

## **BOREIOGLYCASPIS AND SPONDYLIASPIDINE CLASSIFICATION (HOMOPTERA: PSYLLOIDEA)**

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*ABSTRACT.* - *Boreioglycaspis* is revised to include 16 species in the Australian and Oriental Regions. The subgenus is raised to generic rank, five new species are described from East Malaysia: Sabah, and one species is synonymised. A key to species is provided for adults, and characters are discussed which may be useful in species definition in other spondyliaspidine genera. Host plant and biogeographical relationships are briefly discussed. The species develop on *Melaleuca*, *Lophostemon*, *Tristaniopsis*, *Eugenia* (Myrtaceae) and *Sonneratia* (Sonneratiaceae). It is suggested that *Boreioglycaspis* may have originated in tropical Australia/Australasia from where it diversified into subtropical Australia and Laurasian portions of Southeast Asia. There is no congruence between the phylogeny of *Boreioglycaspis* and that of its hosts. Speciation in *Boreioglycaspis* as a response to host diversification must be excluded. The Spondyliaspidini (=Ctenarytainini syn. n.) is redefined based on a series of autapomorphies, and a list of the constituent genera is provided. It is concluded that the tribe forms the sister-group of the Pachypsyllini, the only other tribal member of the Spondyliaspidinae.

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### INTRODUCTION

The mainly tropical and subtropical Myrtaceae, a family of dicotyledonous trees and shrubs with over 140 genera and 3000 species, is particularly diverse in South America and Australia (Cronquist, 1981; Dahlgren & Thorne, 1985; Johnson & Briggs, 1981; Willis, 1980). The radiation of Myrtaceae in Australia is relatively recent. It is likely that, as Australia began its drift to lower latitudes in the Palaeocene (about 50 million years ago), its greater part was covered in a diversifying rain-forest composed of typical Gondwanan taxa with cool-temperate components including araucarians, podocarps, *Phyllocladus*, *Dacrydium*, Proteaceae, Winteraceae and *Nothofagus*, and with elements indicating warmer conditions, e. g. *Cupanieidites* (Sapindaceae), *Anacolosidites* (Olacaceae), *Beaupreadites* (Proteaceae), and Myrtaceae (Walker & Singh, 1981). The mid-Eocene (some 45 million years ago) was, according to Martin (1978), a period of significant change in Australia's flora. By the Oligocene the eucalypts and acacias became important elements in the vegetation. Finally, some ten million years ago, by the end of mid-Miocene, the Australian plate was approaching its present position relative to Southeast Asia, which allowed an exchange with the Malesian flora. Fire resistance probably played an important role in the high diversity of present-day Australian Myrtaceae.

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Similarly diverse and typical for Australia are the homopterous psyllids inhabiting Myrtaceae. A smaller portion of them is referable to the Triozidae but the bulk belongs to the predominantly Australian Spondylaspidinae.

White & Hodkinson (1985) included in the Spondylaspididae the Arepuninae, Euphalerinae, Pachypsyllinae and Spondylaspidinae. Members of the last are gall formers or lerp builders. The Ctenarytainini, with free-living larvae, were included in the Aphalaridae: Euphyllurinae based on the presence of marginal lanceolate setae and a caudal plate in larvae. This concept differed fundamentally from that of Bekker-Migdisova (1973), in which the two groups were included in a single taxon. The base for this change was the conspicuous morphological difference between lerp-building and gall-forming larvae on the one hand and free-living larvae on the other hand; the very homogenous adult morphology was weighted less important. This concept, like previous ones, is not convincing as the characters used may represent sympleisomorphies or parallelisms.

The large spondylaspidine genus *Glycaspis* s.l. includes some 140 described species arranged in three subgenera (Moore, 1983) with gall formers and lerp builders restricted to Australia (*Glycaspis* s. str. and *Synglycaspis*) and free-living species occurring both in Australia and Southeast Asia (*Boreioglycaspis*). Lanceolate setae and a sclerotised caudal plate are absent from the larvae of the former two, whereas they are developed in the latter. Examination of the phylogenetic relationships of *Boreioglycaspis* is, therefore, particularly relevant to the phylogenetic relationships of spondylaspidines.

Species identification in *Glycaspis* s. l. is difficult as differences between species often are minor whereas intraspecific variation may be pronounced. Moore (1970) stated that species are characterised mainly by the shape of the male parameres and the distal portion of the aedeagus, and to a lesser degree by their size. He judged other characters either too variable (e. g. coloration) or too homogenous (e.g. female terminalia). In addition most species show well defined host associations, and sometimes characteristic galls or lerps. The situation in other spondylaspidines is somewhat similar. The following revision of *Boreioglycaspis* discusses additional characters, which may be useful in defining species of related genera, and host plant and biogeographical relationships.

## MATERIAL AND METHODS

Material was examined from following collections and institutions: Australian Museum, Sydney (AMS); Australian National Insect Collection, CSIRO, Canberra (ANIC); Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); the Natural History Museum, London (BMNH); Muséum d'Histoire naturelle, Geneva (MHNG); United States National Museum (psyllid collection in USDA, Beltsville, MD.) (USNM).

Morphological terminology follows mostly Hodkinson & White (1979) and White & Hodkinson (1982). For situating structures on the distal portion of the aedeagus, the side bearing the sclerotised end tube of the ductus ejaculatorius is defined here as the dorsum. Measurements were made from slide mounted material and are given in mm. The following abbreviations are used in the keys and descriptions:

|      |  |
|------|--|
| HW   | head width   |
| AL   | antenna length (including scape and pedicel)             |
| WL   | forewing length  |
| MPP  | length of proximal segment of male proctiger             |
| MPD  | length of distal segment of male proctiger               |
| PL   | male paramere length                                     |
| AEL  | length of distal segment of aedeagus                     |
| FP   | female proctiger length                                  |
| VGCL | vertex length : genal cone length ratio                  |
| ALHW | antenna length : head width ratio                        |
| LLHW | length of apical two labial segments : head width ratio  |
| TLHW | metatibia length : head width ratio                      |
| FTL  | metafemur : metatibia length ratio                       |
| WLHW | forewing length : head width ratio                       |
| WLW  | forewing length : width ratio                            |
| MPPD | proximal : distal segment of male proctiger length ratio |
| FPHW | female proctiger length : head width ratio               |
| FPC  | female proctiger length : circumanal ring length ratio   |
| FSP  | female proctiger length : subgenital plate length ratio  |

### *Glycaspis s. l*

**Status and definitions.** - *Glycaspis* Taylor, 1960 was defined by Tuthill & Taylor (1955; as *Spondylaspis*), Taylor (1960) and Moore (1970). Moore (1961, 1964, 1970) subdivided the genus into three subgenera, viz. *Glycaspis s. str.* (syn. *Alloglycaspis* Moore, 1961), *Synglycaspis* Moore, 1970 and *Boreioglycaspis* Moore, 1964. Members of the former two are gall or lerp formers on *Eucalyptus* spp. restricted to Australia; species of the latter occur also outside Australia and are free-living on other hosts (Moore, 1970, 1983).

The combination of the following adult characters strongly supports the monophyly of *Glycaspis s. l.* which shares the general characters of the Spondylaspidini as defined below: the long and slender genal processes; antennae longer than head width; the long and slender, apically subacute forewings; forewing venation with short veins R+M+Cu1, R and M+Cu1; metacoxae without meracanthus, angular; metatibiae as long as or shorter than the metafemora which bear an apical sclerotised lobe on the inner side (Fig. 74); apical metatibial spurs always grouped.

In contrast to this are differences found in the larvae between *Glycaspis s. str.* and *Synglycaspis* on the one hand and *Boreioglycaspis* on the other hand. Larvae of the latter possess a sclerotised caudal plate and lanceolate setae, both absent in the former two. These larval characters are paralleled by the presence of a long distal segment of the male proctiger, cuneate female terminalia, and wax pores on the abdomen in adult *Boreioglycaspis*. The latter character, by its uniqueness within Psyllidae, constitutes a convincing autapomorphy. Wax pores on the adult abdomen are also found in the homotomid Dynopsyllinae (Hollis & Broomfield, 1989). A long distal segment of the male proctiger and cuneate female terminalia (as opposed to bulbous) occur also in other spondylaspidine genera, e. g. *Anoeconeossa* Taylor, *Leptospermonastes* Taylor, *Blastopsylla* Taylor, *Platyobria* Taylor and *Cryptoneossa* Taylor. The long distal segment of the male proctiger is shared by *Agelaeopsylla* Taylor and most species of

*Eucalyptolyma* Froggatt. The latter character probably represents the primitive condition within the group, and the cuneate female terminalia an adaptation to oviposition biology.

*Glycaspis* and *Synglycaspis* differ from each other mainly in venational characters of the fore and hindwings but constitute otherwise a compact, probably monophyletic group. For these reasons *Boreioglycaspis* is elevated to generic rank forming the sister group of *Glycaspis* which has two subgenera, *Glycaspis* s. str. and *Synglycaspis*. This more restricted definition is in line with those of other genera centered around *Eucalyptolyma* and *Ctenarytaina* (Taylor, 1990).

### ***Boreioglycaspis* Moore, stat. n.**

*Glycaspis* subgenus *Boreioglycaspis* Moore, 1964: 221. Type-species *Glycaspis* (*Boreioglycaspis*) *melaleucae* Moore, 1964, by original designation.

**Diagnosis.** - Forewings with short cells m1+2 and cu1a, bifurcation of M1+2 distal to apex of vein Cu1a. Hindwings with bases of veins R and M close together. Adult abdomen with field of pores (Figs. 79-81), similar to those found on the larval caudal plate (Fig. 82). Distal segment of male proctiger long, MPPD less than 1.2, in most species less than 1.0. Female terminalia cuneate, proctiger with small apical portion which is somewhat separated from the rest of proctiger (Fig. 76). Larvae with nine-segmented antennae and sclerotised caudal plate bearing lanceolate setae.

**Description.** - Adult. Head slightly narrower than mesoscutum, wider than pronotum; in profile weakly inclined up to about 45° to longitudinal body axis. Vertex flat, subrectangular, slightly shorter than wide. Preocular sclerite forming a tubercle of variable size and shape, sometimes very flat (Fig. 73). Antennae ten-segmented with a subapical rhinarium on each of segments four, six, eight and nine; terminal setae unequal, shorter or slightly longer than segment ten; one relatively long, curved and pointed apically, the other one short and truncate apically (Fig. 44). Thorax flattened dorsally; metapostnotum very long with two median tubercles along posterior margin (Fig. 75). Propleurites almost square with subequal epimeron and episternum; suture short with two long dorsal branches. Legs short and stout; basitarsi short; metatibiae with grouped apical spurs (Fig. 74); metabasitarsi with a single outer black spur. Forewings transparent, elongate; vein C+Sc widened, costal break and pterostigma developed; vein M1+2 much shorter than M; cells m1+2 and cu1a small, subequal; surface spinules present in all cells, usually leaving spinule-free stripes along the veins, spaced irregularly, sometimes very faint or partly reduced; in females and on dark back-ground usually better developed and larger; radular spinules usually present in cells rs, m1+2, m3+4 and cu1a. Hindwings (Moore, 1964, Fig. 8) membranous, about two thirds to three quarters forewing length; costal setae ungrouped; vein M+Cu1 developed; vein Cu1a almost straight. Male proctiger two-segmented; hindmargin of basal segment with small rounded lobes apically; apical segment long and slender. Male subgenital plate globular. Aedeagus two-segmented; basal portion widely rounded basally. Parameres elongate bearing black sclerotised pegs on inner surface. Female terminalia in profile cuneate, proctiger with subacute apex, setose laterally and apically. Circumanal ring convoluted, with a double row of pores (Figs. 77-78). Subgenital plate pointed apically, with a group of moderate long setae apically. Valvulae one curved, valvulae two with serrate apical third (Figs. 12, 14).

Larva. Body elongate (Fig. 21). Antennae nine-segmented with a single rhinarium on each of segments three, five, seven and eight. Dorsal thoracic sclerites small. Wing pads long and narrow, outer margin with slender lanceolate setae. Legs short and relatively robust; tarsi well-differentiated from tibiotarsi; tarsal arolium short, membranous without pedicel and visible unguitactor. Abdomen with sclerotised caudal plate. Anus terminal; outer circumanal ring oval, small, consisting of a single row of pores. Additional pore fields present on caudal plate; pores composed of eight symmetrically arranged orifices (Fig. 21), in one specimen with only four orifices (Fig. 24). Outer posterior margin of caudal plate with lanceolate setae.

**Remarks.** - The coloration in adults varies usually within a species depending on age of specimens. In several species there is a notable sexual dimorphism.

The larval morphology differs little between species. The main differences are in the general body coloration and in the extension of the extra pore fields on the caudal plate. With the available material it is possible to define characters to identify *B. forcipata* and *eugeniae*; *B. polymelasma*, *tristaniopsidis* and *borneensis*, which can live together on the same plant, do not differ in any of the examined characters. In the latter three species, only those few larvae could be identified where the adult was already sufficiently developed inside.

#### KEY TO ADULTS OF *BOREIOGLYCASPIS*

1. ALHW less than 1.5. Metatibiae weakly inflated apically, always with 3+1 apical spurs. Inner surface of male parameres with a group of dark pegs in basal third near the foremargin. On *Melaleuca* spp. .... *melaleucae* group ..... 2
- ALHW more than 1.5. Metatibiae strongly inflated apically (Fig. 74), usually with 3+2 apical spurs (in *moorei* with 3+1 spurs). Inner surface of male parameres without group of dark pegs in basal third near foremargin. On *Lophostemon*, *Tristaniopsis*, *Eugenia* and *Sonneratia*. .... *forcipata* group ..... 8
2. Genal cones in a plane parallel to vertex, or weakly deflexed, VGCL more than 1.0. .... 3
- Genal cones strongly depressed from plane of vertex in a 90° angle. VGCL less than 1.0. .... 7
3. Distal segment of aedeagus little expanded apically; sclerotised end tube of ductus ejaculatorius almost straight. Genal processes relatively massive. AL more than 0.8. Australia: New South Wales, Queensland, Northern Territory, Western Australia. On *Melaleuca* spp. .... *Boreioglycaspis melaleucae* Moore
- Distal segment of aedeagus strongly expanded apically; sclerotised end tube of ductus ejaculatorius distinctly sinuous (male of *B. paludis* unknown). Genal processes relatively slender. AL less than 0.8. .... 4

