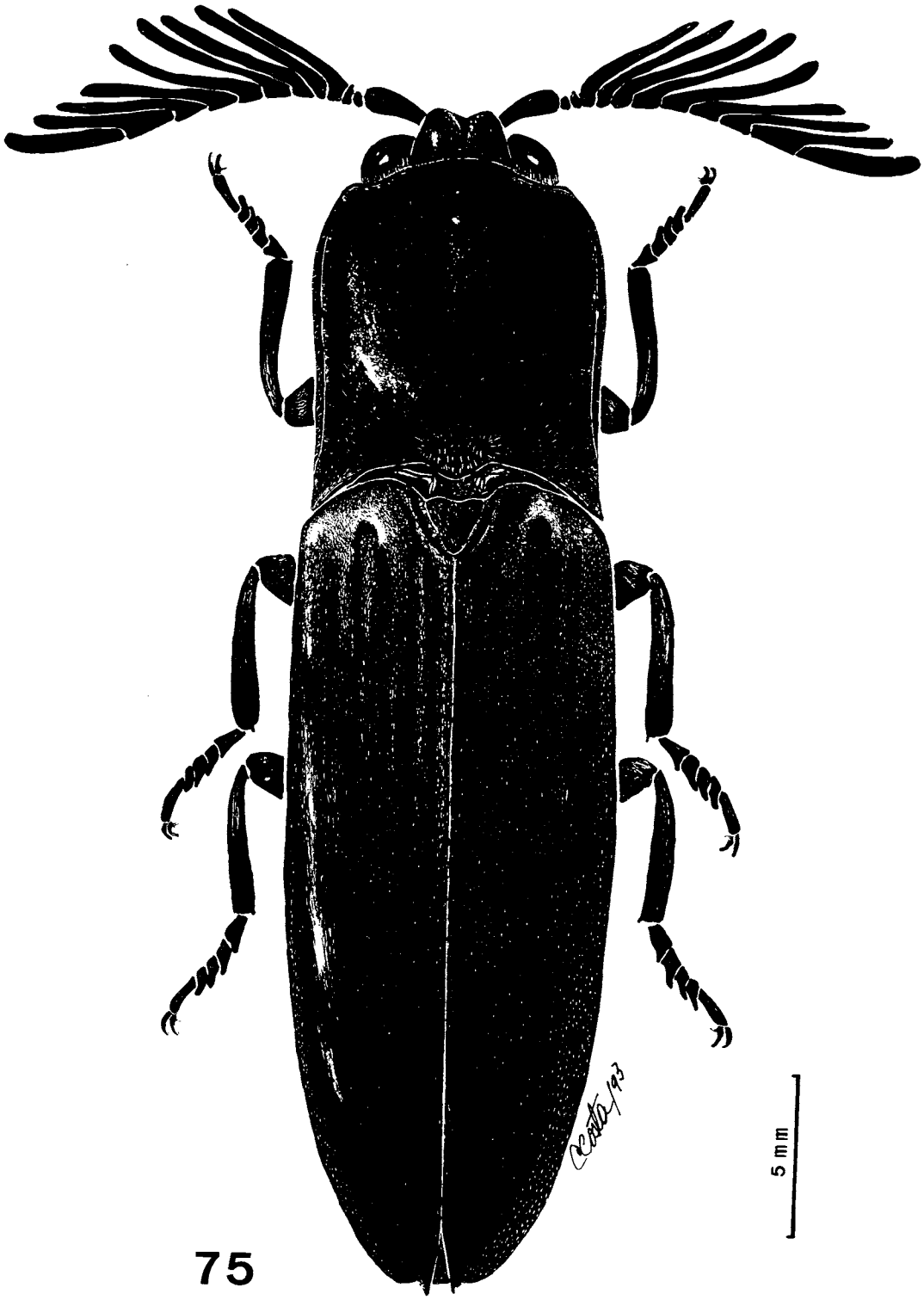
Figs. 44, 45; habitus: *Paratetralobus hemirhipoides*; *Neotetralobus africanus*.



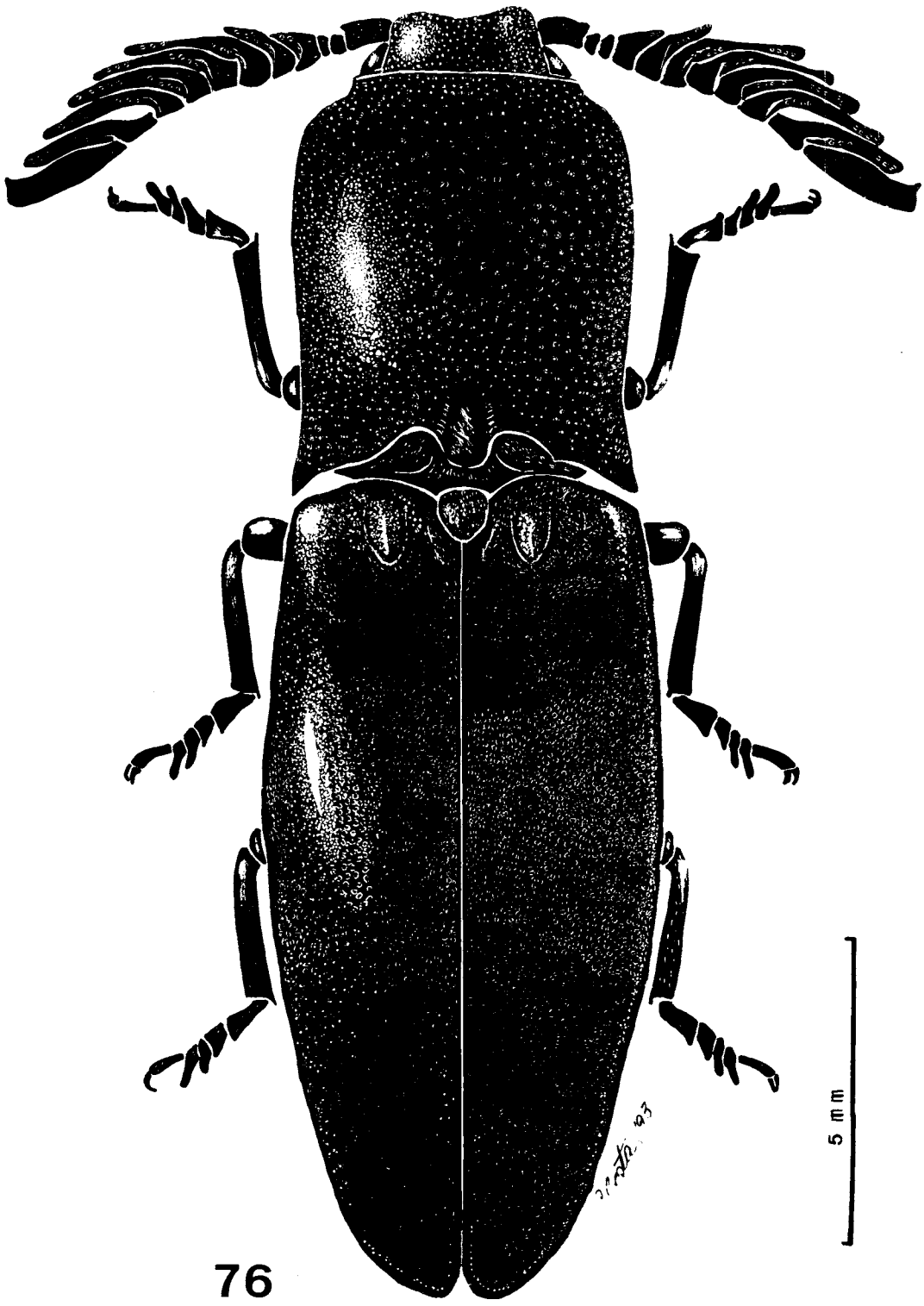
Figs. 46-59; *Paratetralobus hemirhipoides*. ♂ : 46-48, mandible (dorsal, lateral, ventral); 49, labrum and nasal plate; 50, hind wing; 51, prosternum and hypomera; 52, pro-, meso- and metathorax (ventrolateral); 53, urotergite VIII; 54, urosternite VIII; 55, urotergites IX-X; 56, urosternite IX; 57, tibia and tarsal segments (lateral); 58, 59, aedeagus (dorsal, ventral). Figs. 46-48; 51, 52; 53-56, 58, 59, respectively to the same scale.



