

## The larva of *Prospheres aurantiopicta* (Laporte & Gory) with comments on the larval characteristics of Polycestoid taxa (Insecta, Coleoptera, Buprestidae)

With 16 Figures and 1 Table (in pocket)

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**Abstract:** The larva of the Australian buprestid beetle, *Prospheres aurantiopicta* (Laporte & Gory) (Coleoptera: Buprestidae: Polycestinae) is redescribed in detail. Larval characters of taxonomic value used in defining the Polycestoid complex are outlined and their relative importance discussed for the first time. *Prospheres* has apparently the most advanced larva of the Polycestoid complex because it possesses the following set of apomorphic characters: absence of an additional projection (i.e. galea or lacinia) and the presence of a well-developed, large mala; prementum with microspinulae along the anterior margin and additional microspinulate zone in the middle; prothoracic plates with extensive zones of microteeth and asperities along the grooves, body with vast zones of microteeth and microspinulae; prothoracic spiracles typically buprestoid, abdominal ones with interstitial peritreme, without inner trabeculae. The larva of *Prospheres* in many respects is more closely related to those of *Polycetes* and *Thrincopyge* than to the representatives of the Polycestini tribal group, having the most advanced character states which resemble some of those found in the Chalcophorinae and Buprestinae. Hence its position within the Polycestoid complex is rather isolated. It is imperative that study should be made of the larvae of *Astraeus* and *Xyrosclis* as soon as they become available, in order to elucidate the true relationships and taxonomic position of the Australian Polycestinae. The larval characters confirm that the position of *Prospheres* within the Polycestoid complex is somewhat isolated and that *Prospheres* should be attributed to the separate tribe Prospherini Cobos, 1980; the differences between the larvae of *Prospheres* and *Polycetes* are such that they contradict the assignment of these genera within the tribe Polycestini.

**Zusammenfassung:** Die Larve des australischen Prachtkäfers *Prospheres aurantiopicta* (Laporte & Gory) (Coleoptera: Buprestidae: Polycestinae) wird im Detail beschrieben. Die zur Definition des Polycestoid-Komplexes genutzten Larvenmerkmale von taxonomischem Wert wurden herausgearbeitet und erstmalig in ihrer Bedeutung diskutiert.

*Prospheres* hat augenscheinlich die am höchsten entwickelte Larve des Polycestoid-Komplexes, da die Gattung die folgenden apomorphen Merkmale aufweist: das Fehlen eines zusätzlichen Fortsatzes am Unterkiefer (d. h. Galea oder Lacinia) und das Vorhandensein einer gut ausgeprägten, großen Mala; ein Praementum mit feinen Dornen am vorderen Rand und einer zusätzlichen fein bedornen Zone in der Mitte; prothorakale Platten mit ausgedehnten Zonen von Zähnen und Rauigkeiten längs der Furchen, am Körper ausgedehnte Zonen von Zähnen und Dornen; typisch buprestidenartige, prothorakale Tracheen, die abdominalen mit interstitialem Peritreme, ohne innere Trabeculae. Die Larve von *Prospheres* ist in vieler Hinsicht enger verwandt mit jener von *Polycetes* und *Thrincopyge*, als mit den Vertretern des Tribus Polycestini, deren Merkmale jenen der Chalcophorinae und Buprestinae ähnlich sind. Die Stellung von *Prospheres* im Polycestoid-Komplex ist daher ziemlich isoliert. So sollten sobald als möglich die Larven von *Astraeus* und *Xyrosclis* studiert werden, um die Beziehungen und die taxonomische Position der australischen Polycestinae aufzuklären. Die Larvenmerkmale bestätigen die isolierte Stellung von *Prospheres* im Polycestoid-Komplex und daß *Prospheres* zum separaten Tribus Prospherini Cobos, 1980 gestellt werden muß; die Unterschiede zwischen den Larven von *Prospheres* und *Polycetes* widersprechen einer Zuweisung dieser Gattungen zum Tribus Polycestini.