4. Forewings with yellow or brown pattern. .... 5
- Forewings without yellow or brown pattern. .... 6
- 5 Forewings with brown spot on clavus(Fig. 4) and, additionally in females, with brown pattern along outer wing margin and covering large parts of cell cu1a. Australia: Northern Territory. On *Melaleuca viridiflora*. ..... *Boreioglycaspis devicola* Moore
- Forewings of females at most with weakly infusate clavus and with distinct brown band along outer wing margin (Fig. 7); male unknown. Australia: Queensland, New South Wales. On *Melaleuca quinquenervia*.. ..... *Boreioglycaspis paludis* Moore
- 6 Forewings (Fig. 8) short, WLW less than 3.0; radular spinules in cell rs scarce or absent, covering large area in cell cu1a. Male parameres short, PL less than 0.2. FTL more than 1.2. Australia: Queensland. On *Melaleuca acacioides*..... *Boreioglycaspis denigrata* Moore
- Forewings (Fig. 9) long, WLW more than 3.0; radular spinules of cell cu1a scarce or absent, covering large area in cell rs. Male parameres long, PL more than 0.2. FTL less than 1.1. Australia: Queensland, Northern Territory. On *Melaleuca leucadendra, cajuputi*. ..... *Boreioglycaspis devexa* Moore
- 7 Antennae short, AL less than 0.8, ALHW less than 1.2. Forewings (Fig. 10) relatively short, WLHW less than 3.0, WLW more than 2.8. Australia: Northern Territory, Queensland. On *Melaleuca viridiflora* ..... *Boreioglycaspis muminae* Moore
- Antennae long, AL more than 0.8, ALHW more than 1.2. Forewings (Fig. 13) relatively long, WLHW more than 3.0, WLW less than 2.8. Australia: Queensland. On *Melaleuca nervosa*. ..... *Boreioglycaspis abudicola* Moore
- 8 Forewings (Fig. 15) wide, apex blunt, WLW less than 3.0 Terminalia as in Figs. 17-20. Distal portion of aedeagus (Fig. 19) with hook on dorsal side, and slender apical third of proximal portion. Philippines, East Malaysia: Sabah, Singapore. On *Sonneratia* spp. .... *Boreioglycaspis forcipata* (Crawford)
- Forewings slender, apex pointed, WLW more than 3.0. Distal portion of aedeagus without hook on dorsal side; in *polymelasma* dorsal hook present but proximal portion with strongly inflated apical third. On Myrtaceae. .... 9
- 9 Forewings with brown to black pattern consisting of spots, bands or stripes, sometimes ill-delimited, or wing membrane unevenly brown. .... 10
- Forewings yellowish to ochreous, anterior half slightly lighter but without brown pattern. .... 14
- 10 AL more than 1.6. .... 11
- AL less than 1.6. .... 12

- 11 Wing membrane light with ochreous infuscation of the apices of the veins along the outer wing margin, and dark brown pattern consisting of spots in males (Fig. 25), or of a band stretching from base of vein M+Cu1 to apex of Cu 1a in females. Genal processes relatively short, VGCL more than 0.7 (Fig. 26). Smaller species: HW less than 0.8, AL less than 1.8, WL less than 3.3. Terminalia as in Figs. 27-30. Australia: Queensland, New South Wales. On *Lophostemon confertus*. ..... *Boreioglycaspis australiensis* Moore
- Wing membrane brown, fore and hindmargins lighter, with a dark brown, ill-defined band along veins R+M+Cu1 and R (Fig. 31). Genal processes relatively long, VGCL less than 0.7. Larger species: HW more than 0.8, AL more than 1.9, WL more than 3.4. Terminalia as in Figs. 33-35. East Malaysia: Sabah. .... *Boreioglycaspis murphyi*, new species
- 12 Forewings (Fig. 36) with a dark brown pattern consisting of a longitudinal band. Male parameres (Fig. 39) relatively slender. Distal portion of aedeagus (Fig. 40) with a ventral subapical hook. AL less than 1.1, AEL less than 0.2, ALHW less than 1.75, MPBD more than 1.0, FPC more than 2.7. East Malaysia: Sabah..... *Boreioglycaspis fasciata*, new species
- Forewings with light or dark brown pattern consisting of spots. Male parameres relatively broad. Distal portion of aedeagus without ventral subapical hook. AL more than 1.1, AEL more than 0.2, ALHW more than 1.75, MPBD less than 1.0, FPC less than 2.7. .... 13
- 13 Forewings (Fig. 42) with large dark brown spots. Vertex (Fig. 43) with largely reduced surface sculpture. Terminalia as in Figs. 45-48. AL more than 1.4, FSP less than 0.6. East Malaysia: Sabah. On *Tristaniopsis* sp. .... *Boreioglycaspis polymelasma* Moore
- Forewings (Fig. 49) with small brown spots. Vertex (Fig. 50) with developed surface sculpture. Terminalia as in Figs. 51-54. AL less than 1.4, FSP more than 0.6. East Malaysia: Sabah. On *Tristaniopsis* spp. .... *Boreioglycaspis tristaniopsidis*, new species
- 14 Metatibiae with 3+1 apical spurs. Genal cones relatively short, VGCL more than 0.7. Terminalia as in Figs. 57-60. Male parameres long and slender, PL more than 0.35. Female terminalia long, FP more than 0.6, FPHW more than 0.8, FPC more than 3.0. East Malaysia: Sabah. On *Tristaniopsis* sp. .... *Boreioglycaspis moorei*, new species
- Metatibiae with 3+2 apical spurs. Genal cones relatively long, VGCL less than 0.7. Male parameres short, wide, PL less than 0.35. Female terminalia short, FP less than 0.6, FPHW less than 0.8, FPC less than 3.0. .... 15
- 15 Preocular sclerite forming a flattened tubercle (Fig. 62). Terminalia as in Figs. 63-66. Distal portion of aedeagus with subapical hook. FP less than 0.5. East Malaysia: Sabah. On *Tristaniopsis* sp. .... *Boreioglycaspis borneensis* Moore
- Preocular sclerite forming a large tubercle (Fig. 68). Terminalia as in Figs. 69-72. Distal portion of aedeagus without hook. FP more than 0.5. East Malaysia: Sabah. On *Eugenia punctilimba*. .... *Boreioglycaspis eugeniae*, new species

***melaleucae* group**

Members of this group are characterised by their relatively shorter antennae and genal processes, metatibiae weakly expanded apically with 3+1 apical spurs, and the male parameres bearing a group of dark pegs in basal third near the foremargin of their inner surface. Seven species, restricted to Australia, and developing on *Melaleuca* spp., are included.

***Boreioglycaspis melaleucae* Moore**

(Figs. 1-3)

*Glycaspis (Boreioglycaspis) melaleucae* Moore, 1964: 223. Holotype - male (AMS), 12 1/4 miles west along Gwydir Highway, Grafton, New South Wales, Australia, K. M. Moore, 11.i.1964, *Melaleuca quinquenervia* (slide mounted) (not examined).

**Description.** - Adult. Coloration. Vertex and thoracic dorsum ochreous, genal processes, antennae and lower body surface including legs whitish yellow; preocular sclerite, apical two to three antennal segments, a stripe on the profemora and round spots on the female abdomen and terminalia dark brown to almost black. Wings transparent, foremargin and pterostigma whitish, veins ochreous.

Structure. Head (Fig. 2) with relatively massive genal processes, shorter than vertex along mid-line, and subparallel to vertex. Surface sculpture on vertex well developed, setae on vertex very short. Preocular sclerite only slightly raised. Forewings as in Fig. 1, surface spinules leaving broad spinule-free stripes along the veins; radular areas relatively small, spinules sparse. Male genitalia illustrated by Moore (1970). Subgenital plate with a group of setae on either side and a few scattered setae ventrally. Parameres narrow, antero-basally little expanded. Distal portion of aedeagus weakly expanded apically, rounded; sclerotised endtube of ductus ejaculatorius almost straight. Female terminalia (Fig. 3) with relatively massive basal portion of proctiger and slender and short apical portion.

Measurements. (1 male, 1 female). HW 0.59-0.68; AL 0.81-0.89; WL 1.91-2.58; MPP 0.16; MPD 0.18; PL 0.28; AEL 0.22; FP 0.47; VGCL 1.20-1.27; ALHW 1.31-1.37; LLHW 0.32; TLHW 0.46-0.47; FTL 1.15-1.19; WLHW 2.24-3.79; WLW 3.13-3.15; MPPD 0.89; FPHW 0.69; FPC 2.61; FSP 0.60.

Larvae mentioned by Moore (1964), not examined. According to Taylor (in litt.) they do not differ significantly from *B. forcipata* as described and illustrated below (Fig. 21).

**Host plants.** - *Melaleuca quinquenervia* (Cav.) S. T. Blake, *M. leucadendra* (L.), *M. argentea* W. V. Fitzg., *M. nervosa* (Lindl.) Cheel.

**Distribution.** - Australia: New South Wales, Queensland, Northern Territory, Western Australia (Moore, 1964, 1970).

**Materials examined.** - Paratype - 1 male (AMS), Palm Beach, Queensland, K. M. Moore, 12.i.1964, on *Melaleuca quinquenervia*; 5 males, 13 females (ANIC), 70 miles South Charters Tower, Cape River, Queensland, K. M. Moore, 3.v.1966, on *Melaleuca leucadendra*, det. K. M. Moore 1966; 3 males, 7 females (ANIC) Toowoomb Bay, New South Wales, K. M. Moore,

28.iv.1967, on *Melaleuca quinquenervia*, det. K. M. Moore 1966; 20 males, 24 females (ANIC), Lennard River, Western Australia, K. M. Moore, 20.vii.1966, on *Melaleuca ? leucadendra*, det. K. M. Moore 1966; 2 males, 9 females (MHNG), Cooina, Northern Territory, K. M. Moore, 23.vi.1966, on *Melaleuca ? argentea*, det. K. M. Moore 1966. All localities in Australia.

***Boreioglycaspis devicola* Moore**

(Figs. 4-6)

*Glycaspis (Boreioglycaspis) devicola* Moore, 1970: 332. Holotype - male (ANIC), 17 miles SW East Alligator River Crossing, Northern Territory, Australia, 24.iv.1966 on *Melaleuca ? viridiflora* (slide mounted) (examined).

**Description.** - Adult. Coloration. Head and genal processes light brown dorsally, whitish to yellowish ventrally. Antennal segments eight and nine brown, apices of segments four to eight light brown. Thorax yellowish to ochreous dorsally, brown laterally, and whitish to yellowish ventrally. Pro- and metanotum each two with brown spots, mesoscutum with four brown longitudinal stripes. Legs whitish-yellow with a brown stripe on profemora and a brown spot on metacoxae. Forewings transparent, foremargin including pterostigma whitish, other veins light brown or ochreous; apex of clavus infuscate, vein A with small brown, indistinctly delimited spot in the middle; in addition females with brown, indistinctly delimited pattern consisting of spots in the cells  $r_1$ ,  $m_1+2$ ,  $m_3+4$ , and  $cu_1$ , and a broad band in cell  $cu_1b$ . Abdomen brown to dark brown and ochreous above, whitish beneath; terminalia brown.

**Structure.** Head (Fig. 5) with relatively massive genal processes shorter than vertex along mid-line, and weakly inclined relative to vertex, at most at an angle of 45°. Surface sculpture on vertex well-developed; setae on vertex very short, on genal processes longer, particularly apically. Preocular tubercle very flat, almost absent. Forewings as in Fig. 4, surface spinules scarce, leaving broad, spinule-free stripes along the veins, concentrated mainly on basal and marginal regions; radular areas large, spinules dense. Male genitalia illustrated by Moore (1970). Subgenital plate with a group of setae on either side forming a double row, and a few setae ventrally. Parameres narrow, strongly expanded antero-basally. Distal portion of aedeagus with strongly dilated apex, forming a small ventral hook; sclerotised end tube of ductus ejaculatorius weakly sinuous. Female terminalia (Fig. 6) similar to those of *melaleucae*.

**Measurements.** (1 male, 1 female). HW 0.59-0.64; AL 0.70-0.75; WL 1.89-2.49; MPP 0.16; MPD 0.16; PL 0.26; AEL 0.21; FP 0.46; VGCL 1.17-1.24; ALHW 1.17-1.19; LLHW 0.25-0.31; TLHW 0.42-0.44; FTL 1.24-1.50; WLHW 3.20-3.89; WLW 2.95-3.19; MPPD 1.00; FPHW 0.72; FPC 2.88; FSP 0.63.

Larva unknown.

**Host plant.** - *Melaleuca viridiflora* Sol. ex Gaertn.

**Distribution.** - Australia: Northern Territory (Moore, 1970).

**Materials examined.** - holotype - male (ANIC), 17 miles SW East Alligator River Crossing, Northern Territory, Australia, K. M. Moore, 24.vi.1966, on *Melaleuca ? viridiflora*.

Paratypes - 4 males, 6 females (ANIC, MHNG), Cooina, Northern Territory, Australia, K. M. Moore, 23.vi.1966, on *Melaleuca viridiflora*.

**Remarks.** - *B. devicola*, *paludis*, *denigrata* and *devexa* are morphologically similar. They differ mainly in their body and wing coloration, in the distribution of surface and radular spinules of the forewings, the relative lengths of the genal processes, the antennae, the hindlegs, the forewings and the parameres, and, to some extent, in the shape of the parameres and the distal portion of the aedeagus (male of *B. paludis* unknown). At present, it is difficult to decide whether the four taxa are distinct, mostly monophagous species or if they are populations of the same, morphologically variable, oligophagous species. More material, including larvae, is necessary to answer this question.

***Boreioglycaspis paludis* Moore**

(Fig. 7)

*Glycaspis (Boreioglycaspis) paludis* Moore, 1964: 224. Holotype - female (AMS), 100 yards west of Pacific Highway, Palm Beach, Queensland, Australia, K. M. Moore, 12.i.1964, *Melaleuca quinquenervia* (slide mounted) (examined).

**Description.** - Adult. Coloration. Similar to *devicola* but vertex, thoracic and abdominal dorsum orange and brown pattern on forewings (Fig. 7) very light and diffuse marginally, absent from cell cu1b.

Structure. As *devicola*. Male unknown.

Larva unknown.

**Host plant.** - *Melaleuca quinquenervia* (Cav.) S. T. Blake.

**Distribution.** - Australia: Queensland, New South Wales (Moore, 1964, 1970).

**Materials examined.** - holotype - female (AMS), Palm Beach, Queensland, Australia, K. M. Moore, 12.i.1964, on *Melaleuca quinquenervia*; 1 female, (ANIC), 2 miles South Tweed Heads, New South Wales, Australia, K. M. Moore, 11.iv.1966, on *Melaleuca quinquenervia*.

***Boreioglycaspis denigrata* Moore**

(Fig. 8)

*Glycaspis (Boreioglycaspis) denigrata* Moore, 1970: 332. Holotype - male (ANIC), 33 miles W Croydon, Queensland, Australia, K. M. Moore, 25.v.1966, on *Melaleuca acacioides*. (slide mounted) (examined).

**Description.** - Adult. Coloration. General body coloration whitish, vertex yellow, thoracic and abdominal dorsum ochreous. Antennal segments nine and ten, apex of female terminalia and in males also vertex and genal processes brown.

**Structure.** Similar to *devicola*. Forewings as in Fig. 8, radular spinules in cell rs scarce or absent. Male terminalia figured by Moore (1970). Distal portion of aedeagus somewhat less expanded and hooked apically than in *devicola*, sclerotised end tube of ductus ejaculatorius more sinuous.

**Measurements.** (1 male, 1 female). HW 0.47-0.54; AL 0.59-0.62; WL 1.48-1.89; MPP 0.13; MPD 0.19; PL 0.19; AEL 0.21; FP 0.42; VGCL 1.00; ALHW 1.15-1.26; LLHW 0.28-0.32; TLHW 0.43-0.46; FTL 1.24-1.55; WLHW 3.15-3.50; WLW 2.79-2.82; MPPD 0.92; FPHW 0.78; FPC 2.80; FSP 0.62.

Larva unknown.

**Host plant.** - *Melaleuca "acacioides"* F. Muell. Barlow (1986) split *M. acacioides* s. l. into *M. citrolens* Barlow and *M. acacioides* s. str. with the two subspecies *acacioides* and *alsophila* (Cunn. ex Benth.) Barlow. It is unknown to which of these taxa the host record refers.