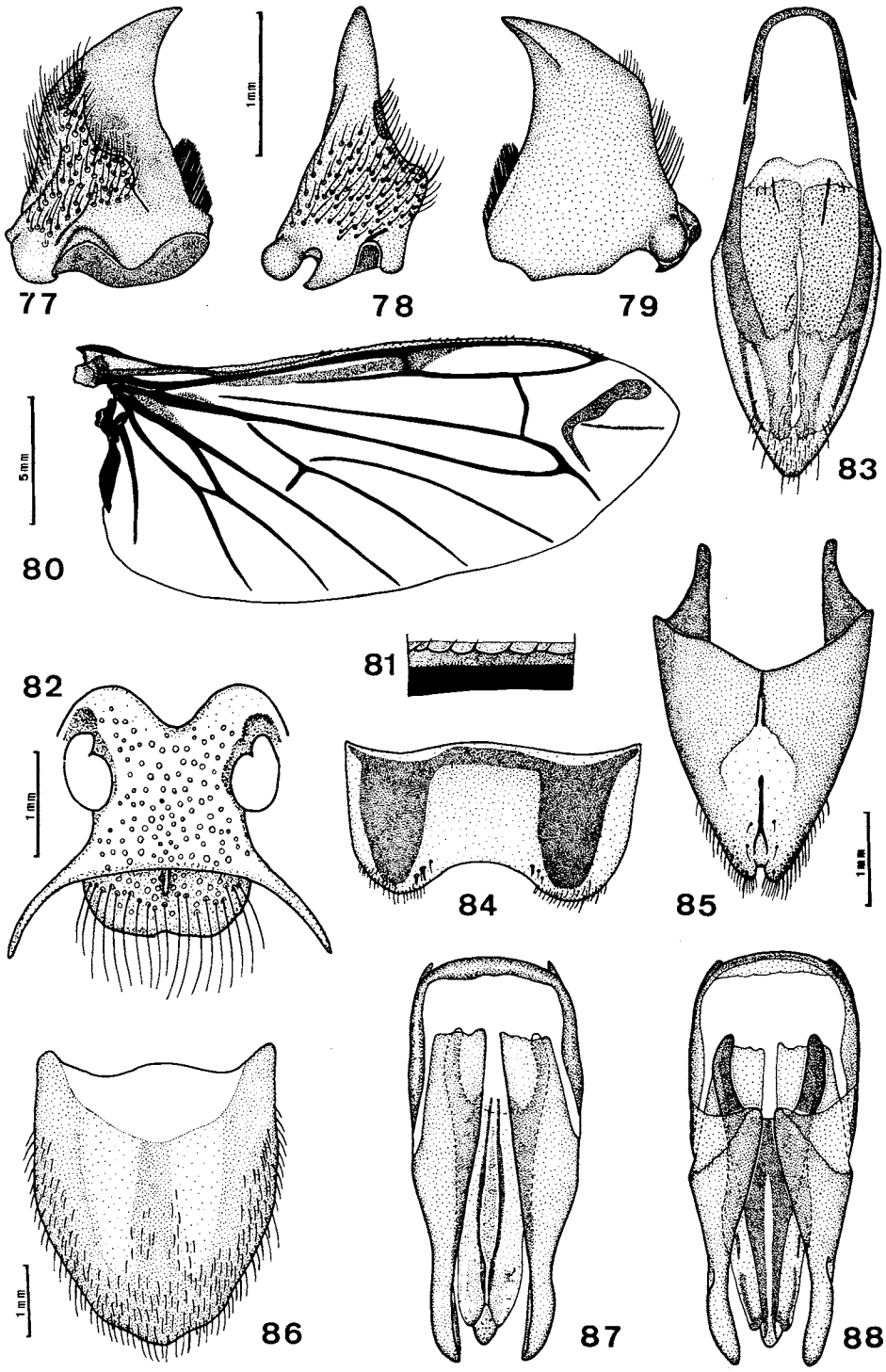
Figs. 60-74; *Neotetralobus africanus*. ♂ : 60-62, mandible (ventral, lateral, dorsal); 63, labrum and nasal plate; 68, urosternite VIII; 69, urotergite VIII; 70, urosternite IX; 71, urotergites IX, X; 72, 73, aedeagus (ventral, dorsal); 74, hind wing. ♀ : 64, genitalia; 65, omega-like sclerite; 66, urosternite VIII; 67, urotergite VIII. Figs. 60-62; 63, 68, 71-73; 66, 67, 74, respectively to the same scale.