### Introduction

The genus *Prospheres* Saunders, 1868 (type species *Buprestis aurantiopicta* Laporte & Gory, 1838, by monotypy), according to the recent revision of LEVEY (1978), comprises 4 species which occur exclusively in the Australian region. These are *P. aurantiopicta* Laporte & Gory (continen-

tal Australia and New Zealand), *P. chrysocomus* Fauvel (New Caledonia), *P. norfolkensis* Levey (Norfolk I.) and *P. alternecostata* Levey (New Guinea). *Prospheres aurantiopicta* (Laporte & Gory) is the most widely distributed and most relatively well known species among them; the distributional and biological data for this species have been generalised by LEVEY (1978) and HAWKESWOOD & PETERSON (1982); the larva was described by LEVEY (1978) for the first time. *Prospheres aurantiopicta* is widely distributed in eastern Australia (Queensland, New South Wales, Australian Capital Territory, South Australia, Northern Territory and New Zealand). Its larvae is known to develop inside the wood of *Araucaria cunninghamii* Don. (Araucariaceae, Araucariales), as well as *Pinus patula* Schlecht. & Cham. (Pinaceae, Pinales), an introduced species to Australia; there are also some data recorded concerning emergence of adults from processed timber manufactured from conifer wood, but in one case, a maple (*Acer*, Aceraceae) chair was recorded as a larval host (LEVEY 1978), which tends to suggest that *P. aurantiopicta* is potentially polyphagous. It is supposed that *P. alternecostata* also develops in *Araucaria* (LEVEY 1978). It is apparent that *Araucaria* is the native host plant for *Prospheres* and the coincidence of their distributional ranges in the Australian region confirms this assumption.

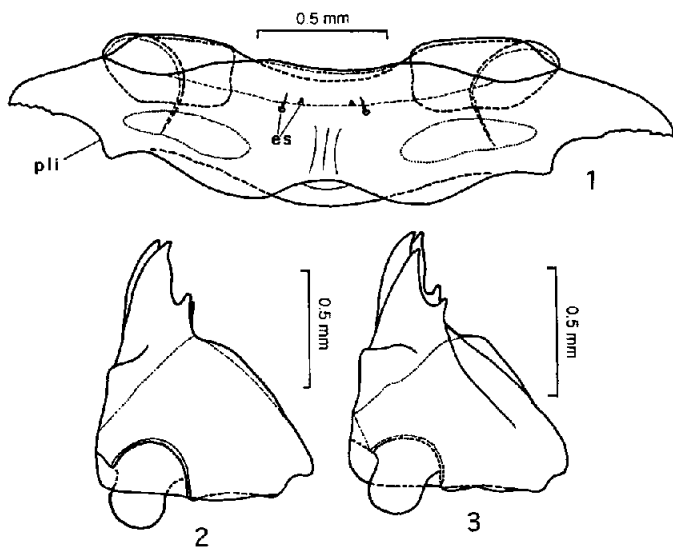
The taxonomic position and relationships of *Prospheres* remain debatable. Until recently *Prospheres* was attributed to the tribe Polycestini (KERREMANS 1906; OBENBERGER 1926; COBOS 1955), but then LEVEY (1978) transferred it to the Polyctesini, highlighting its close relationship to *Euleptodema* Obenberger, 1928 (= *Blepharum* Thomson, 1878), which was placed in Paraleptodemini Cobos, 1975 (= Cinyrini Cobos, 1979) (Chalcophorinae) by COBOS (1975). Later, COBOS (1980) erected the separate monogeneric tribe Prospheresini for *Prospheres* but since this spelling does not correspond to recent rules of zoological nomenclature, the spelling was changed to Prospherini (BELLMAY 1985; 1986). HOLYNSKI (1993) attributed both *Prospheres* and *Euleptodema* to the subtribe Prospherina which he included within the tribe Tyndarini of the subfamily Buprestinae [Buprestinae, (sensu HOLYNSKI 1993) comprises the traditional subfamilies Polycestinae, Acmaeoderinae, Thrinopyginae, Mastogeninae, Chalcophorinae, Sphenopterinae, Buprestinae, and Chrysobothrinae]. Although the larva of *Euleptodema* remains unknown, its close relationship to *Prospheres* is confirmed by many adult characters, including antennal morphology (Volkovitsh, unpublished data). The taxonomic position and relationships of *Prospheres* based on larval morphology will be discussed below. Due to the kindness of Dr. Brain Levey we received the opportunity of studying the larva of *P. aurantiopicta* and comparing it with other known Polycestoid larvae to perform a new analysis and to reevaluate its characters, which has assisted us to make clearer its taxonomic position and relationships within the Polycestinae. The larva of *P. aurantiopicta* is described in detail below.