**Distribution.** - Australia: Queensland.

**Materials examined.** - holotype - male, paratypes - 1 male, 16 females (ANIC, 1 female in MHNG), 33 miles W Croydon, Queensland, Australia, K. M. Moore, 25.v.1966, on *Melaleuca acacioides*.

### ***Boreioglycaspis devexa* Moore**

(Fig. 9)

*Glycaspis (Boreioglycaspis) devexa* Moore, 1970: 332. Holotype - male (ANIC), 6 miles S Quamby, Queensland, Australia, K. M. Moore, 30.v.1966, *Melaleuca leucadendra* (slide mounted) (examined).

**Description.** - Adult. Coloration. Similar to *denigrata* but lacking dark vertex and genal processes in males.

**Structure.** Similar to *devicola*. Forewings as in Fig. 9, surface spinules covering most of the cells, leaving narrow spinule-free stripes along the veins; radular spinules in cell cula scarce or absent. Male terminalia figured by Moore (1970). Distal portion of aedeagus as in *denigrata*.

**Measurements.** (1 male, 1 female). HW 0.48-0.62; AL 0.63-0.78; WL 1.61-2.42; MPP 0.13; MPD 0.16; PL 0.25; AEL 0.22; FP 0.45; VGCL 1.08-1.15; ALHW 1.26-1.31; LLHW 0.31-0.35; TLHW 0.52-0.53; FTL 1.03-1.08; WLHW 3.35-3.90; WLW 3.22-3.23; MPPD 0.81; FPHW 0.73; FPC 3.00; FSP 0.67.

Larvae mentioned by Moore (1970), not examined. The species differs from *B. melaleucae* in the presence of an additional group of pores on the dorsum of the caudal plate near the circumanal ring (Taylor, in litt.).

**Host plants.** - *Melaleuca leucadendra* (L.), *M. cajuputi* Powell.

**Distribution.** - Australia: Queensland, Northern Territory (Moore, 1970).

**Material examined.** - holotype - male, paratypes - 2 males, 12 females (ANIC; 1 male, 1 female in MHNG), 6 miles S Quamby, Queensland, Australia, K. M. Moore, 30.v.1966, on *Melaleuca leucadendra*.

***Boreioglycaspis muminae* Moore**

(Figs. 10-12)

*Glycaspis (Boreioglycaspis) muminae* Moore, 1970: 333. Holotype - male (ANIC), 28 miles North Road Junction Camooweal - Darwin, Northern Territory, Australia, K. M. Moore, 12.vi.1966, *Melaleuca viridiflora* (slide mounted) (examined).

**Description.** - Adult. Coloration. Vertex, genal processes, pronotum, tibiae and tarsi whitish. Foremargin of vertex orange, base of genal processes brown. Antennal segments one and two light brown, three to eight dirty greyish, nine and ten almost black. Thorax orange with brown and white spots, metapostnotum, femora and metacoxae dark brown. Wings whitish, veins slightly darkened apically. Abdomen orange with brown sclerites and white intersegmental membranes ventrally.

Structure. Head (Fig. 11) with strongly inclined, slender genal processes, deflexed to a 90° angle relative to vertex, longer than vertex along mid-line. Surface sculpture on vertex well developed, setae on vertex very short, on genal processes longer. Preocular sclerite flattened, not tubercular. Forewings as in Fig. 10, surface spinules faint and sparse in distal two thirds, leaving broad spinule-free stripes along the veins; radular spinules forming relatively small fields, particularly in cells *rs* and *cu1a*. Male terminalia figured by Moore (1970). Subgenital plate with a group of setae on either side forming a double row, and a few scattered setae ventrally. Parameres large, strongly expanded antero-basally. Distal segment of aedeagus expanded apically with small ventral hook; sclerotised end tube of ductus ejaculatorius strongly sinuous. Female terminalia (Fig. 12) with relatively slender basal portion and bold apical portion.

Measurements. (1 male, 1 female). HW 0.63-0.69; AL 0.69-0.74; WL 1.85-2.21; MPP 0.18; MPD 0.16; PL 0.24; AEL 0.21; FP 0.44; VGCL 0.76-0.79; ALHW 1.07-1.10; LLHW 0.37-0.41; TLHW 0.33-0.43; FTL 1.18-1.30; WLHW 2.21-2.94; WLW 2.89-3.03; MPPD 1.13; FPHW 0.64; FPC 2.93; FSP 0.57.

Larva unknown.

**Host plant.** - *Melaleuca viridiflora* Sol. ex Gaertn.

**Distribution.** - Australia: Northern Territory, Queensland.

**Material examined.** - holotype - male (ANIC), 28 miles North Road Junction Camooweal - Darwin, Northern Territory, Australia, K. M. Moore, 12.vi.1966, *Melaleuca viridiflora*.

Paratypes - 1 male, 2 females (ANIC). 32 miles W Soudan, Northern Territory, Australia, K. M. Moore, 10.vi.1966, on *Melaleuca viridiflora*.

***Boreioglycaspis abudicola* Moore**

(Figs. 13, 14)

*Glycaspis* (*Boreioglycaspis*) *abudicola* Moore, 1970: 333. Holotype - male (ANIC), 30 miles W Duaringa, Queensland, K. M. Moore, 29.iv.1966, *Melaleuca nervosa*. (slide mounted) (examined).

**Description.** - Adult. Coloration. Vertex and thoracic and abdominal dorsum orange, otherwise whitish; antennal segments eight to ten brown.

Structure. Similar to *muminae*. Forewings as in Fig. 13, surface and radular spinules slightly more expanded. Male terminalia figured by Moore (1970). Setae on subgenital plate less distinctly grouped than in *muminae*. Distal portion of aedeagus more expanded apically than in *muminae*. Female terminalia (Fig. 14) with gradually narrowing proctiger.

Measurements. (1 male, 1 female). HW 0.59-0.71; AL 0.81-0.90; WL 1.79-2.38; MPP 0.15; MPD 0.18; PL 0.24; AEL 0.23; FP 0.55; VGCL 0.86-0.88; ALHW 1.27-1.37; LLHW 0.32-0.38; TLHW 0.58-0.62; FTL 1.02-1.12; WLHW 3.03-3.35; WLW 2.59-2.74; MPPD 0.83; FPHW 0.70; FPC 3.33; FSP 0.62.

Larva unknown.

**Host plant.** - *Melaleuca nervosa* (Lindl.) Cheel.

**Distribution.** - Australia: Queensland.

**Material examined.** - holotype - male, paratypes - 7 males, 14 females (ANIC) (1 male, 1 female in MHNG), 30 miles W Duaringa, Queensland, K. M. Moore, 29.iv.1966, *Melaleuca nervosa*; .

***forcipata* group**

Members of this group are characterised by their relatively longer antennae and genal processes, which are at most weakly inclined, the apically strongly expanded metatibiae with usually 3+2 apical spurs (3+1 in *moorei*), and the male parameres lacking a group of dark pegs in basal third near the foremargin of their inner surface. The nine included species occur in Australia and tropical Asia where they develop on *Sonneratia*, *Lophostemon*, *Tristaniopsis* and *Eugenia* spp.

***Boreioglycaspis forcipata* (Crawford)**

(Figs. 15-21)

*Epipsylla forcipata* Crawford, 1917: 167. Lectotype - male (USNM), Palawan Island, Puerto Princesa, Palawan Island, Philippine Islands, Baker (D. L. Crawford collection, 1943), designated by Moore, 1964: 228. (slide mounted) (examined)

*Glycaspis* (*Boreioglycaspis*) *forcipata* (Crawford); Moore, 1964: 227; Moore, 1970: 334.

*Glycaspis* (*Boreioglycaspis*) *penangensis* Moore, 1964: 227. Holotype - female (BPBM), Island of Penang, West Malaysia, Baker. (slide mounted) (examined). Syn. n.

**Description.** - Adult. Coloration. Ochreous with black genal processes, abdominal tergites and a longitudinal median black stripe on the dorsum of head and thorax. Patches on profemora, metacoxae and abdominal pleurites brown. Antennae ochreous with segments nine and ten, and apices of segments four to eight dark brown to black. Forewings ochreous with whitish vein C+Sc and pterostigma. Immature specimens with less expanded or without dark colour.

Structure. Head (Fig. 16) with very flat, small preocular tubercle; surface sculpture well developed, slightly weaker in the middle of the vertex. Genal processes conical. Setosity on vertex very short, on genal processes longer, particularly apically. Forewings (Fig. 15) relatively broad, with surface spinules forming extended fields leaving narrow, spinule-free stripes along the veins; radular spinules covering moderately wide areas. Metatibiae with 3+2 apical spurs. Male terminalia as in Figs. 17-19. Subgenital plate evenly covered in long setae. Parameres lanceolate, truncate apically; inner surface with few dark pegs. Distal segment of aedeagus with dorsal hook in apical third, weakly widened apically; sclerotised end tube of ductus ejaculatorius short, sinuous. Female terminalia as in Fig. 20. Apical portion of proctiger short.

Measurements. (2 males, 2 females). HW 0.67-0.88; AL 1.76-1.88; WL 2.36-3.23; MPP 0.17-0.21; MPD 0.22; PL 0.31-0.35; AEL 0.30-0.32; FP 0.61-0.64; VGCL 0.63-0.71; ALHW 2.14-2.63; LLHW 0.31-0.36; TLHW 0.48-0.57; FTL 1.23-1.55; WLHW 3.23-3.84; WLW 2.62-2.81; MPPD 0.77-0.95; FPHW 0.73; FPC 2.65-2.67; FSP 0.48-0.59.

Larva. Coloration. Sclerites, wing buds and caudal plate brown; membranes yellowish.

Structure. Body as in Fig. 21. Setosity sparse and short. Forewing pads rounded apically, relatively wide, bearing very slender lanceolate setae. Extra pore fields on caudal plate forming many small patches; marginal lanceolate setae numerous, relatively slender.

**Host plants.** - *Sonneratia alba* J. J. Smith, *Sonneratia* sp. (Sonneratiaceae).

**Distribution.** - Philippines: Palawan, Balabak Island; East Malaysia: Sabah as *forcipata*; and West Malaysia: Penang as *penangensis* (Moore, 1964).

**Materials examined.** - Philippines: lectotype male of *forcipata*, Palawan Island, Puerto Princesa (Baker) (D. L. Crawford collection, 1943) (USNM); 4 males, 2 females, 23 larvae, Palawan, Puerto Princesa City, White Beach, 27.i.1988, *Sonneratia* sp. (J. H. Martin) (BMNH; 3 larvae in MHNG).; 2 females, Balabac Island, Pasig, 4.iii.1957 (Yoshio Kondo), det. K. M. Moore, 1963 (MHNG). Singapore: 13 males, 7 females, 35 larvae, Sembawang, 2.i.1987, *Sonneratia alba* (D. Burckhardt) (MHNG). West Malaysia: holotype female of *penangensis*, Island of Penang (Baker) (BPBM).

**Remarks.** - Described on a single female only, *B. penangensis* differs according to Moore (1964) from *B. forcipata* in the distinctively convex edge of the scutellum. The comparison of the types with fresh material showed that this difference is trivial and expresses intraspecific variation. *B. penangensis* is therefore synonymised with *forcipata*.

***Boreioglycaspis australiensis* Moore**

(Figs. 25-30)

*Glycaspis (Boreioglycaspis) australiensis* Moore, 1964: 227. Holotype - female (BPBM), Coolangatta, on the New South Wales - Queensland border, Queensland, Australia, F. Muir, viii.1919 (dry mounted) (examined).

**Description.** - Adult. Coloration. Yellowish; antennae with light brown segments five to eight and dark brown segments eight and nine. Forewings pale with yellow stripes along the marginal veins and a dark brown spot in the middle of vein A. In addition males with brown vertex and spots on abdomen, thorax and at the base of cell rs of forewings, and females with reddish genal processes and abdominal tergites, orange thorax, a dark brown band on the forewings, stretching from base of cell rs to apex of vein Cu1b, and brown spots on the thorax and the terminalia.

**Structure.** Head (Fig. 26) with relatively short genal processes compared to other members of the *forcipata* group; surface sculpture in male reduced laterally towards the eyes, in females more expanded but weaker towards eyes. Preocular sclerite forming small tubercle. Forewings as in Fig. 25, surface spinules sparse, reduced at the bases of cells, leaving broad spinule-free stripes along the veins; radular spinules forming large patches in cells rs, m1+2 and m3+4, and a small patch in cell cu1a. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 27-30. Male subgenital plate with a group of long setae on either side and a few setae ventrally. Parameres very narrow; inner surface with irregularly arranged dark pegs in apical half. Distal segment of aedeagus bent in apical quarter, weakly expanded and rounded apically. Basal portion of female proctiger only weakly humped apically, apical portion relatively long.

**Measurements.** (1 male, 1 female). HW 0.70-0.78; AL 1.60-1.74; WL 2.63-3.28; MPP 0.17; MPD 0.25; PL 0.39; AEL 0.28; FP 0.55; VGCL 0.74-0.76; ALHW 2.23-2.29; LLHW 0.41; TLHW 0.50-0.55; FTL 1.05-1.09; WLHW 3.76-4.12; WLW 3.22-3.29; MPPD 0.68; FPHW 0.71; FPC 3.06; FSP 0.58.

Larva unknown.

**Host plant.** - *Lophostemon confertus* (R. Br.) P. G. Wilson & J. T. Waterhouse.

**Distribution.** - Australia: Queensland, New South Wales (Moore, 1964, 1970).

**Material examined.** - holotype - female (BPBM), Coolangatta, on the New South Wales - Queensland border, Queensland, Australia, F. Muir, viii.1919.

Other material - 5 males, 15 females (ANIC; 2 males, 2 females in MHNG), Mt. Archer summit, Rockhampton, Queensland, Australia, K. M. Moore, 28.iv.1966, *Lophostemon confertus*.

***Boreioglycaspis murphyi*, new species**

(Figs. 31-35, 80, 81)

**Material examined** - holotype. - male (MHNG), 1750-1850 m, Mt. Kinabalu, Sabah, East Malaysia, C. Lienhard, 20.iii.1983.

**Description.** - Adult. Coloration. General body colour brown, forewings with a dark brown stripe along vein R+M+Cu1; foremargin lighter.

Structure. Head (Fig. 32) with distinct, rounded preocular tubercle; surface sculpture almost completely absent. Genal processes long, tubular. Setosity long and regular. Forewings as in Fig. 31, surface spinules relatively dense, reaching veins; radular spinules forming low triangular patches which are almost as wide as cells, patch in cell *rs* distinctly higher. Male terminalia as in Figs. 33-35. Subgenital plate with very few, mainly ventral setae. Parameres narrow, curved backwards; inner surface with a row of dark pegs along the foremargin and apically. Distal portion of aedeagus with dorsal kink in apical fifth and ventral subapical hook; sclerotised end tube of ductus ejaculatorius short. Female unknown.

Measurements. (1 male). HW 0.87; AL 1.99; WL 3.46; MPP 0.20; MPD 0.32; PL 0.50; AEL 0.37; VGCL 0.65; ALHW 2.29; LLHW 0.31; TLHW 0.60; FTL 1.08; WLHW 3.98; WLW 3.12; MPPD 0.63.

Larva and host plant unknown.