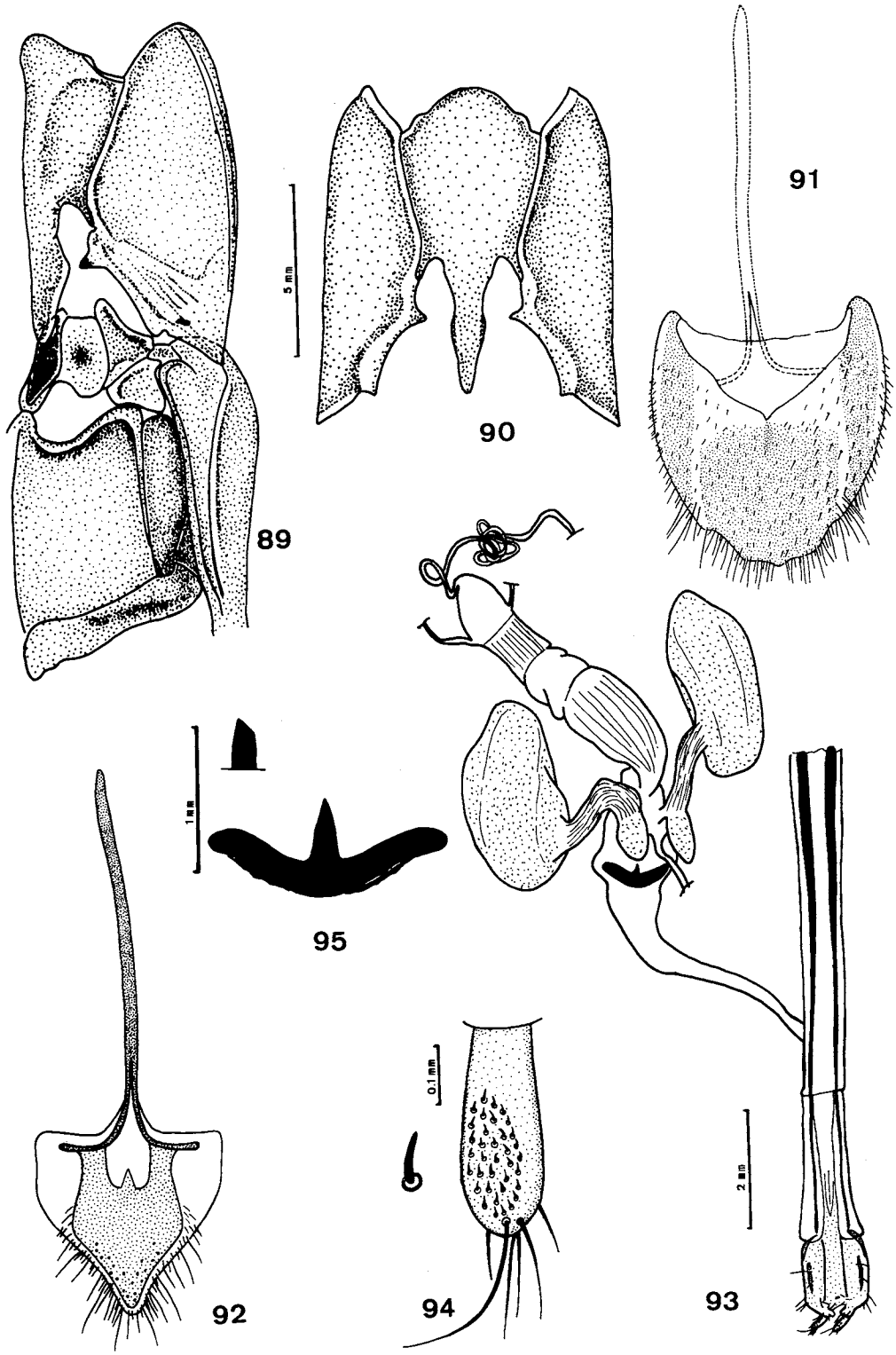
Figs. 75, habitus: *Pseudotetralobus dohrni*.



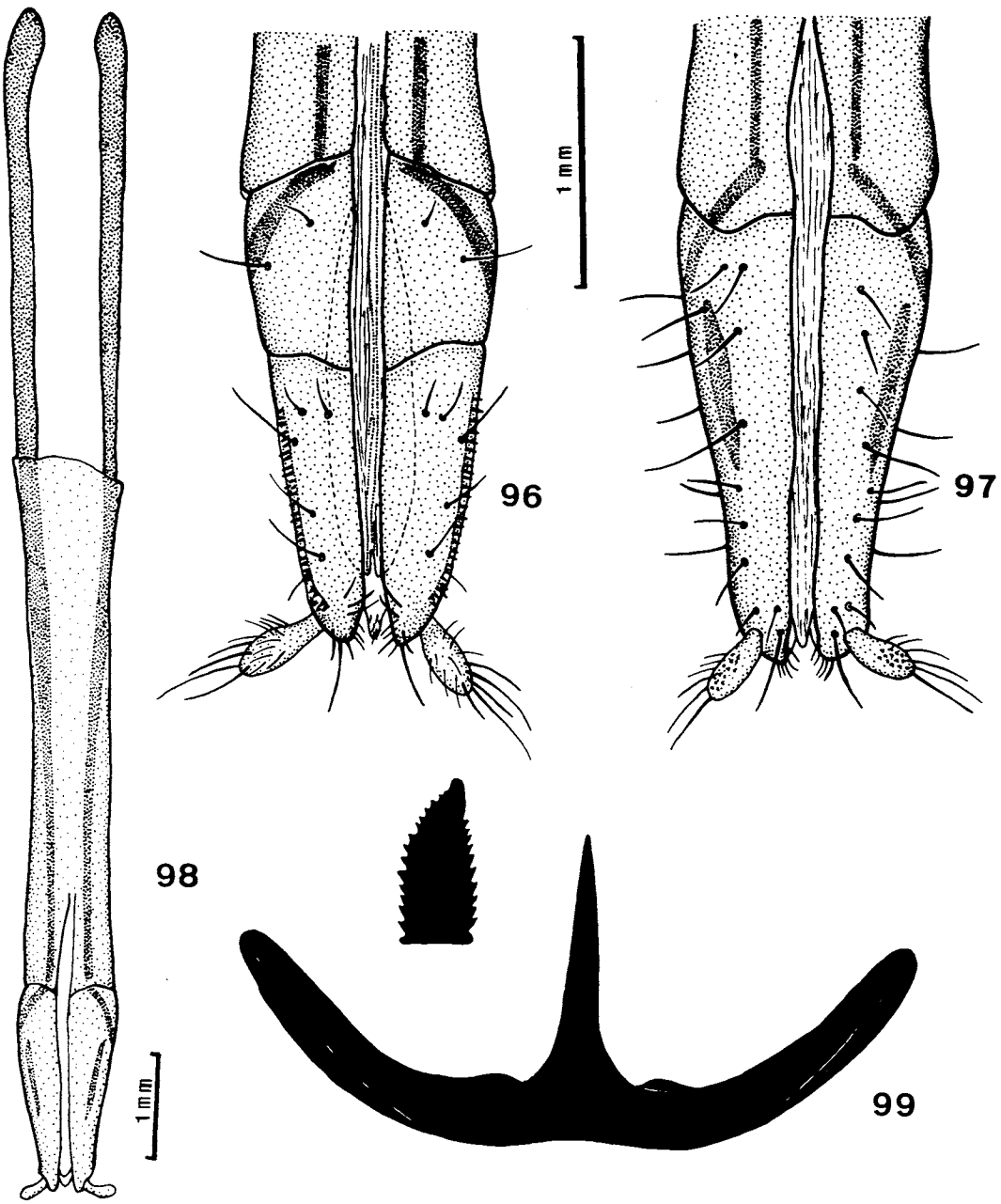
Figs. 76, habitus: *Pseudalaus dohrni*.