### Description of the larva of *Prospheres aurantiopicta* (Laporte & Gory)

#### *Prospheres aurantiopicta* (Laporte & Gory) (Figs. 1-16)

Length of the single larva studied, (presumably last instar) = 18.6 mm. Larva (Fig. 10) of the usual buprestid type with prominently enlarged prothorax into which the head capsule is retracted; this larva corresponds to the 1<sup>st</sup> morpho-ecological type of *Acmaeoderella* larva (VOLKOVITSH 1979). Body of preserved larva whitish with weakly sclerotized mouthparts, spiracles and areas around the prothoracic grooves; prothoracic grooves colourless.

Head and mouthparts. Epistome (Fig. 1) narrow, about 4.7 times wider than long, with very weakly sclerotized, brownish anterior and lateral margins and mandibular condyles; remaining surface semi-transparent, yellowish, with poorly demarcated posterior margin rather shallowly emarginate, almost completely concealing the mandibular condyles; posterior margin slightly bisinuate, indistinct; latero-posterior corners blunt, nearly rectangular, bearing a long seta situated at the place of attachment of the antennal articular membrane (not shown); epistome bearing two pairs of closely arranged epistomal sensillae (Fig. 1, es), situated anterior to the middle of epistome; each pair consists of one short trichoid lateral sensilla and one campaniform median sensilla, each at about the same level; the distance between each pair of sensillae is much greater than the distance between each sensilla in the same pair.



Figs. 1-3. *Prosppheres aurantiopicta* (Laporte and Gory) mouthparts. 1: Epistome showing postero-lateral (antennal) incision (pli) and epistomal sensillae (es), 2: Left mandible, dorsal view; 3: Right mandible, ventral view. (Illustration: M. G. Volkovitsh).

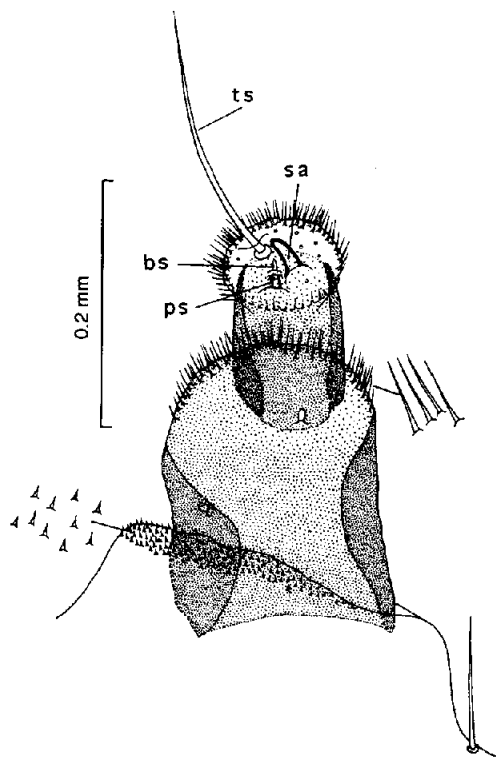


Fig. 4. *Prosppheres aurantiopicta* (Laporte and Gory). Left antenna showing trichosensilla (ts), sensory appendage (sa), palmate (ps), and basiconic (bs) sensillae (Illustration: M. G. Volkovitsh).