**Etymology.** - Named in honour of Assoc. Prof. D. H. Murphy on the occasion of his 60th birthday.

***Boreioglycaspis fasciata*, new species**

(Figs. 36-41)

**Materials examined** - male (MHNG), 1750-1850 m, Mt. Kinabalu, Sabah, Malaysia, C. Lienhard, 20.iii.1983.

Paratypes. - 2 males, 1 female (MHNG), same data as holotype; female (BMNH), 5,225 ft, Pinasuk Plateau, Mt. Kinabalu, Sabah, East Malaysia, (Royal Soc. Exped., coll. S. Kueh., B. M. 1964-250) 14-17.iii.1964.

**Description.** - Adult. Coloration. Dark brown with two ochreous longitudinal lines reaching from bases of genal processes to mesonotum. Antennae yellowish, segments nine and ten and apices of segments six to eight dark brown. Metanotum ochreous; longitudinal lines on thorax and abdominal venter whitish to yellow-grey. Wings transparent with dark brown pattern as in Fig. 36. Tibiae, tarsi and metafemora pale ochreous.

Structure. Head (Fig. 37) with conical genal processes; surface sculpture of vertex relatively distinct, covering the whole vertex; setosity shorter than in *B. tristaniopsidis*, about as long as or slightly shorter than in *B. polymelasma*; preocular tubercle narrower than in *B. tristaniopsidis*. Forewings as in Fig. 36, surface spinules sparse and fine, mostly confined to coloured areas, leaving broad spinules-free stripes along the veins; radular spinules covering large

triangular areas, densely spaced. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 38-41. Male subgenital plate sparsely setose laterally and ventrally. Parameres lamellar, slender; inner surface with a row of dark pegs along the apical third of foremargin and apically. Distal segment of aedeagus with large apical dilatation which bears a small ventral hook. Basal portion of female proctiger slightly dilated apically, apical portion small.

Measurements. (1 male, 1 female). HW 0.61-0.63; AL 1.02-1.09; WL 2.69-2.89; MPP 0.16; MPD 0.14; PL 0.23; AEL 0.19; FP 0.45; VGCL 0.55-0.61; ALHW 1.67-1.73; LLHW 0.33-0.39; TLHW 0.57-0.64; FTL 1.13-1.19; WLHW 4.41-4.59; WLW 3.21-3.43; MPPD 1.14; FPHW 0.71; FPC 2.81; FSP 0.62.

Larva and host plant unknown.

**Etymology.** - Latin *fasciatus* = bearing a band.

### ***Boreioglycaspis polymelasma* Moore**

(Figs. 22, 24, 42-48, 73-78)

*Glycaspis* (*Boreioglycaspis*) *polymelasma* Moore, 1964: 225. Holotype - female (BPBM), Kota Kinabalu 30 miles East, 1460 m, Tenompok, Sabah, East Malaysia, T. C. Maa, 10-19.ii.1959, (slide mounted) (examined).

**Description.** - Adult. Coloration. Head and genal processes black, shiny; antennal segments one and two yellow, three to eight yellow-grey, nine and ten black. Body yellow to ochreous, with dark brown mesoscutum and metapostnotum, and two black spots on either side of thorax. Forewings transparent with ochreous veins and dark pattern as in Fig. 42. Abdominal tergites brown to black.

Structure. Head (Fig. 43) with long, tubular genal processes; surface sculpture on vertex almost absent, restricted to anterior and posterior margin of vertex; setae longer than in *B. australiensis*. Preocular sclerite forming a distinct tubercle which is larger than in *australiensis*. Forewings as in Fig. 42, surface spinules fine and reduced apart from dark areas and in apical third of wing where they are thicker, covering a larger surface, leaving broad spinule-free stripes along the veins; radular spinules covering large triangular areas, in cell m1+2 forming comparatively low triangle. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 45-48. Male subgenital plate with a group of a few setae on either side and a few setae ventrally. Parameres relatively wide, broadly rounded apically, with a row of dark pegs along foremargin and apically. Proximal segment of aedeagus thickened in apical third; distal segment with large dorsal hook in apical third weakly expanded and rounded apically. Female terminalia relatively short, proctiger strongly concave dorsally.

Measurements. (2 males, 2 females). HW 0.65-0.72; AL 1.45-1.54; WL 2.71-3.34; MPP 0.14-0.17; MPD 0.19-0.22; PL 0.35-0.37; AEL 0.27; FP 0.46-0.52; VGCL 0.58-0.77; ALHW 2.01-2.28; LLHW 0.38-0.44; TLHW 0.50-0.65; FTL 1.18-1.29; WLHW 4.10-4.91; WLW 3.44-3.99; MPPD 0.74-0.77; FPHW 0.68-0.72; FPC 2.19-2.60; FSP 0.54-0.57.

Larva. Coloration. Sclerites, wing pads and caudal plate light brown, membranes yellowish.

Structure. Similar to *B. forcipata* but marginal lanceolate setae on caudal plate more slender at base and more widened in the middle (Fig. 22), less numerous, and forewing pads more slender.

**Host plants.** - *Tristaniopsis* sp.

**Distribution.** - East Malaysia: Sabah (Moore, 1964).

**Material examined.** - East Malaysia: holotype female, Sabah, Tenompok, 1460 m, Kota Kinabalu 30 miles East, 10-19.ii.1959 (T. C. Maa) (BPBM); 7 males, 6 females, Sabah, Mt. Kinabalu, near headquarters, Liwagu trail, 1840 m, 22.v.1987, *Tristaniopsis* (Burckhardt & Löbl) (MHNG); 1 female, Sabah, Mt. Kinabalu, 1900 m, 26.iv.1987, *Tristaniopsis* (Burckhardt & Löbl) (MHNG); 25 males, 28 females, Sabah, Mt. Kinabalu, 1700-1850 m, 20-22.iii.1983 (Lienhard & Nagai) (MHNG; 2 males, 2 females, in ANIC; 1 male, 1 female, in BPBM; 2 males, 2 females, in BMNH).

#### ***Boreioglycaspis tristaniopsidis*, new species**

(Figs. 49-54)

**Materials examined.** - Holotype. - male (MHNG), headquarters, 1740 m, Mt. Kinabalu, Sabah, East Malaysia, Burckhardt, 3.v.1982, *Tristaniopsis grandifolia*.

Paratypes. - 2 females (MHNG), headquarters, 1730 m, Mt. Kinabalu, Sabah, Burckhardt, 28.iv.1982; 3 males, 3 females (MHNG; 1 male, 1 female, in ANIC; 1 male, 1 female, in BMNH), 1700 m, Mt. Kinabalu, Sabah, coll. Nagai, 22.iii.1983; 1 male (MHNG), 1500 m, Liwagu trail, near headquarters, Mt. Kinabalu, Sabah, Burckhardt & Löbl, 22.v.1987, *Tristaniopsis*; 8 males, 6 females (MHNG) 1500 m, Mt. Kinabalu, Sabah, Burckhardt & Löbl, 30.iv.1987, *Tristaniopsis*; 6 males, 2 females, same but 1550-1650m, 24.iv.1987; 3 males, same but 30.iv.1987; 5 males, 1 female, same but 1750 m, 27.iv.1987; 1 male (MHNG), 1560 m, HQ, Mt. Kinabalu Nat. Park, Sabah, A. Smetana 30.iv.1987. All localities in East Malaysia.

**Description.** - Adult. Coloration. Head and thorax ochreous dorsally and ventrally, almost black laterally. Antennal segments one to seven ochreous, eight to ten dark brown to black. Legs and abdominal venter yellowish. Forewings transparent with yellow veins, brown pattern as in Fig. 49; spots in cell rs very faint. Abdominal tergites dark brown to black.

Structure. Head (Fig. 50) with conical genal processes; surface sculpture on vertex covering the whole surface, faint; setae distinctly longer than in *B. australiensis*, slightly longer than in *B. polymelasma*. Preocular sclerite forming distinct, slightly flattened lobe. Forewings as in Fig. 49, surface spinules very sparse and reduced; radular spinules forming triangular patches smaller than in *B. polymelasma*. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 51-54. Male proctiger with a group of setae on either side and a few scattered setae ventrally. Parameres broad; inner surface with dark pegs anteriorly and apically. Proximal portion of aedeagus weakly expanded in apical third; distal portion with globular dilatation apically; sclerotised end tube of ductus ejaculatorius short, sinuous. Female proctiger longer and less concave dorsally than in *B. polymelasma*; apical portion slender.

Measurements. (3 males, 3 females). HW 0.60-0.68; AL 1.20-1.34; WL 2.51-3.27; MPP 0.13-0.17; MPD 0.10-0.20; PL 0.28-0.31; AEL 0.26-0.29; FP 0.43-0.47; VGCL 0.54-0.64; ALHW 1.78-2.09; LLHW 0.30-0.47; TLHW 0.46-0.59; FTL 1.05-1.35; WLHW 4.18-4.81; WLW 3.49-3.80; MPPD 0.68-0.85; FPHW 0.63-0.69; FPC 2.24-2.53; FSP 0.62-0.63.

Larva. As *B. polymelasma*.

**Host plants.** - *Tristaniopsis grandifolia* (Ridl.) P. G. Wilson) & J. T. Waterhouse, *Tristaniopsis* sp.

**Etymology.** - Named after its host genus *Tristaniopsis*.

***Boreioglycaspis moorei*, new species**

(Figs. 55-60)

**Materials examined.** - Holotype. - male (MHNG), 1840 m, Liwagu trail, near headquarters, Mt. Kinabalu, Sabah, East Malaysia, Burckhardt & Löbl, 22.v.1987, *Tristaniopsis*.

Paratypes. - 7 males, 5 females, same data as holotype; 5 males, 5 females (MHNG; 2 male, 2 female, in ANIC; 1 male, 1 female, in BPBM; 2 males, 2 females, in BMNH), 1700-1850 m, Mt. Kinabalu, Sabah, East Malaysia, Lienhard & Nagai, 20-22.iii.1983.

**Description.** - Adult. Coloration. Ochreous; vertex, antennal flagellum and abdominal tergites brown.

Structure. Head (Fig. 56) with conical genal processes; surface sculpture on vertex weak, restricted to foremargin and stripe along the eyes, setae long. Preocular sclerite forming indistinct small tubercle. Forewings as in Fig. 55, surface spinules reduced in the basal part of cells, distinct apically, leaving broad spinule-free stripes along the veins; radular spinules covering very broad triangular areas in cells m1+2 and m3+4, slightly narrower in cells rs and cu1a. Metatibiae with 3+1 apical spurs (one specimen with 3+2 on one leg). Terminalia as in Figs. 57-60. Male subgenital plate sparsely setose laterally and ventrally. Parameres long, narrow and curved; inner surface with dark pegs along foremargin and apically. Distal portion of aedeagus dilated apically bearing a ventral subapical hook. Sclerotised end tube of ductus ejaculatorius short, straight. Female terminalia long; proctiger with straight dorsal margin and long, slender apical portion.

Measurements. (2 males, 2 females). HW 0.64-0.73; AL 1.18-1.33; WL 2.69-3.49; MPP 0.14-0.15; MPD 0.21-0.23; PL 0.39-0.40; AEL 0.27-0.28; FP 0.61-0.63; VGCL 0.75-0.82; ALHW 1.80-2.27; LLHW 0.37-0.41; TLHW 0.59-0.64; FTL 1.03-1.22; WLHW 4.20-4.78; WLW 3.20-3.45; MPPD 0.61-0.71; FPHW 0.86-0.88; FPC 3.00-3.05; FSP 0.59-0.61.

Larva unknown.

**Host plants.** - *Tristaniopsis* sp.

**Etymology.** - Named in honour of the late Mr. K. M. Moore.

***Boreioglycaspis borneensis* Moore**

(Figs. 61-66)

*Glycaspis* (*Boreioglycaspis*) *borneensis* Moore, 1964: 227. Holotype - female (BPBM), 1460 m, 30 miles East Kota Kinabalu, Tenompok, Sabah, East Malaysia, T. C. Maa, 2-4.ii.1959. (slide mounted) (examined).

**Description.** - Adult. Coloration. Ochreous; antennal flagellar segments with brown apices or entirely brown. Older males with dark genal processes and spots on thorax and abdomen; older females with dark brown or black vertex and brown spots on thorax and abdomen.

Structure. Head (Fig. 62) with long conical genal processes. Surface sculpture on vertex weak, sometimes covering entire vertex, sometimes absent from most parts and restricted to foremargin; setae long. Preocular sclerite forming flattened tubercle. Forewings as in Fig. 61, surface spinules forming extended fields, leaving spinule-free stripes along the veins; radular spinules covering broad triangular fields. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 63-66. Male subgenital plate sparsely setose laterally and ventrally. Parameres expanded apically, relatively broad, with dark pegs on the inner surface forming a row along the apical half of foremargin and apically. Distal segment of aedeagus dilated apically bearing a subapical ventral hook. Female proctiger relatively short, basal portion weakly bulbous apically, distal portion short.

Measurements (4 males, 4 females). HW 0.61-0.72; AL 1.16-1.63; WL 2.54-3.24; MPP 0.13-0.15; MPD 0.16-0.20; PL 0.21-0.33; AEL 0.20-0.27; FP 0.44-48; VGCL 0.52-0.70; ALHW 1.77-2.36; LLHW 0.33-0.43; TLHW 0.50-0.63; FTL 1.10-1.24; WLHW 3.90-4.62; WLW 3.30-3.72; MPPD 0.70-0.94; FPHW 0.64-0.70; FPC 2.32-2.56; FSP 0.60-0.72.

Larva. As *B. polymelasma*.

**Host plants.** - *Tristaniopsis* sp.

**Distribution.** - East Malaysia: Sabah (Moore, 1964, 1970).

**Material examined.** - East Malaysia: holotype female, Sabah, Tenompok, 30 miles East Kota Kinabalu, 1460 m, 2-4.ii.1959 (T. C. Maa) (BPBM); 9 males, 8 females, Sabah, Mt. Kinabalu, near headquarters, Liwagu trail, 1840 m, 22.v.1987, *Tristaniopsis* (Burckhardt & Löbl) (MHNG); 1 female, Sabah, Mt. Kinabalu, 1900 m, 26.iv.1987, *Tristaniopsis* (Burckhardt & Löbl) (MHNG); 13 males, 12 females, same but 1750 m, 27.iv.1987 (2 males, 2 females, in ANIC; 1 male, 3 females, in BMNH); 4 males, 2 females, Sabah, Mt. Kinabalu, 1950 m, 2.v.1982, *Tristaniopsis* (Burckhardt) (MHNG); 13 males, 17 females, Sabah, Mt. Kinabalu, 1700-1850 m, 20-22.iii.1983 (Lienhard & Nagai) (MHNG; 1 male, 1 female, in BPBM).

***Boreioglycaspis eugeniae*, new species**

(Figs. 23, 67-72, 79, 82)

**Materials examined.** - holotype male (MHNG), 2600 m, Mt Kinabalu, Sabah, East Malaysia, Burckhardt & Löbl, 1-2.v.1987, *Eugenia punctilimba*.

Paratypes - 11 males, 16 females, 14 larvae, same data as holotype; 2 females, 10 larvae (MHNG), 2700m, Mt. Kinabalu, Sabah, East Malaysia, Burckhardt, 4.v.1982; 1 larva, same but 2020 m, 2.v.1982.