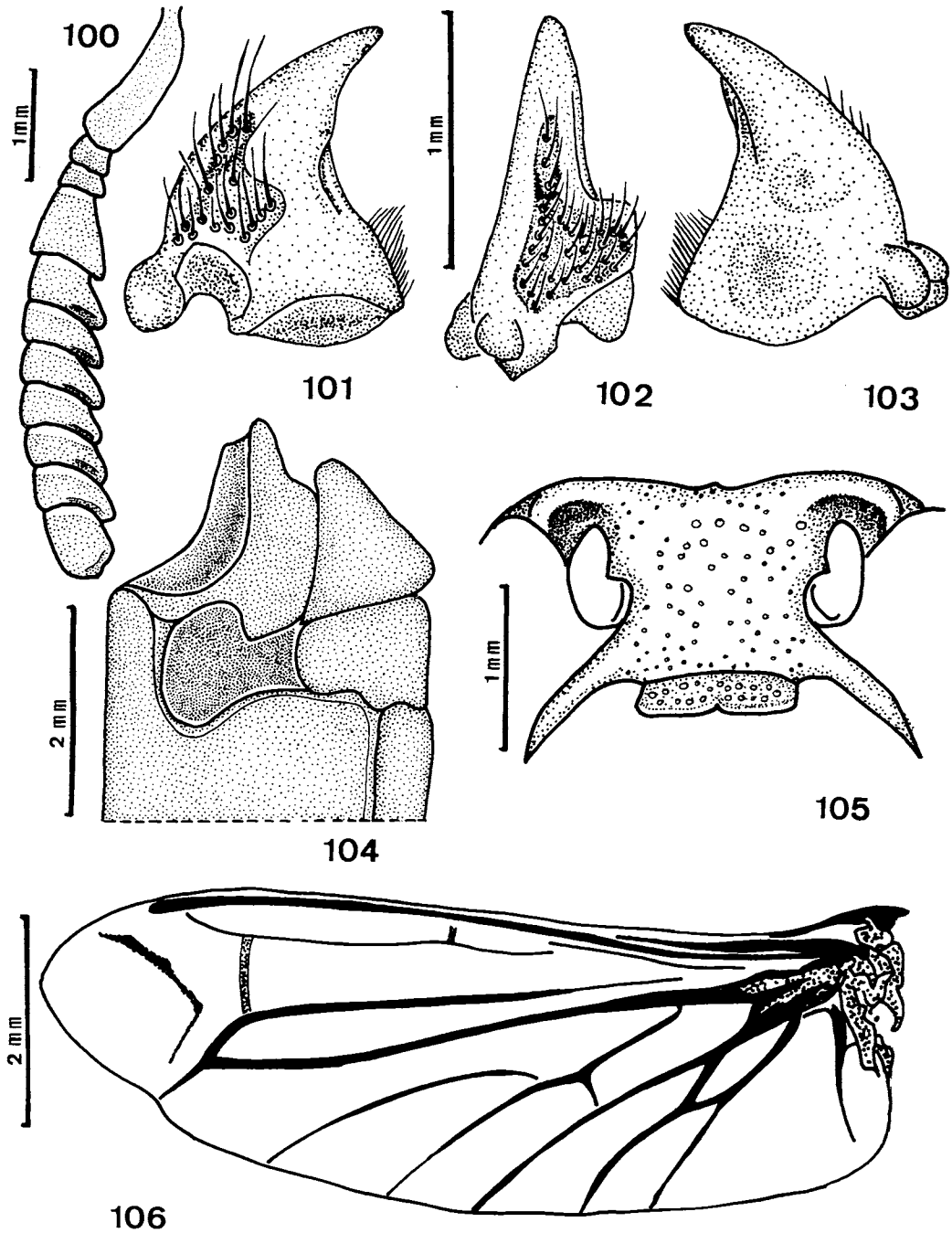
Figs. 77-88; *Pseudotetralobus dohrni*. ♂ : 77-79, mandible (dorsal, lateral, ventral); 80, hind wing; 81, spines near costal margin of hind wing; 82, labrum and nasal plate; 83, urosternite IX; 84, urosternite VIII; 85, urotergites IX, X; 86, urotergite VIIII; 87, 88, aedeagus (dorsal, ventral). Figs. 77-79; 82, 87, 88; 83-85, respectively to the same scale.