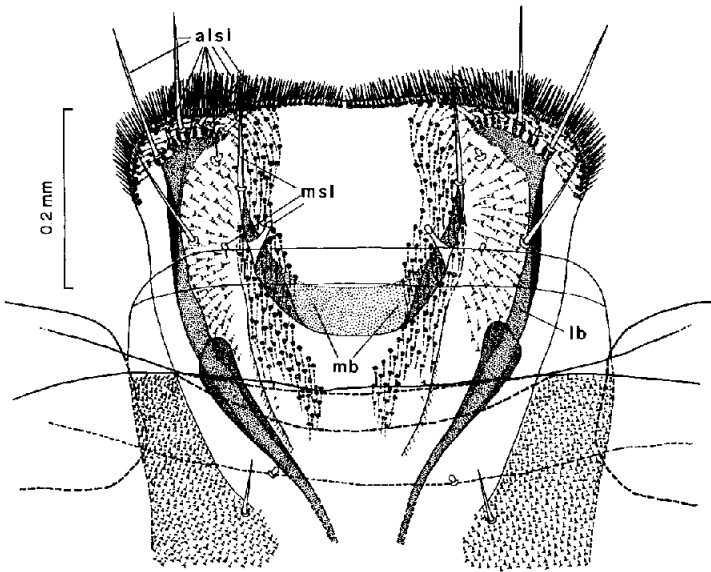


Fig. 5. *Prosppheres aurantiopicta* (Laporte and Gory) mouthparts. Labrum, showing armature, median (mb) and lateral (lb) branches of palatine sclerite, median sensillae of the labrum (msl), and antero-lateral sensillae of the labrum (alsl). (Illustration: M. G. Volkovitch).

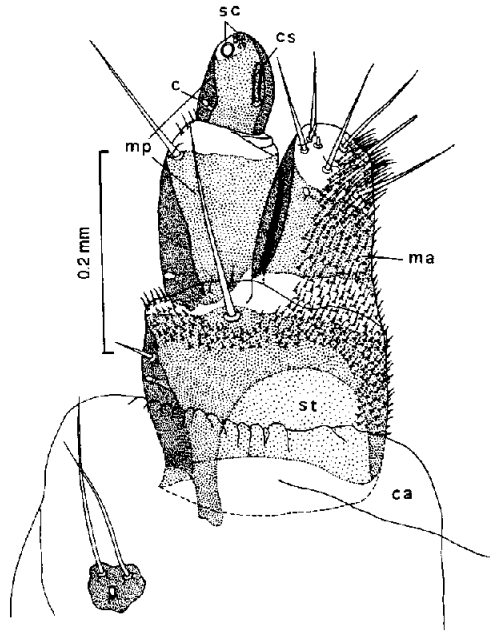


Fig. 6. *Prosppheres aurantiopicta* (Laporte and Gory) mouthparts. Left maxilla showing cardo (ca), stipes (st), maxillary palpus (mp) with modified (cs) and campaniform (c) sensillae, sensory structures (sc), and mala (ma). (Illustration: M. G. Volkovitch).

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Clypeus (Fig. 5) narrow, collar-shaped, membranous, glabrous, with inner structure clearly visible through transparent epistome; inner surface covered with very dense, small microspinulae laterally.

Labrum (Fig. 5) subquadrate, slightly broadened anteriorly, mostly membranous, bearing poorly sclerotized palatine sclerites internally; with setae, trichoid and campaniform sensillae, connected to branches of palatine sclerites or attached freely to membrane, as well as with zones of microspinulae and microsetae on both surfaces. Anterior margin weakly emarginate between broadly rounded antero-lateral corners, which form poorly developed lateral lobes, with slightly diverging anterior sides. Palatine sclerites divided into two isolated branches, i.e. median internal branch (Fig. 5, mb) and lateral external branch (Fig. 5, lb), which are almost parallel to each other and to the median line of labrum; not connected posteriorly and with free-ended posterior processes. Median sensillae of labrum (Fig. 5, msl) (VOLKOVITSH & HAWKESWOOD 1994) consist of one long apical seta situated at anterior third of labrum and extending to anterior margin of labrum, and two campaniform sensillae, situated at about the latitudinal mid-line of labrum almost on same level, external campaniform sensilla attached freely to membrane, the distance between apical seta and both campaniform sensillae slightly longer than the distance between each campaniform sensilla. Anterior-lateral sensillae (Fig. 5, als) comprise three sharp setae and one campaniform sensilla externally, three blunt setae and one campaniform sensilla near anterior-lateral margin of labrum internally. External sensillae arranged as follows on each side: (a) two long setae, situated very close to each other but not fused at their bases, (b) one campaniform sensilla situated between the two long setae immediately above the apex lateral branches of palatine sclerite, and (c) one sharp seta situated near inner margin of lateral branches of palatine sclerite anterior to latitudinal mid-line of labrum. Internal sensillae arranged as follows on each side: (a) three blunt setae, situated close to each other but not fused at their bases, arising from the apex of lateral branches of palatine sclerite and directed medianally towards external setae, (b) one campaniform sensilla freely attached to membrane posterior to bases of the three blunt setae. The composition and position of anterior-lateral sensillae are as follows:

$$\frac{1t + 2c + 3t - 4t}{1c - 2t + 3t + 4t}$$

(The external sensillae designations are in the numerator and the internal ones in the denominator of this formula; 1, 2, 3 ... = the ordinal number of sensillae from most median to lateral ones; t = trichoid, c = campaniform sensillae, + = with closely situated bases, - = with distant bases; see VOLKOVITSH & HAWKESWOOD 1994).

External surface of labrum with a very narrow, transverse band of very dense microsetae (Fig. 5) bordering the entire anterior margin which are longer and denser at anterior-lateral corners of labrum and shorter and less dense in middle; remaining surface glabrous. Labrum ventrally (epipharynx) with a rather dense and complicated armature consisting of zones of microsetae on anterior-lateral corners, a region of dense, short microspinulae on sides between lateral and median branches of palatine sclerites, and subparallel curved zones of microsetae extending in a narrow band to base of labrum and surrounding pharynx.

Antennae (Fig. 4), 2-segmented, situated in a shallow, posterior-lateral (antennal) incisure (Fig. 1, pli) in posterior-lateral corners of epistome; articular membrane well-developed, bearing a narrow band of very short microspinulae along anterior-lateral margin externally and a long, sharp seta internally; articular membrane not forming a cover around 1<sup>st</sup> segment, which is weakly invaginated by membrane at base only. Segment 1 broadly cylindrical, about 1.3 times as long as wide and longer than segment 2, weakly sclerotized, with a narrow fringe of microspinulae along the rounded anterior margin and a prominent campaniform sensilla on external surface towards apex of segment in base of segment 2, and another one on internal surface near external margin. Segment 2 elongate, cylindrical, about 1.8 times as long as wide, attached to inner surface of segment 1 (near apex); apex disc-like, broader than rest of segment and bearing a fringe of microspinulae around margin and without a distinct apical cavity; disc bearing the following sensory structures which arise from small tubercles: (a) a long, sharp seta (trichosensilla) (Fig. 4, ts), which is about 1.3 times longer than the length of segment 2; (b) a relatively slender sensory appendage

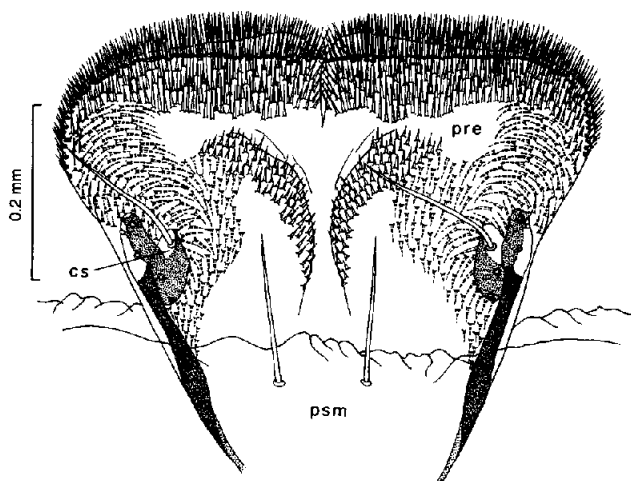


Fig. 7. *Prosppheres aurantiopicta* (Laporte and Gory) mouthparts. Labium, showing prementum (prm) with its armature, corner sclerites (cs), and postmentum (psm) with 2 sharp setae. (Illustration: M. G. Volkovitsh).