**Description.** - Adult. Coloration. Dark brown with orange mesoscutum and ochreous scutellum. Antennae ochreous, segment nine and ten, and apices of segments four to eight dark brown. Legs yellowish with brown patches on femora.

Structure. Head (Fig. 68) with long tubular genal processes. Surface sculpture on vertex distinct, fully developed; setosity long. Preocular sclerite forming a large tubercle. Forewings as in Fig. 67, surface spinules similar to the ones in *B. borneensis* but more reduced and more sparse; radular spinules covering broad triangular areas. Metatibiae with 3+2 apical spurs. Terminalia as in Figs. 69-72. Male terminalia similar to those in *B. borneensis* but parameres wider with a larger field of dark pegs on the inner surface, and lacking a ventral hook on the distal segment of the aedeagus. Female terminalia elongate; proctiger with long apical portion.

Measurements (1 male, 1 female). HW 0.69-0.71; AL 1.25-1.40; WL 3.12-3.20; MPP 0.16; MPD 0.17; PL 0.28; AEL 0.23; FP 0.52; VGCL 0.56-0.60; ALHW 1.76-2.03; LLHW 0.30-0.41; TLHW 0.39-0.54; FTL 1.27-1.54; WLHW 4.51-4.52; WLW 3.56-3.59; MPPD 0.94; FPHW 0.73; FPC 2.60; FSP 0.60.

Larva. Coloration. Sclerites, wing pads and caudal plate dark brown; membrane yellowish.

Structure. Similar to *B. polymelasma* but with extra pore fields on caudal plate forming three transverse bands, and with lanceolate setae on caudal plate more slender basally and wider in the middle (Fig. 23).

**Host plant.** - *Eugenia punctilimba* Merr.

**Etymology.** - Named after its host genus *Eugenia*.

#### *Incertae sedis*

The following list of material contains females and larvae which cannot be identified with certainty. The females probably belong to three, yet undescribed, species; the taxonomically important males are required to confirm this.

#### *Boreioglycaspis* spp.

**Materials examined.** - 8 larvae, 1620-1740 m, Headquarters, Mt. Kinabalu, Sabah, D. Burckhardt, 28.iv-3.v.1982, *Tristaniopsis grandifolia*; 12 larvae, 1920-1950 m, summit trail, Mt. Kinabalu, Sabah, Burckhardt, 29.iv-2.v.1982; 4 larvae, 1700-1850 m, Mt. Kinabalu, Sabah, Lienhard & Nagai, 20-22.iii.1983; 23 larvae, 1500 m, Mt. Kinabalu, Sabah, Burckhardt & Löbl, 24-30.iv.1987, *Tristaniopsis*; 10 larvae, same but 1840 m, Liwagu trail, 22.v.1987; (All material in MHNG). All localities in East Malaysia.

**Remarks.** - The larvae may belong to *B. polymelasma*, *tristaniopsidis*, *borneensis* or another species; at present there are no reliable characters known to separate these sympatric species.

***Boreioglycaspis* sp. 1**

**Materials examined.** - 1 female (BMNH), strand biotope, PW27, Molibagu, Sulawesi, 6.xi.1985; 1 female (BMNH), coastal vegetation, PW1, Manado, Sulawesi, 17.x.1985. Both localities in Indonesia.

**Remarks.** - The two females resemble *B. forcipata* from which they differ mainly in the presence of a brown band along the apical and posterior margin in the forewings.

***Boreioglycaspis* sp. 2**

**Materials examined.** - 1 female (BMNH), N. C. Seram, Manusela N. P. Wae Mual Plain, Indonesia, Spray 10 (Operation Raleigh, M. J. D. Brendell, B. M. 1987-262), 25.vii.-2.ix.1987.

**Remarks.** - The single female is similar to specimens of *B. forcipata* but differs in the broader genal processes.

***Boreioglycaspis* sp. 3**

**Materials examined.** - 1 male (BMNH), Botanical Gardens, Cairns, Queensland, Australia, Asche & Hoch, 4.vi.1987.

**Remarks.** - The single female resembles superficially *B. fasciata* from which it differs in the more extended and delimited dark brown pattern on the forewings, the body coloration, the more robust genal processes, and the longer apical process of the female terminalia.

**DISCUSSION**

In members of the *B. melaleucae* group, the differences in the male terminalia are small. They are particularly homogenous in the three species *devicola*, *denigrata* and *devexa* which differ only in relative size and coloration. Based on head and wing characters, *B. paludis*, whose male is unknown, is closely related to these species. It is not possible to decide at the moment whether the four represent distinct species or forms of one species. In contrast to this are pronounced differences in the male terminalia between species of the *forcipata* group. Apart from relative size the species of both groups are characterised by surface sculpture and setosity of the vertex, the shape of the preocular sclerite, the shape of the genal processes, extent and arrangement of surface and radular spinules of the forewings, number of apical metatibial spurs, arrangement of the setae on the male subgenital plate, and, to a lesser degree, the shape of the female terminalia. Perhaps these characters are also useful in defining species in related genera. The larval morphology within *Boreioglycaspis* is very homogenous and not very helpful in species definition.

*Boreioglycaspis* is composed of two monophyletic species groups, the *melaleucae* and *forcipata* group respectively. This grouping is similar to the classification of Moore (1983) who recognises four groups, viz. the "melaleucae group" (*melaleucae*, *paludis*, *devicola*, *denigrata*),

the “*devexa* group” (*devexa*, *muminae*, *abudicola*), the “*forcipata* group” (*penangensis*, *forcipata*), and the “*australiensis* group” (*australiensis*, *borneensis*, *polymelasma*). Based on the short antennae, the weakly deflexed, slender genal processes and the male terminalia, *devexa* is close to *paludis* (male unknown), *devicola* and *denigrata*. The relationships between *melaleuca*, the *devexa* - *denigrata* complex, and the *muminae* - *abudicola* complex of species are obscure. Genital characters, in particular the shape of the male parameres, the arrangement of the dark pegs on the inner paramere surface, and the size of the postero-apical lobes of the distal proctiger segment in males (probable synapomorphies), subdivide the *forcipata* group into four units with, again, unknown relationships among each other: *forcipata*, *australiensis* + *fasciata*, *murphyi* + *moorei*, and *polymelasma* + *tristaniopsidis* + *borneensis* + *eugeniae*.

The *B. melaleuca* group with seven species is restricted to Australia and to the host genus *Melaleuca*. The *B. forcipata* group with nine species is distributed over insular Southeast Asia and one species occurs in Australia; the hosts belong to the not closely related genera *Sonneratia* (Sonneratiaceae), *Lophostemon*, *Tristaniopsis* and *Eugenia* (Myrtaceae). In the formal classification of Briggs & Johnson (1979), *Eugenia* is attributed to the subfamily Myrtoideae, *Lophostemon* and *Tristaniopsis* to the *Metrosideros* alliance of the subfamily Leptospermoideae, and *Melaleuca* to the *Leptospermum* alliance of the same subfamily. Johnson & Briggs (1984) abandoned this subfamily concept and suggested closer relationship of the *Leptospermum* group to the Myrtoideae s. str. than to the *Metrosideros* group. Wilson & Waterhouse (1982) when analysing *Tristania* s. l. concluded that *Lophostemon* and *Tristaniopsis* have no very close links. The *Melaleuca* hosts, with the exception of *M. acacioides*, belong to the primitive tropical *leucadendra* complex, morphologically probably close to the ancestral condition (Barlow, 1988, and in litt.). The *M. leucadendra* group and the *M. acacioides* complex are phylogenetically not very close but have both, in contrast to most of the other 200 odd *Melaleuca* spp., relatively large leaves and a tropical/subtropical distribution (Barlow, in litt.).

It is interesting to note that several members of the *forcipata* group can cohabit on the same host tree, whereas other members of the group utilise unrelated host genera of Sonneratiaceae and Myrtaceae (both Myrtales). The comparison of the phylogenies of *Boreioglycaspis* and of its hosts shows no congruence between the two. Speciation in *Boreioglycaspis* cannot, therefore, be explained as a response to host diversification. *Boreioglycaspis* species may be physiologically best suited to tropical Myrtales species with relatively broad leaves. The host associations as well as the predominantly tropical present-day distribution of *Boreioglycaspis* suggest a tropical Australian/Australasian origin and relatively recent colonisation of subtropical Australia and Laurasian parts of Southeast Asia.

Seven of the nine species of the *forcipata* group occur on Mt. Kinabalu. Even though this mountain belongs to one of the better studied places in Southeast Asia from an entomological point of view, this large number of *Boreioglycaspis* spp. is surprising. According to Holloway (1978), at higher altitudes Mt. Kinabalu is part of an “upland archipelago” of montane habitats incorporating Central Borneo, much of Sulawesi and Seram, and a large area of New Guinea, consisting, theoretically, of a blend of Himalayan and temperate Australian elements. Lowland flora and fauna in Borneo would be in contrast predominantly Asian. This hypothesis holds for the flora but not for the birds and moths where the upland species are almost entirely of Himalayan affinity (Holloway, 1978). In psyllids both elements are well represented: *Boreioglycaspis* and *Ctenarytaina* as Australian elements, and species of *Psylla* s. l. feeding on Ericaceae as Himalayan elements (unpublished data in MHNG). On a recent visit to Mt. Gede in Java and Mt. Kerinci in Sumatra, I paid particular attention to *Boreioglycaspis* but was unable

to find any specimens. The genus may thus be absent from these islands, quite in contrast to New Guinea where its occurrence is very likely.

### Spondyliaspidine classification

The Spondyliaspidinae were defined by Heslop-Harrison (1954) who used a name proposed by Schwarz (1898). He included 13 genera from Australia, New Zealand, Central and North America, and the Indo-Malayan Archipelago. Apart from the American genera which develop on *Celtis* spp., and the New Zealand *Atmetocranium* with unknown host relationships, all listed genera, at least in part, develop on Myrtaceae. In an earlier paper, Heslop-Harrison (1949) suggested that the Spondyliaspidinae may be a very ancient group of psyllids going back directly to a Permian ancestor.

Klimaszewski (1964) accepted Heslop-Harrison's concept and raised the group to family level. This classification was adopted by Bekker-Migdisova (1973) who subdivided it into the predominantly Australian Spondyliaspidinae and the predominantly American Pachypsyllinae. Neither of these authors provided sufficient information on defining characters and content which makes their classifications difficult to test.

Based on a cladistic analysis of adult and larval characters, White & Hodkinson (1985) redefined the Spondyliaspididae, to include the Arepuninae, the Euphalerinae, the Pachypsyllinae and the Spondyliaspidinae. They transferred one group, the Ctenarytainini, included in the former classifications to the Aphalaridae: Euphyllurinae. A simplified version of their cladogram is given in Fig. 83 and Tab. 1. Their family Spondyliaspididae (clade 55 + *Arepuna*) is for following reasons polyphyletic and has to be rejected in a phylogenetic classification:

1. Clade 17, including the Diaphorininae, Pauropsyllinae, Euphyllurinae and Aphalaroidinae of the Aphalaridae, the Spondyliaspididae and the Psyllidae, is defined by characters 59, 90 and 123. None of these characters is shared by all members of the included taxa; the absence of a rhinarium from antennal segment five is probably plesiomorphic within Psylloidea (character 58) (Hollis, 1984).

2. The presence in larvae of capitate setae on body and wing pads (character 118), and the absence from the larval antennae of sectasetae or derivable structures (character 147) constitute synapomorphies of the Spondyliaspididae + Psyllidae + *Aphalaroida* of the Aphalaridae (clade 53), and the three together form the sister-group of Diaphorininae + Paurocephalinae + Euphyllurinae (clade 48) of the Aphalaridae. Character 118, principally a convincing character, is, however, subsequently reduced (characters 158, 159) in Spondyliaspididae minus Arepuninae (clade 55). This makes the monophyly of clade 53 questionable.

3. The characters 58 and 76 given as synapomorphy for the Diaphorininae + Paurocephalinae + Euphyllurinae (clade 48) are not convincing as they are subject to homoplasy.

4. The presence of extra pore fields on the larval caudal plate (character 108) defines both clades 47 and 55, viz. Euphyllurinae and Spondyliaspididae minus Arepuninae respectively. Also this character is likely to be subject to homoplasy.

5. Characters 95, 109 (clade 66), 96 (clade 67), 100 (clade 68), and 99 (clade 70) concern the morphology of the larval abdominal apex or larval chaetotaxy. The former is strongly dependent on larval biology and not conclusive for phylogenetical purposes, the latter is present also in other groups and not convincing as such.

6. The remaining characters are not discussed here as they are “loss” characters which are not convincing synapomorphies a priori.

Ctenarytainini larvae differ significantly in the morphology of the tarsal arolium from those of Euphyllurini and Dicliodiphlebiini, the two other members of the Euphyllurinae. As in other Spondyliaspidini (sensu Taylor) the larval tarsal arolium of Ctenarytainini is membranous, without pedicel and visible unguitactor.

Burckhardt (1987) synonymised the Spondyliaspididae and Aphalaridae with the Psyllidae without clarifying the status of the constituent groups. The Arepuninae were synonymised with the Aphalaroidinae which, on the basis of the structure of larval tarsal arolia, are related to legume-feeding Psyllidae of the subfamilies Acizziinae, Ciriacreminae, Arytaininae, and to the Psyllinae developing on a variety of host families.

Taylor (1990), in discussing the phylogenetic relationships, transferred the tribe Ctenarytainini to the Spondyliaspidinae, together with the Spondyliaspidini and Euphalerini. He emphasizes that adult Spondyliaspidini and Ctenarytainini are similar, and differences are limited to the absence or presence of a caudal plate and lanceolate setae in the larvae.

A critical analysis of adult and larval characters yielded some characters which, in combination, diagnose the Spondyliaspidini with a slightly altered composition: 1. meracanthi of metacoxae always tubercular or absent; 2. preocular sclerite developed, often tubercular; 3. terminal setae on antennal segment ten strongly subequal: one long and curved, the second short and truncate apically; 4. male proctiger two-segmented, even though the apical portion may be small and membranous; 5. larval tarsal arolium membranous, without visible pedicel and unguitactor, sometimes difficult to see; 6. pro and mesobasitarsi very short, in profile almost globular; their ventro-apical area modified to form a large contractile pulvillus. Carver (1987) observed that species of *Anoeconeossa*, *Australopsylla*, *Blastopsylla*, *Ctenarytaina*, *Glycaspis* and *Spondylaspis* stand and walk on their basitarsi and carry the apical tarsi aloft. When stationary the apical tarsi are rapidly oscillating or vibrating.