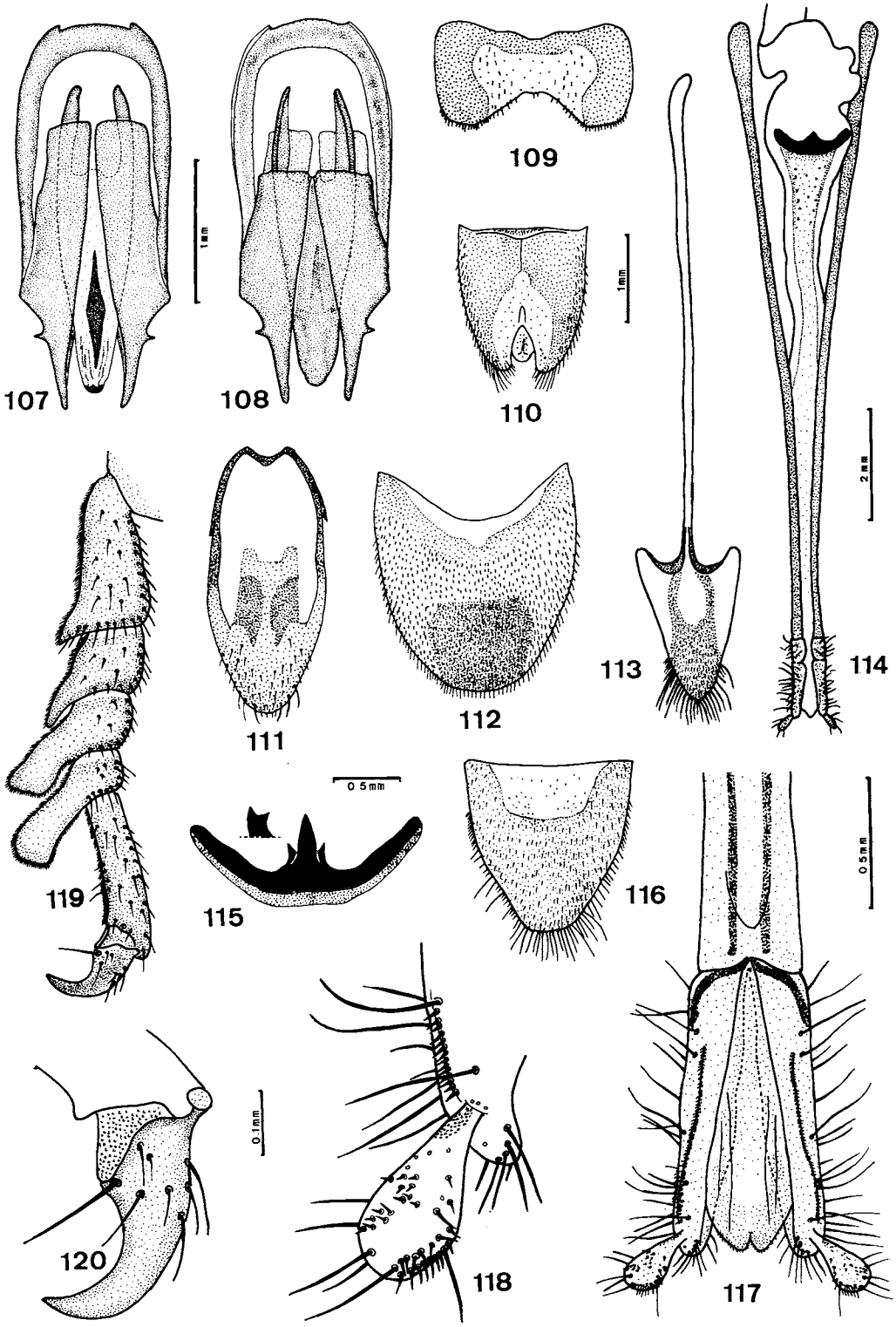
Figs. 89-95; *Pseudoteiralobus dohrni*. ♂ : 89, pro-, meso- and metathorax (ventrolateral); 90, prosternum and hypomera; ♀ : 91, urotergite VIII; 92, urosternite VIII; 93, genitalia; 94, stylus; 95, omega-like sclerite. Figs. 89, 90; 91-93, respectively to the same scale.



Figs. 96-99; *Pseudotetralobus australasiae*. ♀ : 96, 97, coxites (dorsal, ventral); 98, ovipositor and baculi; 99, omega-like sclerite. Figs. 96-99 to the same scale.

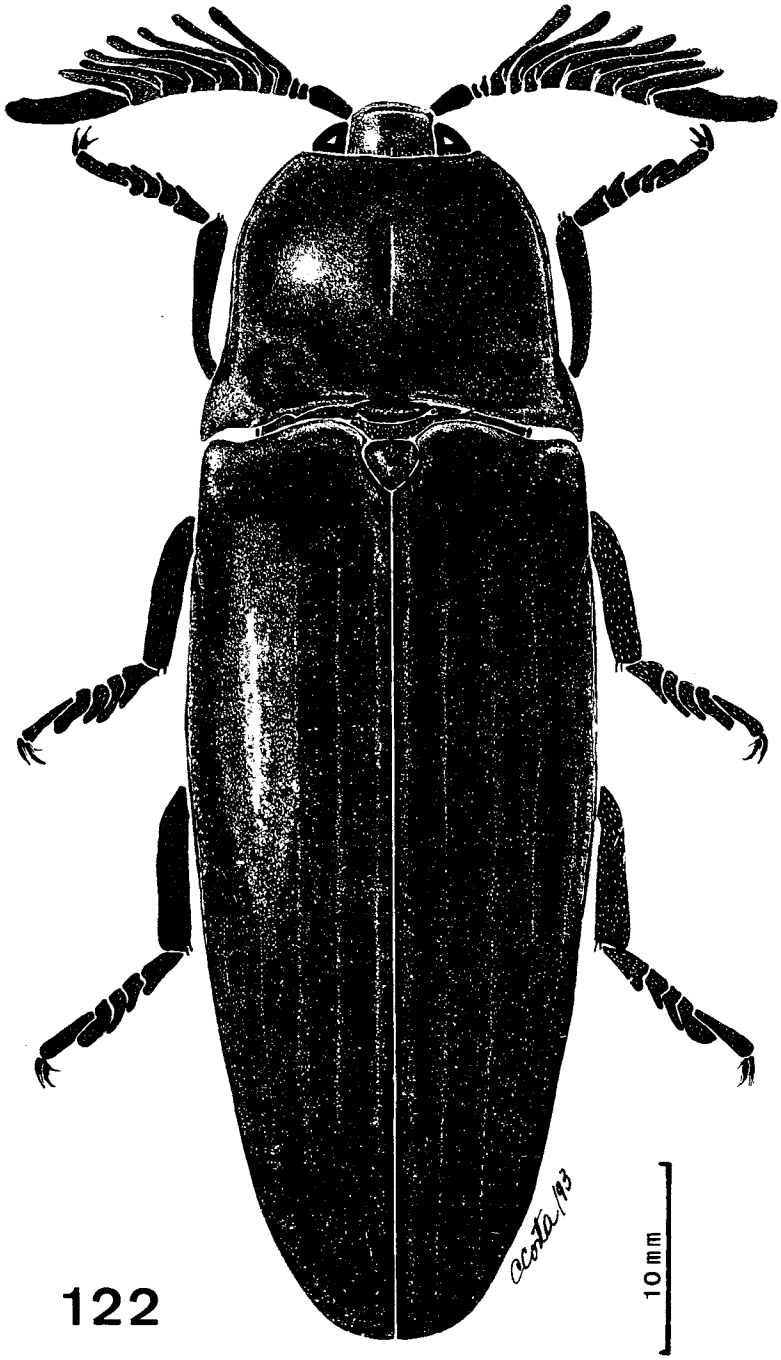


Figs. 100-106; *Pseudalaus dohrni*. ♀ : 100, antenna. ♂ : 101-103, mandible (dorsal, lateral, ventral); 104, mesosternum and anterior region of metasternum; 105, labrum and nasal plate; 106, hind wing. Figs. 101-103 to the same scale.