Following taxa are included: *Agelaeopsylla* Taylor, *Anoeconeossa* Taylor, *Australopsylla* Tuthill & Taylor, *Blastopsylla* Taylor, *Boreiogycaspis* Moore, *Cardiaspina* Crawford, *Creiis* Scott, *Cryptoneossa* Taylor, *Ctenarytaina* Ferris & Klyver, *Dasypsylla* Froggatt, *Eriopsylla* Froggatt, *Eucalyptolyma* Froggatt, *Eurhinocola* Crawford, *Glycaspis* Taylor, *Hyalinaspis* Taylor, *Kenmooreana* Taylor, *Lasiopsylla* Froggatt, *Leptospermonastes* Taylor, *Phellopsylla* Taylor, *Phyllolyma* Walker (= *Cometopsylla* Froggatt), *Platyobria* Taylor, *Spondylaspis* Signoret and *Syncarpiolyma* Froggatt (material was examined of at least one species of all genera except for the two monobasic genera *Eurhinocola* and *Syncarpiolyma*, which both are similar to *Ctenarytaina*). This classification differs from those of White & Hodkinson and of Taylor mainly in the inclusion of the Ctenarytainini and the genera *Phellopsylla*, *Phyllolyma* (from Euphalerini) and *Platyobria* (from Diaphorininae). The remainder of the Euphalerini sensu White & Hodkinson have larval tarsal arolia with pedicel and visible unguitactor. The

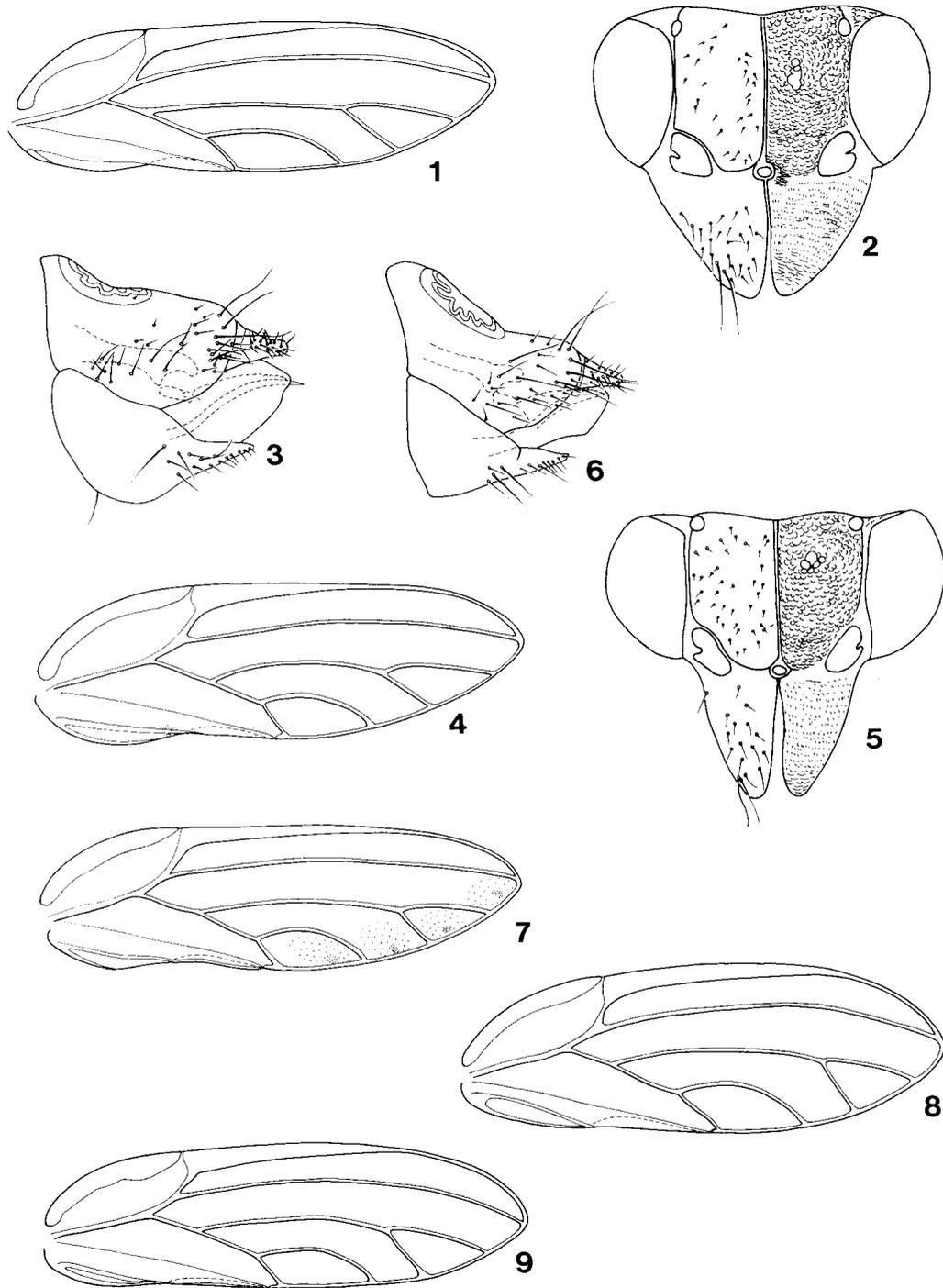
similarity of *Platyobria* to members of the Diaphorininae is superficial and does not express phylogenetic relationship.

A further subdivision within the tribe seems premature. The Ctenarytainini sensu White & Hodkinson and Taylor is probably not a natural group. The presence of a caudal plate and lanceolate setae in larvae is plesiomorphic; the gall-forming and lerp-building habit on the other hand almost certainly evolved several times independently. This character reflects thus only differences in the larval biology, and should not be used for phylogenetical purposes. The Ctenarytainini is therefore synonymised with the Spondyliaspidini.

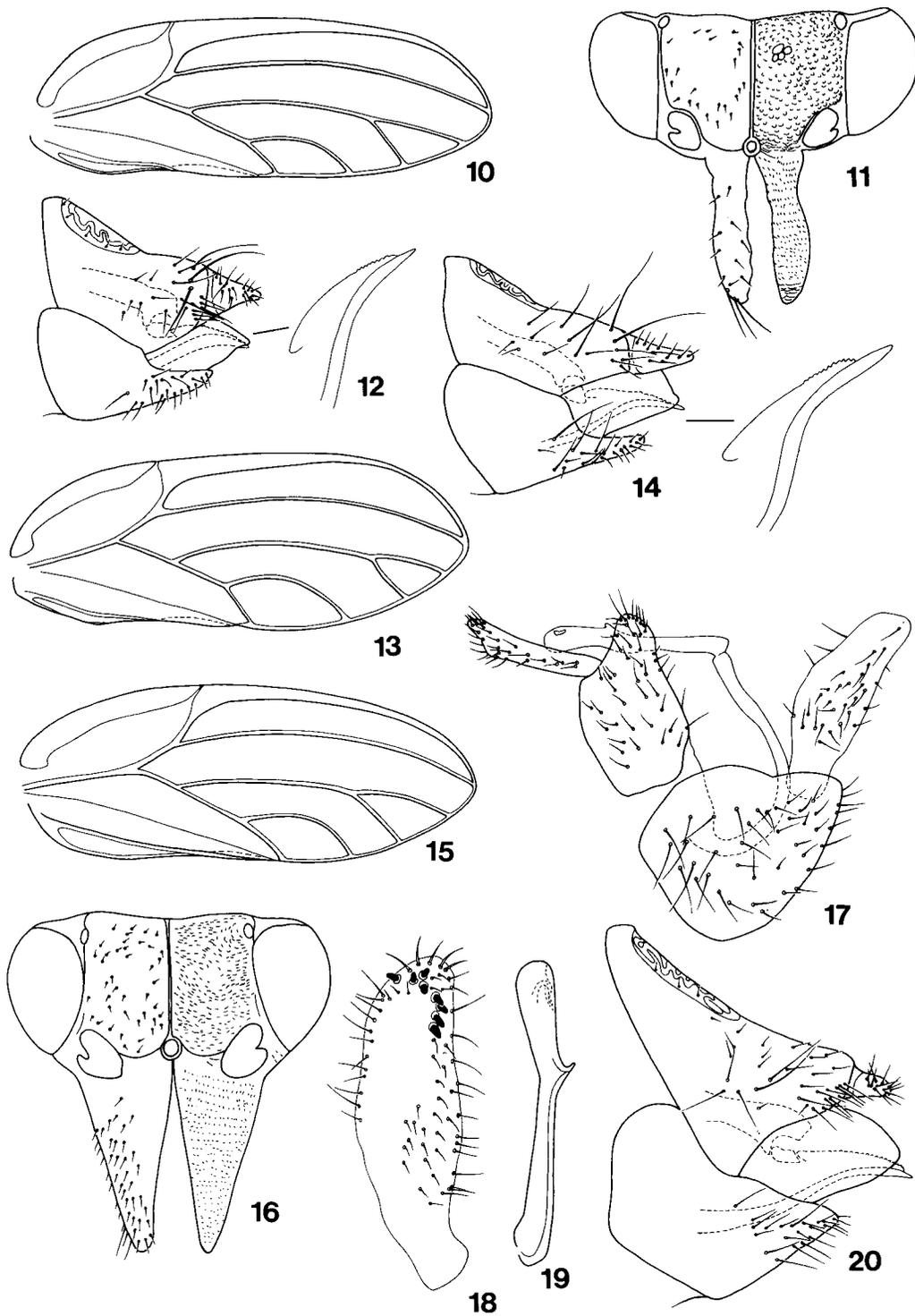
*Pachypsylla* spp. possess similar larval tarsal arolia to members of the Spondyliaspidini as defined above. It is suggested that, together with the other two genera included in the tribe Pachypsyllini (*Celtisaspis* and *Tetragonocephala*) it forms the sister-group of the Spondyliaspidini and, that the two together constitute the Spondyliaspidinae. The remainder of the Euphalerinae sensu White & Hodkinson do not share this character and are therefore excluded from the subfamily. Their phylogenetic relationship is uncertain.

Unlike Heslop-Harrison (1949) who thought the Spondyliaspidini a very ancient group of psyllids, it is suggested here that their diversification may have occurred, together with that of their myrtaceous hosts, during the mid-Eocene.

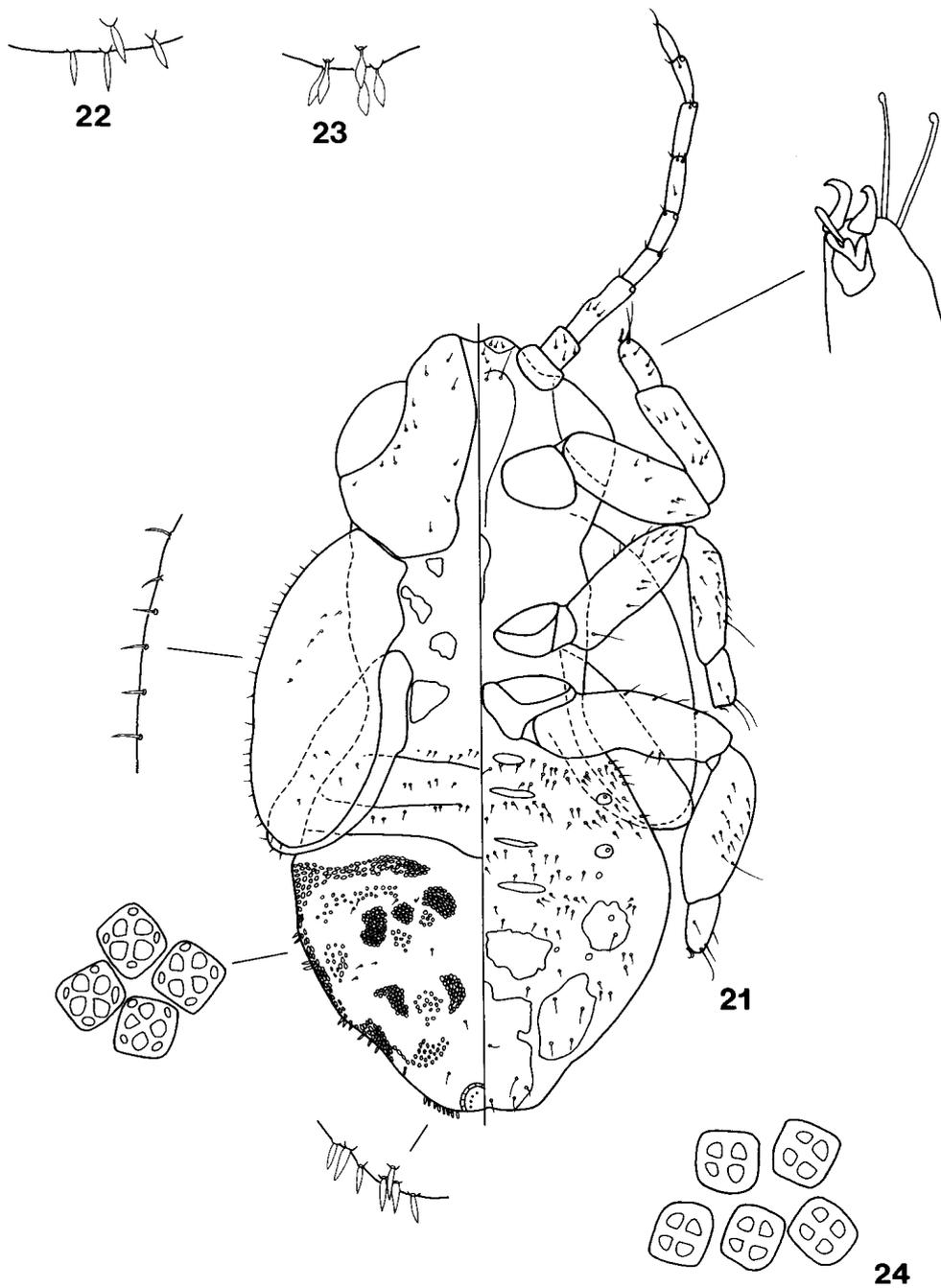
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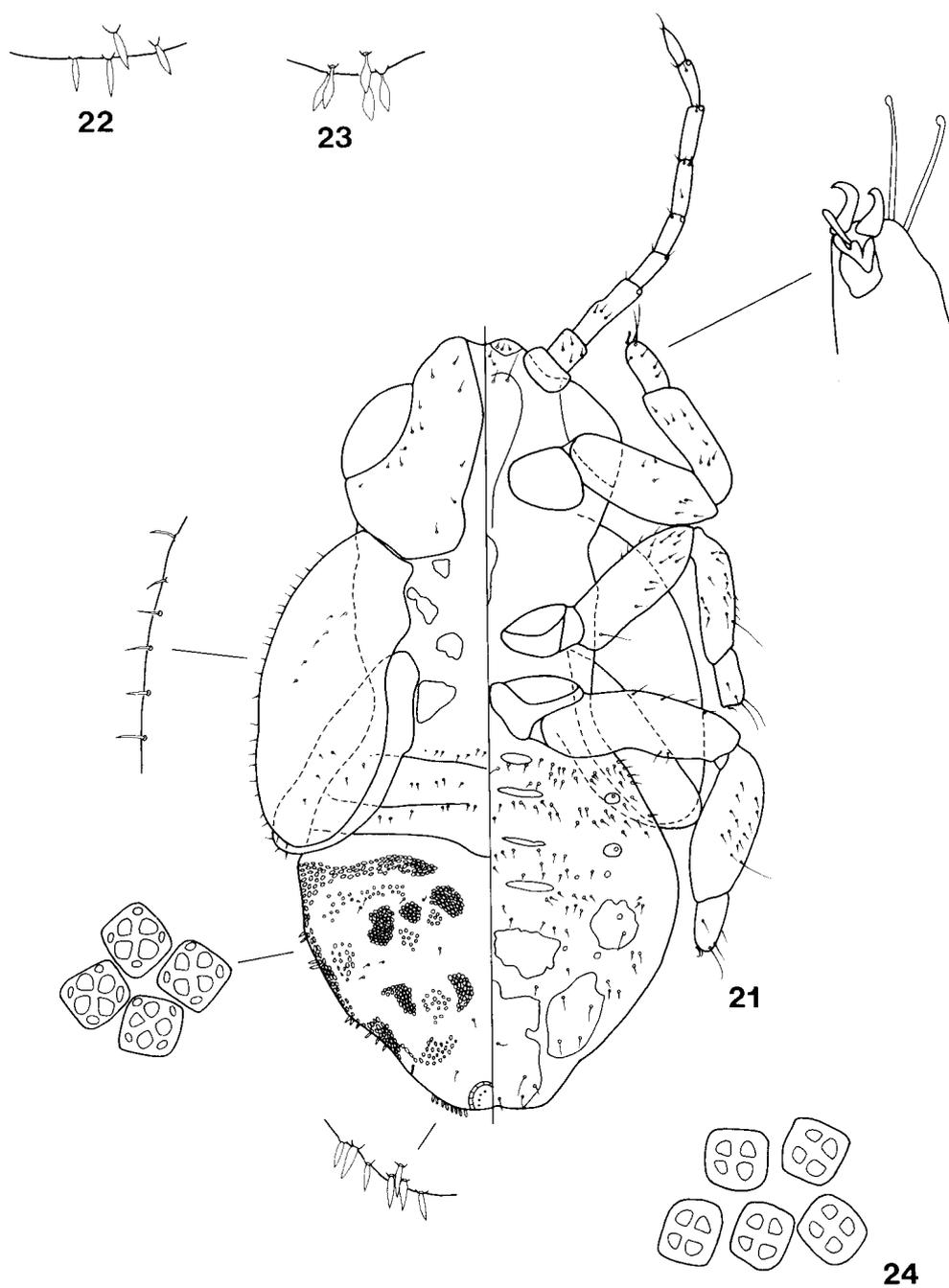
Figs. 1-9. *Boreioglycaspis* spp. 1-3 - *B. melaleuca* Moore; 4-6 - *B. devicola* Moore; 7 - *B. paludis* Moore; 8 - *B. denigrata* Moore; 9 - *B. devexa* Moore; 1, 4, 7-9 - forewing; 2, 5 - head; 3, 6 - female terminalia.



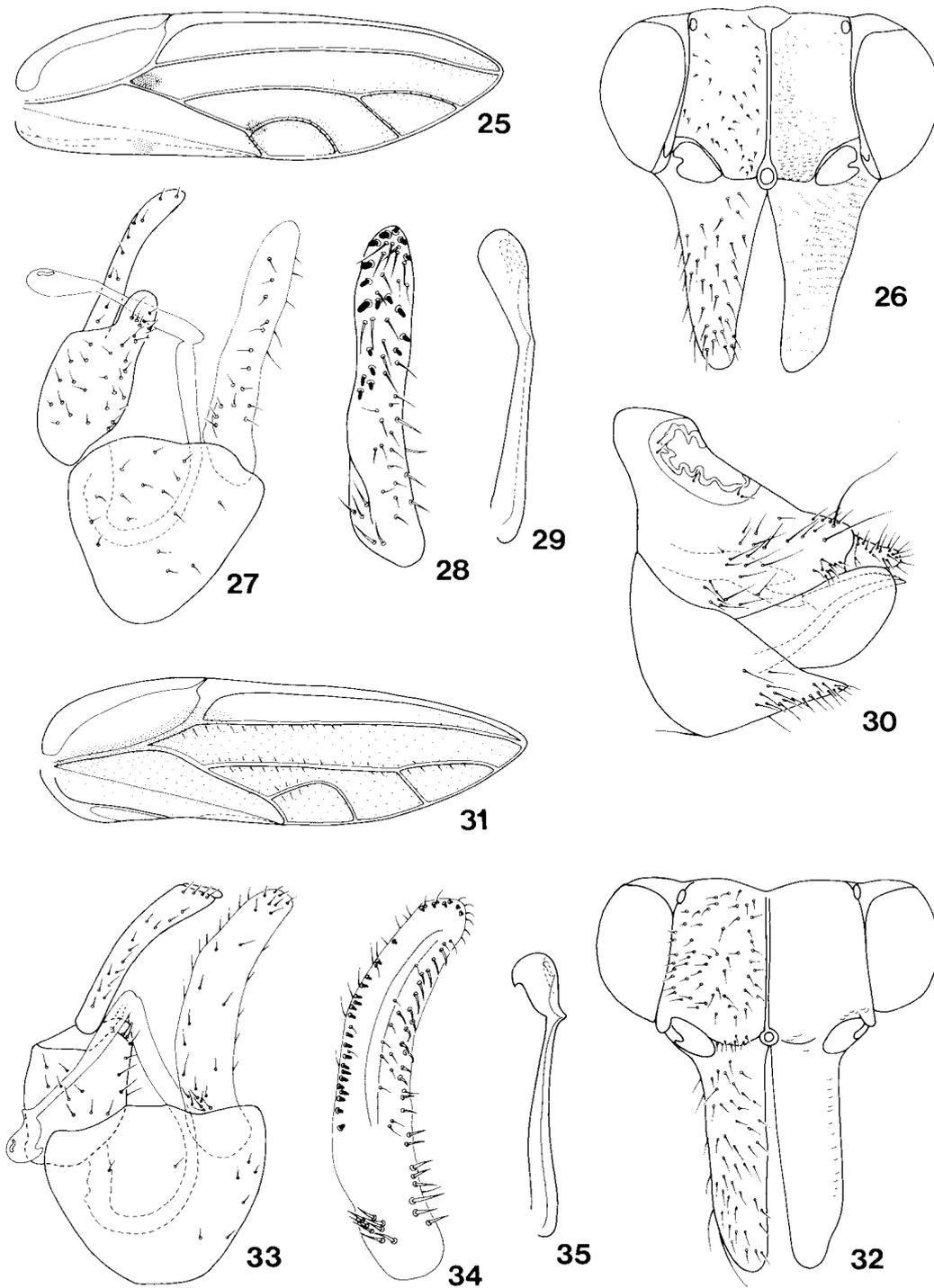
Figs. 10-20. *Boreioglycaspis* spp. 10-12 - *B. muminae* Moore; 13-14 - *B. abudicola* Moore; 15-20 - *B. forcipata* (Crawford); 10, 13, 15 - forewing; 11, 16 - head; 12, 14, 20 - female terminalia; 17 - male terminalia; 18 - paramere, inner surface; 19 - distal portion of aedeagus.



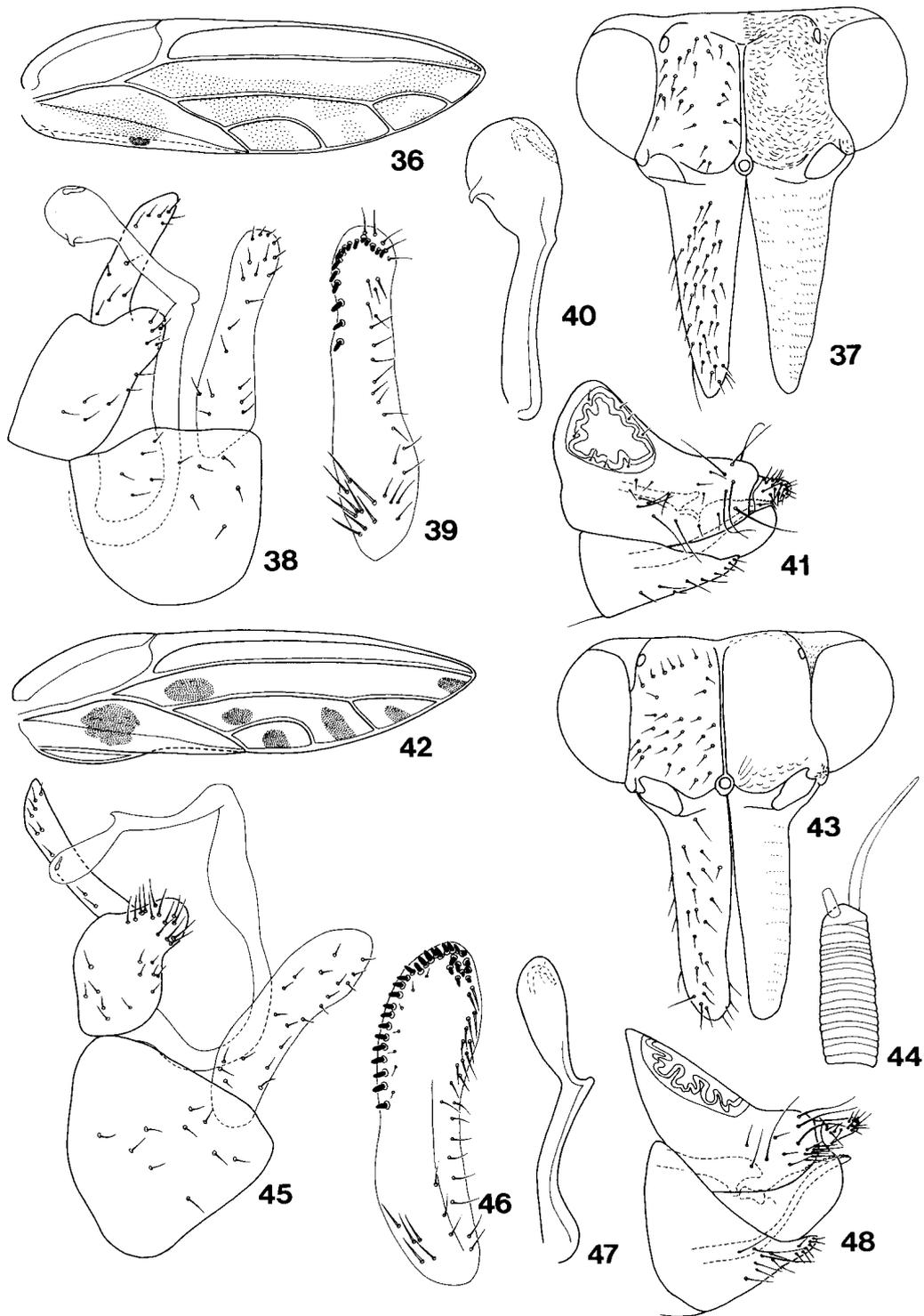
Figs. 21-24. *Boreioglycaspis* spp., last instar larva. 21 - *B. forcipata* (Crawford); 22, 24 - *B. spp.*; 23 - *B. eugeniae*, new species; 21 - left, dorsal surface, right, ventral surface; 22, 23 - lanceolate setae on apex of caudal plate; 25 - pores on caudal plate.



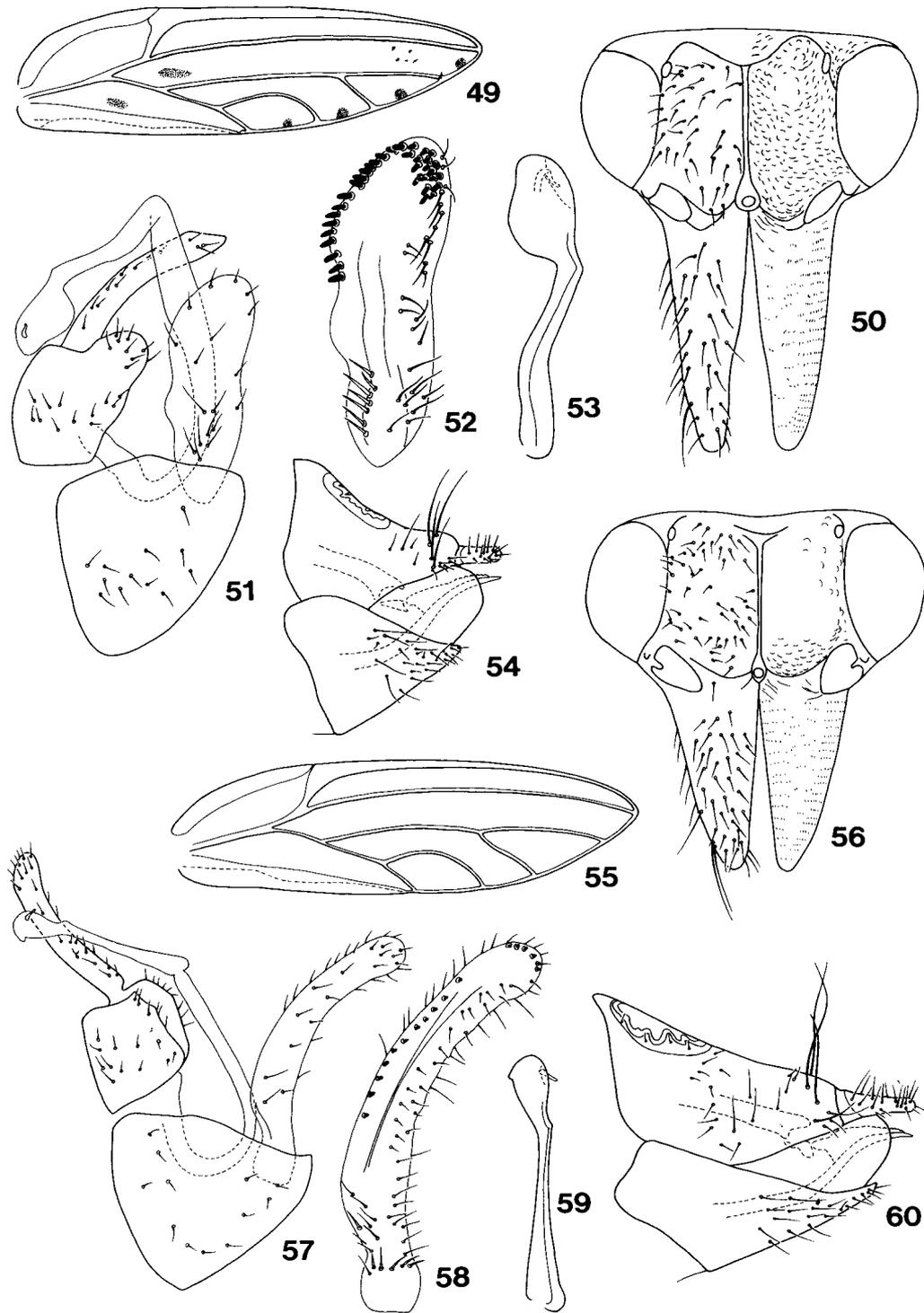
Figs. 21-24. *Boreioglycaspis* spp., last instar larva. 21 - *B. forcipata* (Crawford); 22, 24 - *B. spp.*; 23 - *B. eugeniae*, new species; 21 - left, dorsal surface, right, ventral surface; 22, 23 - lanceolate setae on apex of caudal plate; 25 - pores on caudal plate.