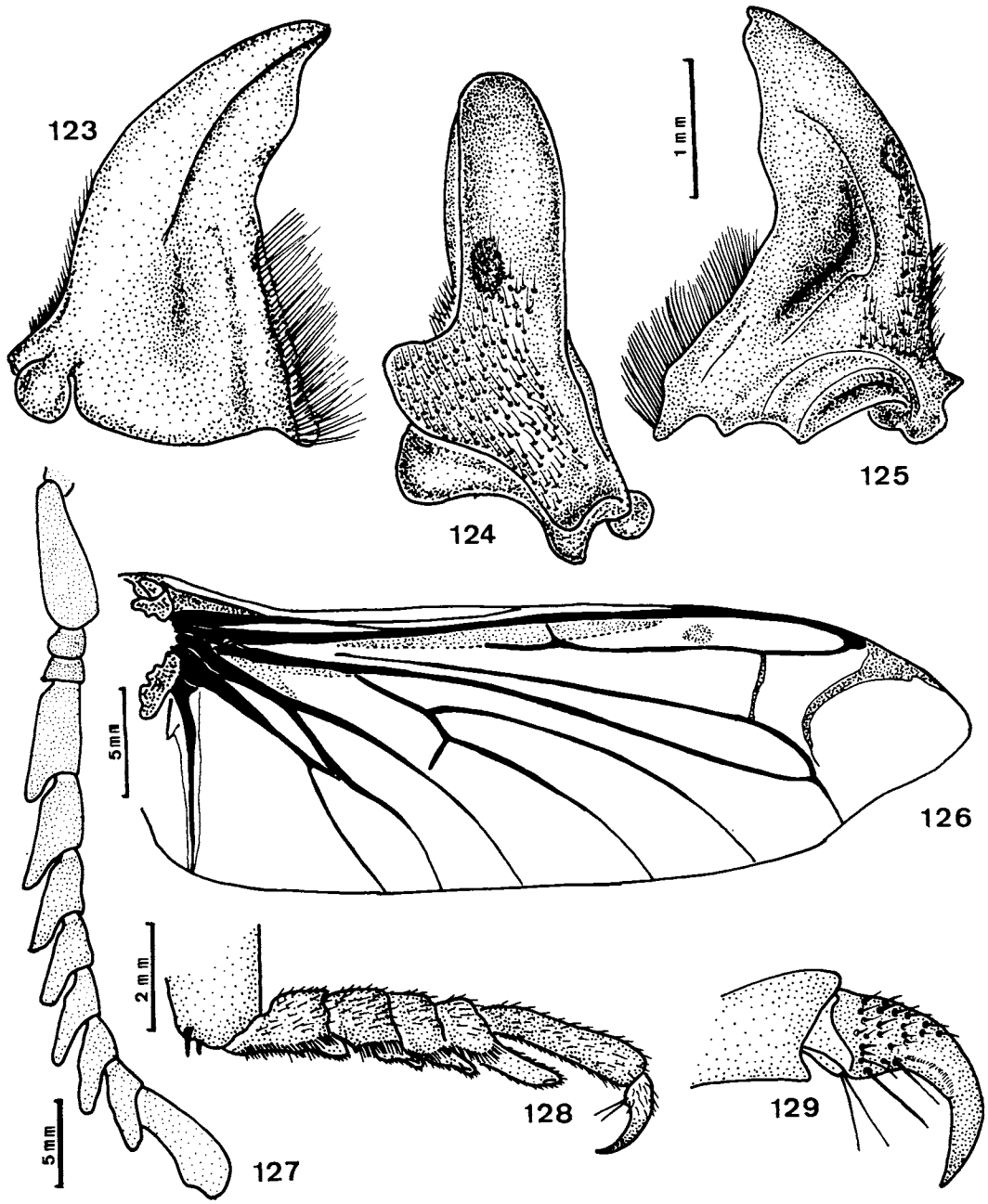


Figs. 107-120; *Pseudalaus dohrni*. ♂ : 107-108, aedeagus (dorsal, ventral); 109, urosternite VIII; 110 urotergites IX, X; 111, urosternite IX; 112, urotergite VIII; 119, tarsal segments; 120, claw. ♀ : 113, urosternite VIII; 114, genitalia; 115, omega-like sclerite; 116, urotergite VIII; 117, coxites; 118, stylus. Figs 107, 108; 109-112; 113, 114, 116; 118, 120; 117, 117, respectively, to the same scale.