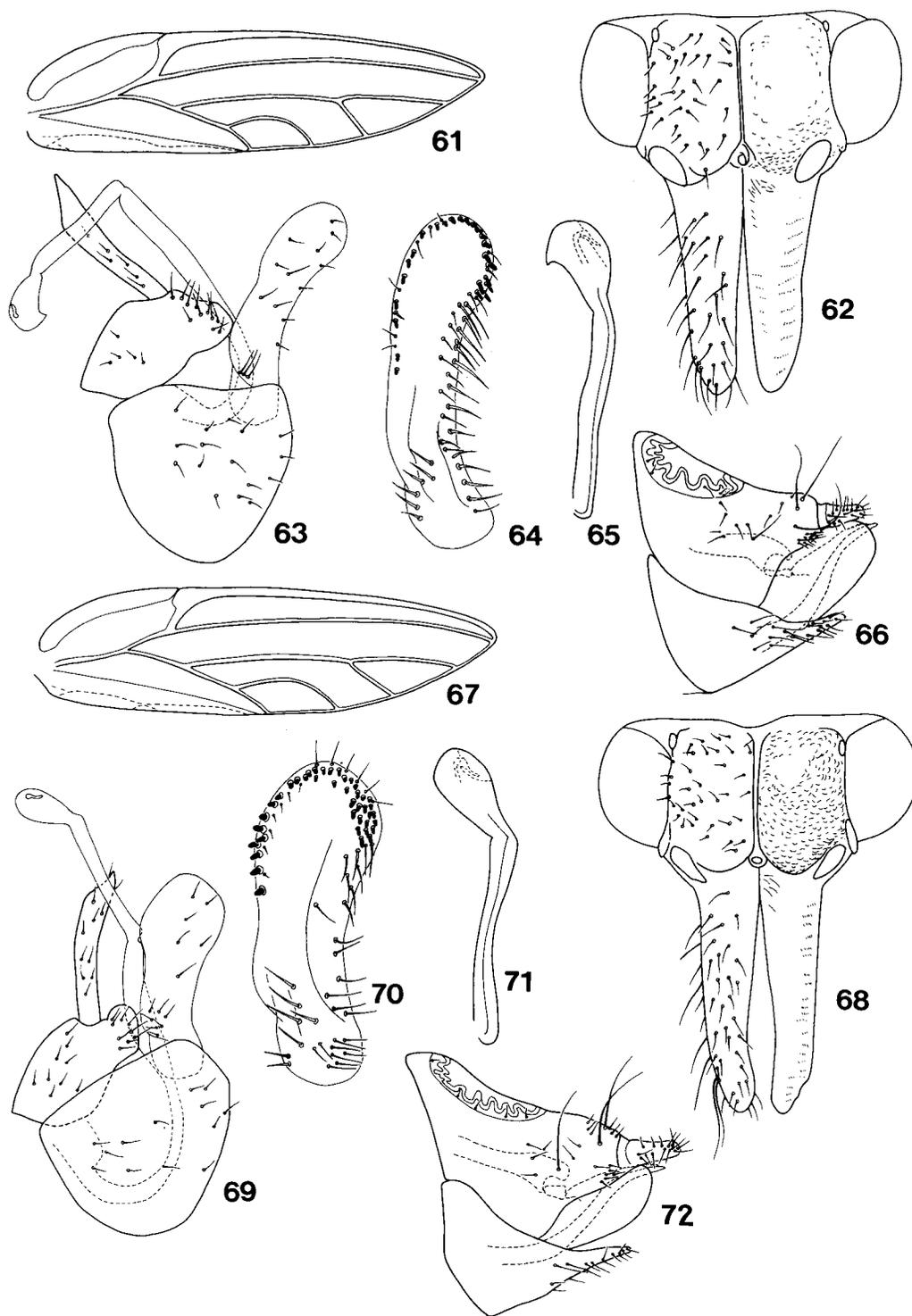
Figs. 25-35. *Boreioglycaspis* spp. 25-30 - *B. australiensis* Moore; 31-35 - *B. murphyi*, new species; 25, 31 - forewing; 26, 32 - head; 27, 33 - male terminalia; 28, 34 - paramere, inner surface; 29, 35 - distal portion of aedeagus; 30 - female terminalia.



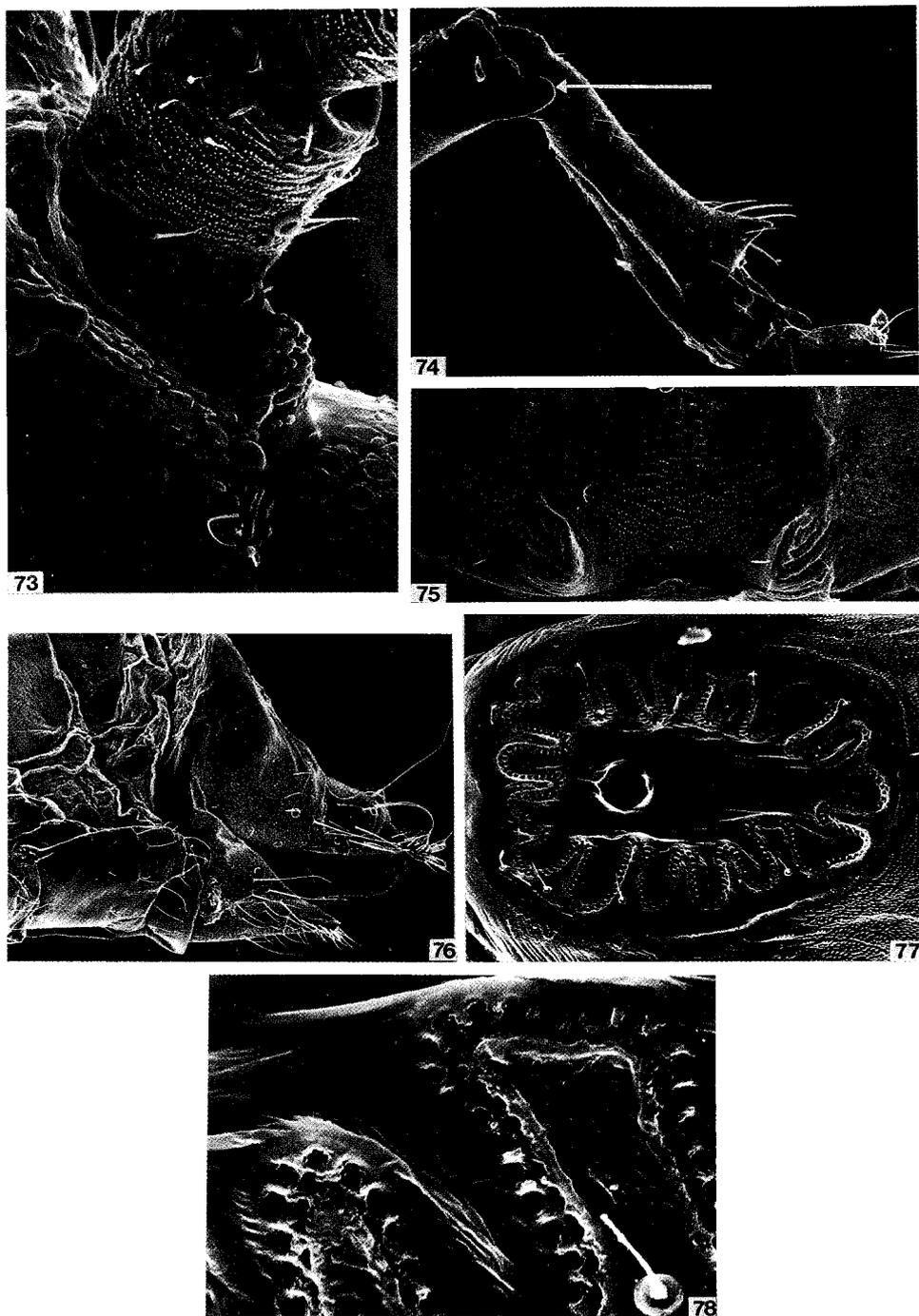
Figs. 36-48. *Boreioglycaspis* spp. 36-41 - *B. fasciata*, new species; 42-48 - *B. polymelasma* Moore; 36, 42 - forewing; 37, 43 - head; 38, 45 - male terminalia; 39, 46 - paramere, inner surface; 40, 47 - distal portion of aedeagus; 41, 48 - female terminalia; 44 - antennal segment 10.



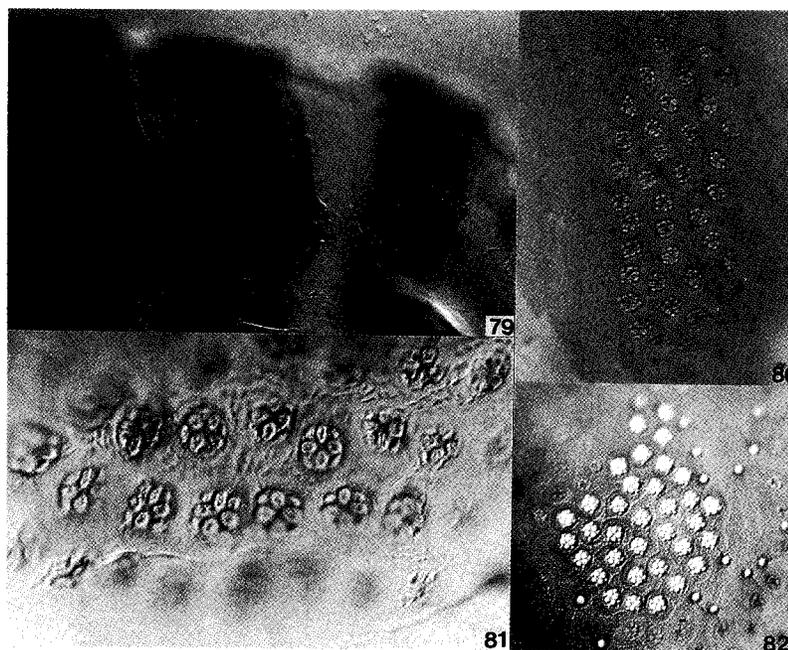
Figs. 49-60. *Boreioglycaspis* spp. 49-54 - *B. tristaniopsidis*, new species.; 55-60 - *B. moorei*, new species; 49-55 - forewing; 50, 56 - head; 51, 57 - male terminalia; 52, 58 - paramere, inner surface; 53, 59 - distal portion of aedeagus; 54, 60 - female terminalia.



Figs. 61-72. *Boreioglycaspis* spp. 61-66 - *B. borneensis* Moore; 67-72 - *B. eugeniae*, new species; 61-67 - forewing; 62, 68 - head; 63, 69 - male terminalia; 64, 70 - paramere, inner surface; 65, 71 - distal portion of aedeagus; 66, 72 - female terminalia.



Figs. 73-75. *Boreioglycaspis polymelasma* Moore. 73 - preocular sclerite; 74 - apex of metafemur with sclerotised lobe (arrow), metatibia and metatarsi; 75 - postmetanotum. Figs. 76-78. *Boreioglycaspis polymelasma* Moore. 76 - female terminalia, in profile; 77 - female circumanal ring; 78 - detail of circumanal ring.



Figs. 79-82. *Boreioglycaspis* spp., wax pores on abdomen. 79 - *B. eugeniae*, new species, adult; 80, 81 - *B. murphyi*, new species, adult; 82 - *B. eugeniae*, new species, larva.

**Table 1. Characters used in the cladogram in Fig. 83, strongly simplified from Hodkinson & White (1985). Only derived state of each character is given.**

**Adult "loss" character**

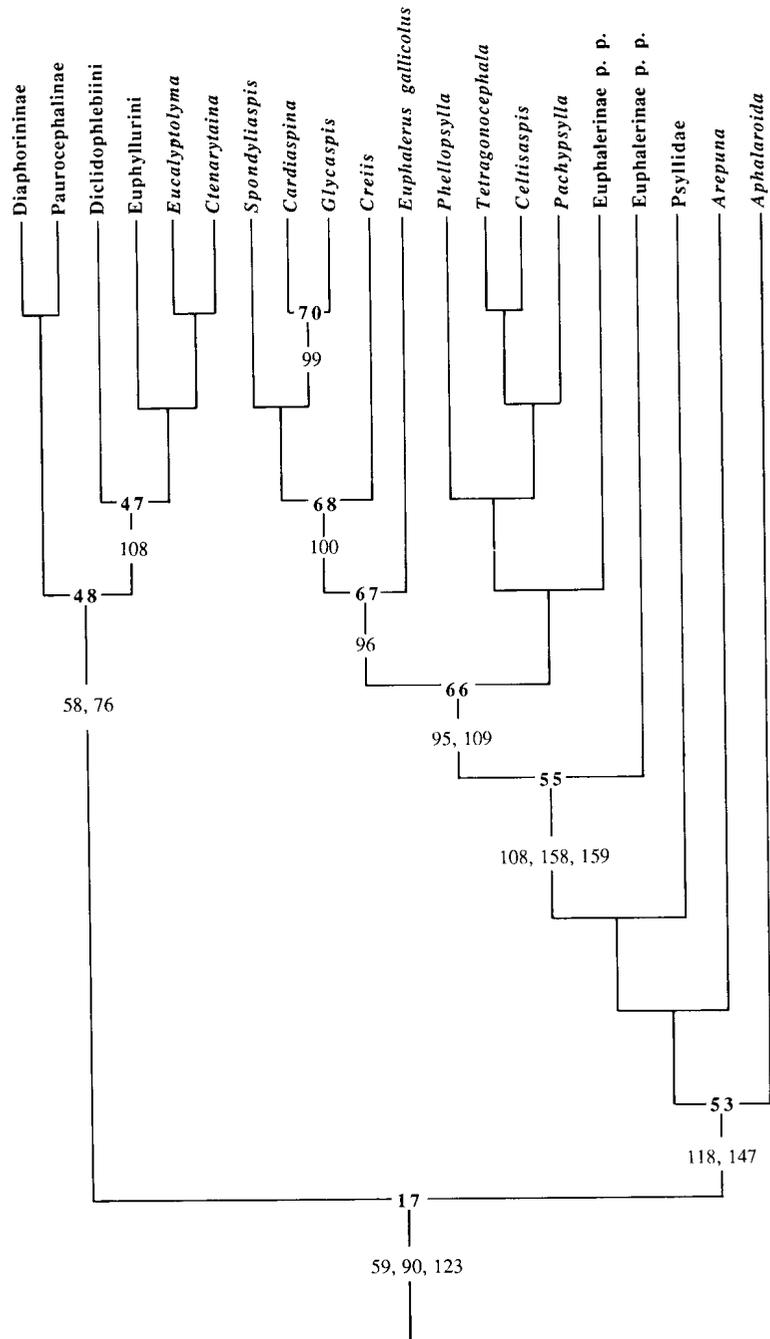
- 58 Rhinarium absent from segment V.  
 59 Rhinarium absent from segment seven.  
 76 Metatibia basal (genual) spine absent.

**Larval "gain" characters**

- 90 Unguitractor long.  
 95 Abdominal apex serrate.  
 96 Abdominal apex with large "teeth" at lateral extremities of serrate area (follows from character 95).  
 99 Abdominal segments produced laterally as rounded or "tooth" like projections.  
 100 Cauda pointed.  
 108 Anal pore-field (other than circum-anal ring) arranged as 1 + 1 rings or derivable from (discount characters 102 and 103). Rings placed ventrally or dorso-ventrally, i.e. each ring is partly dorsal and partly ventral).  
 109 Anal pore field (other than circum-anal ring) arranged as 2 + 2 rings or of derivable form. The rings are arranged ventrally 1 + 1 and dorsally 1 + 1.  
 118 Capitae setae present on body plus wing-pad margins and dorsal surfaces.

**Larval "loss" characters**

- 123 Basal area of arolium reduced to a thin membrane.  
 147 Antennae without sectasetae or derivable structures.  
 158 Body margin without capitae setae (except in some species which retain one seta behind each eye) (derived from character 118).  
 159 Body dorsal surface without capitae setae (derived from character 118).



83

Fig. 83. Strongly simplified cladogram by Hodkinson & White (1985) illustrating relationships of Spondyliaspidae. For explanations see Tab. 1 and text.

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