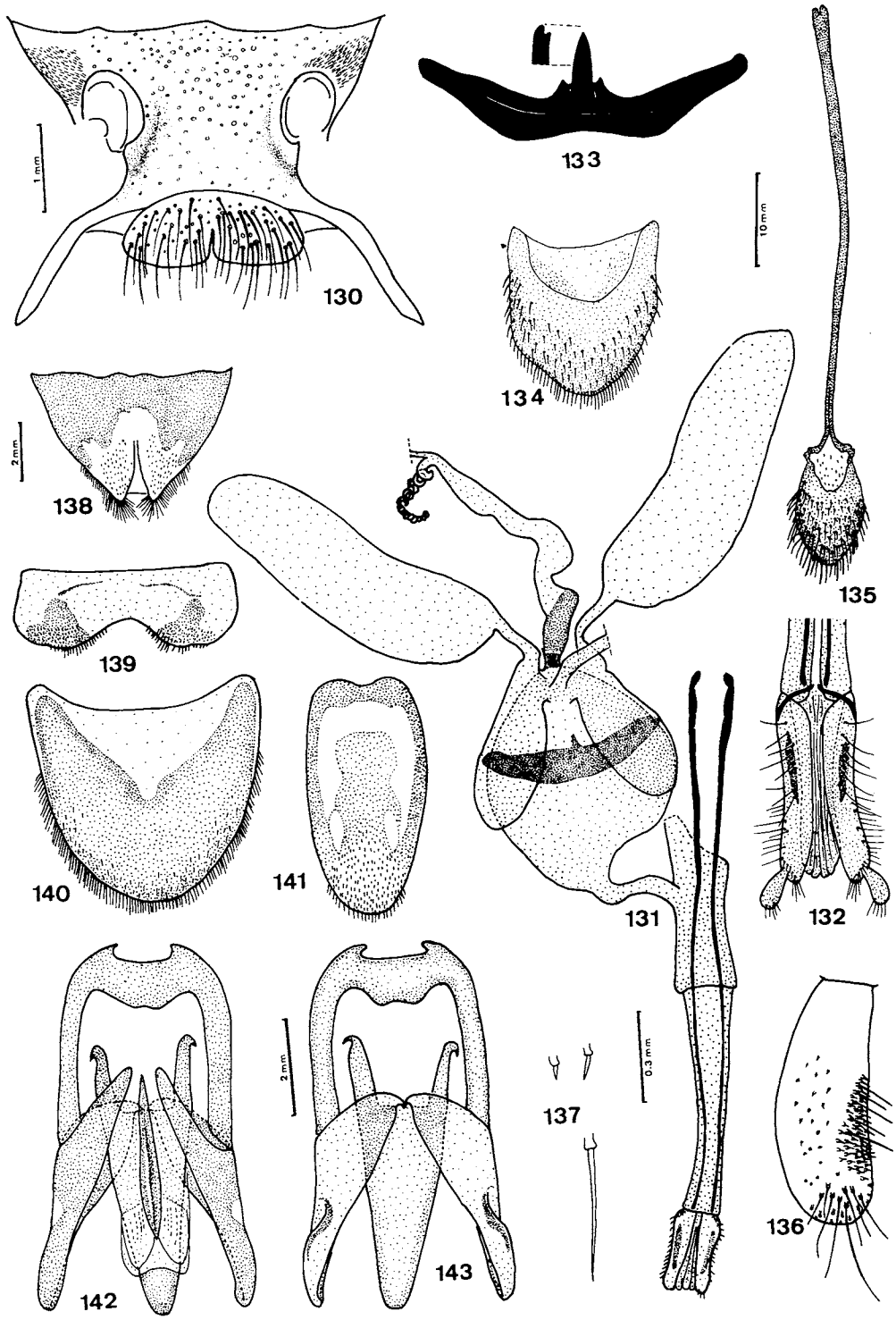
Figs. 121, habitus: *Tetralobus flabellicornis*.



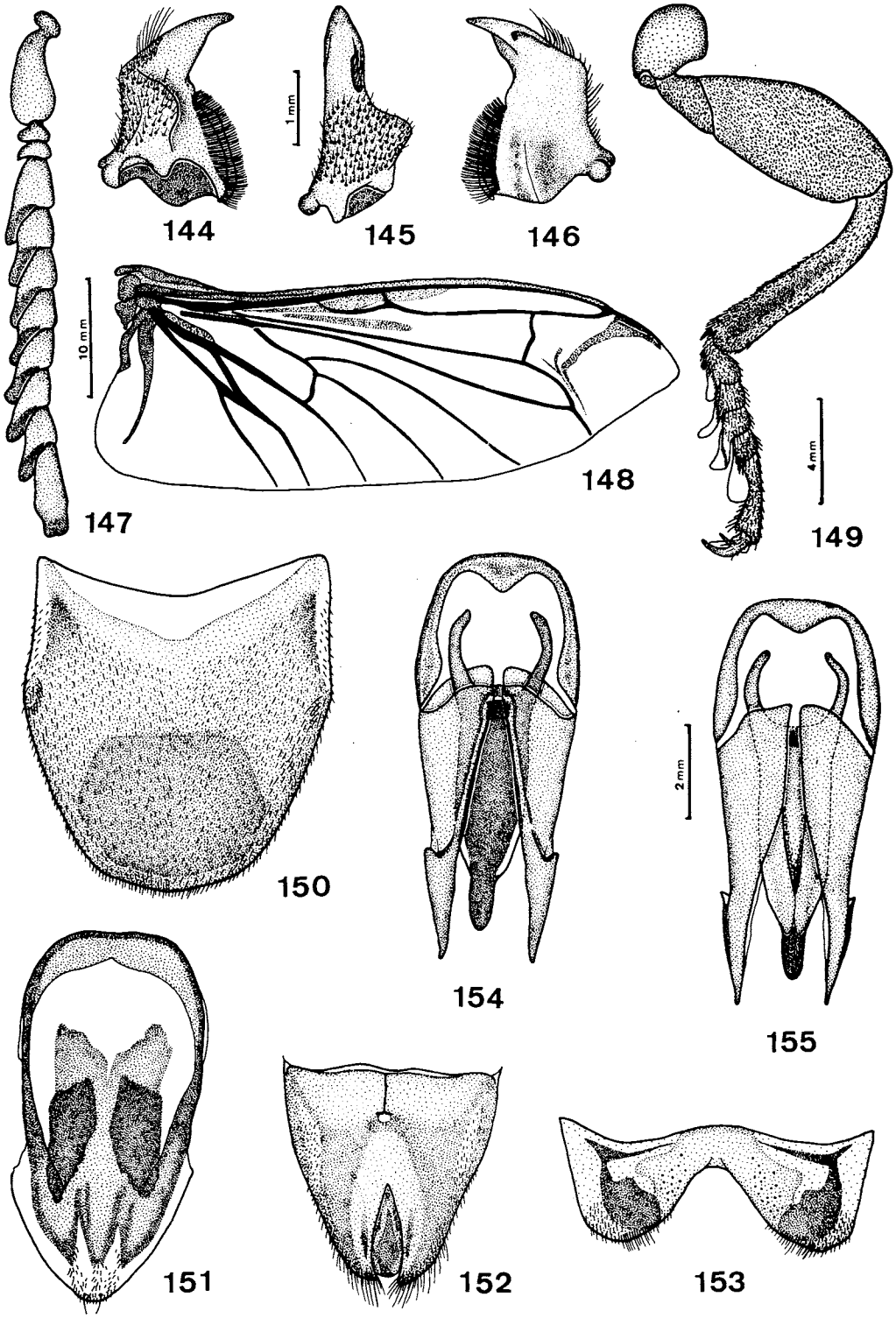
Figs. 122, habitus: *Sinelater perroti*.



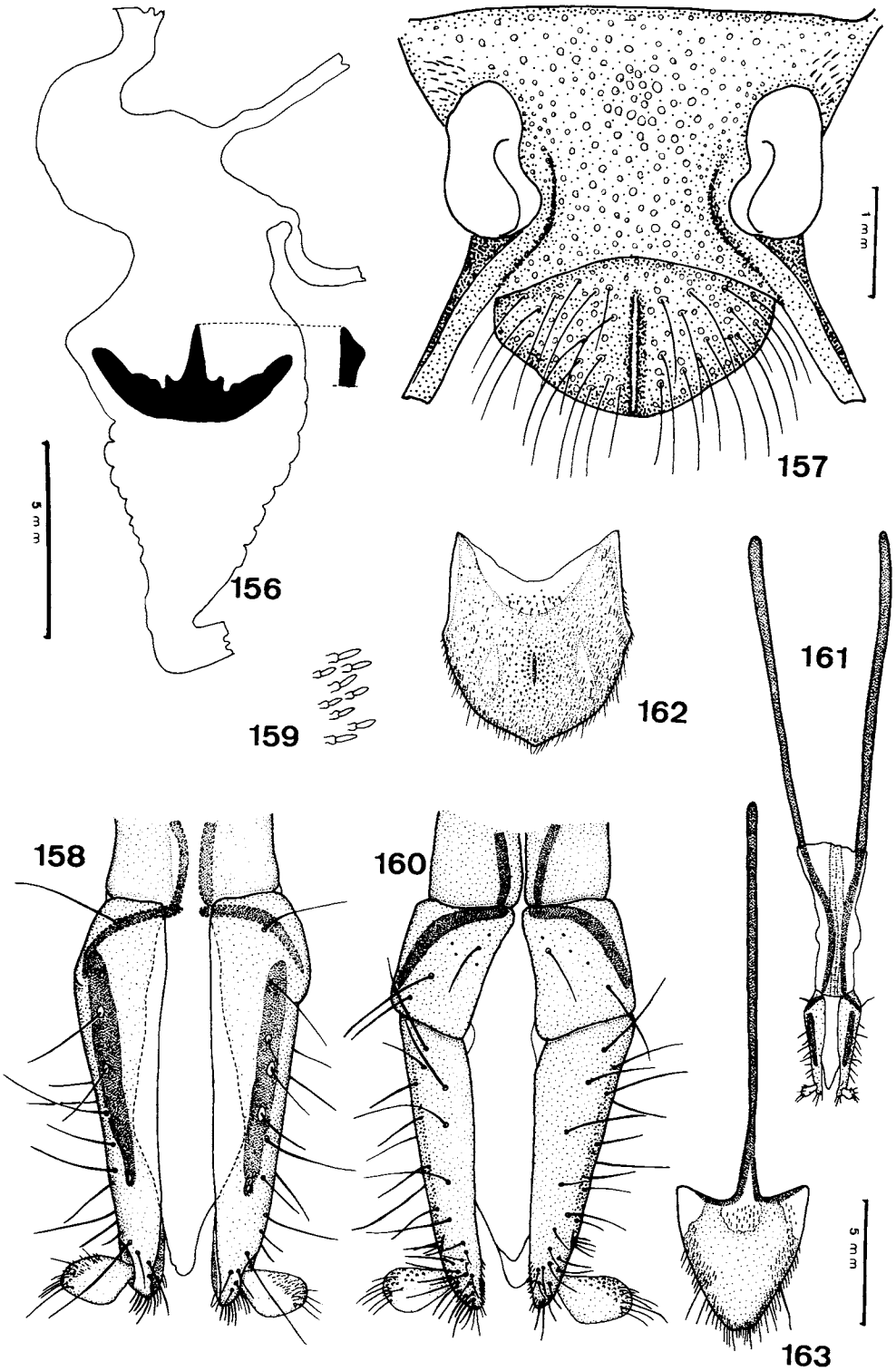
Figs. 123-129; *Tetralobus flabellicornis*. ♂ : 123-125, mandible (ventral, lateral, dorsal); 126, hind wing; 128, apex of tibia and tarsal segments; 129, claw. ♀ : 127, antenna. Figs. 123-125, 129, to the same scale.



Figs. 130-143; *Tetralobus flabellicornis*. ♂ : 130, labrum and nasal plate; 138, urotergites IX, X; 139, urosternite VIII; 140, urotergite VIII; 141, urosternite IX; 142, 143, aedeagus (dorsal, ventral). ♀ : 131, genitalia; 132, coxites; 133, omega-like sclerite; 134, urotergite VIII; 135, urosternite VIII; 136, stylus; 137, setae of stylus. Figs 131, 134, 135; 132, 142, 143; 133, 136; 138-141, respectively to the same scale.



Figs. 144-155; *Sinelater perroti*. ♂ : 144-146, mandible (dorsal, lateral, ventral); 148, hind wing; 149, metathoracic leg; 150, urotergite VIII; 151, urosternite IX; 152, urotergites IX, X; 153, urosternite VIII: 154, 155, aedeagus (ventral, dorsal). ♀ : 147, antenna. Figs. 144-146; 147, 149; 150-153, respecively to the same scale.



Figs. 156-163; *Sinelater perroti*. ♂ : 157, labrum and nasal plate. ♀ : 156, bursa copulatrix; 158, 160, coxites (ventral, dorsal); 159, setae of coxites; 161, ovipositor and baculi; 162, urotergite VIII; 163, urosternite VIII. Figs. 157, 158, 160; 161, 162, 163, respectively to the same scale.

Median lobe wide, abruptly narrow near the apex, dorsal region membranous like a sheath with a large longitudinal median sclerite; furcae longer than parameres.

Female genitalia. Urotergite VIII (Fig. 162) membranous basally; distal half tapered apicad; covered by short setae, and with scattered long setae on distal margin. Urosternite VIII (Fig. 163) sub-triangular, partially membranous; a marginal band of setae, the distal ones longer; basal sclerite approximately 2.7 times longer than distal area. Ovipositor (Figs. 158, 160-161) with styli; baculus 4.3 times longer than coxites; coxites with three or four rows of pedunculate microsetae (Fig. 159) on ventral lateral margins; simple long setae, dorsal and ventral; stylus with distal long setae and several ventral pedunculate short setae. Omega-like sclerite (Fig. 156) of anterior bursa copulatrix with lateral arms curved and central arm sharp, with one small tooth on each side, apex obliquely truncate.

Material examined. South Vietnam. (Tonkin), N.O. de Bao-Loc, Dr. Battarel 1897-1898, ex-col. Oberthur, 1 ♂, 1 ♀ (MNHN).

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