(Fig. 4, sa) not extending outside but covered by membrane; (c) two small palmate sensilla situated very close to each other (Fig. 4, ps); and (d) one very small, peg-like basiconic sensilla (Fig. 4, bs). [According to LEVEY (1978), the antennae of *Prosppheres* consist of 4 segments since he incorrectly regarded the articular membrane and sensory appendage (sa) as antennal segments].

Mandibles (Figs. 2, 3) each with a weakly sclerotized, yellowish, semi-transparent base and a strongly sclerotized, black apex; base broad, strongly narrowed towards apex, almost forming the shape of a right-angled triangle; apex bearing five teeth consisting of three, sharp, elongate, almost equal, apical teeth and two distinct, sharp, lateral teeth.

Hypostome very slightly sclerotized, almost totally membranous except for condylar recesses for attachment of mandibles, and anterior margin; posterior margin indistinct; ocelli absent; singular trichoid, campaniform and deeply set sensillae present.

Labiomaxillary complex (Figs. 6, 7). Maxillae (Fig. 6): maxillary basis (cardo) (Fig. 6, ca) membranous, glabrous, with two very long sharp setae and one campaniform sensilla situated on a small, isolated, slightly sclerotized but distinct sclerite on the post-lateral corner near base of cardo. Stipes (Fig. 6, st) with a weakly sclerotized internal sclerite and bearing one campaniform sensilla and one very short, sharp seta near lateral external margin, and one long, sharp seta near the anterior margin below the maxillary palpus and extending to base of 2<sup>nd</sup> segment of maxillary palpus; stipes externally with a fringe of short, very sparse microspinulae at anterior-lateral corners; stipes internally with a sparse covering of very short microspinulae along anterior and internal margins. Maxillary palpus (Fig. 6, mp) 2-segmented; basal segment strongly sclerotized, elongate, cylindrical, about 1.7 times as long as wide, bearing a long, sharp seta arising from near anterior-lateral corner and extending to apex of segment 2, and a campaniform sensilla situated near posterior-lateral corner; anterior margin with a fringe of sparse, indistinct microspinulae in anterior-lateral corner; 2<sup>nd</sup> segment slightly elongate, about 1.4 times longer than wide, strongly sclerotized, with one long, modified sensilla (Fig. 6, cs) internally near internal margin and one campaniform sensilla (Fig. 6, c) on external margin at base; apically with 10 small, conical sensory structures (Fig. 6, sc), one of which is much larger than the others. Mala (Fig. 6, ma): weakly sclerotized except for external margin, without a distinct internal sclerite; elongate, slightly longer than 1<sup>st</sup> segment of maxillary palpus, slightly converging to apex, about 1.6 times wider than long; externally almost glabrous, without microspinulae; with one small campaniform sensilla, close to internal margin above middle, four long, sharp setae, equal in length to length of 2<sup>nd</sup> segment of maxillary palpus, at or near apex of mala, and two peg like, basiconic sensillae near anterior-lateral margin, one of them, situated more apically and longer than the other; internally with very dense,

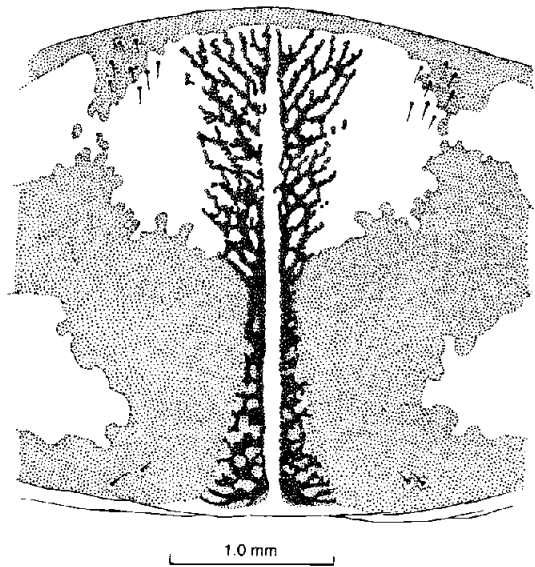


Fig. 8. *Prosppheres aurantiopicta* (Laporte and Gory). Pronotal plate showing the groove zones of micro-teeth (dotted), bristles, and asperities along the groove. (Illustration: M. G. Volkovitsh).

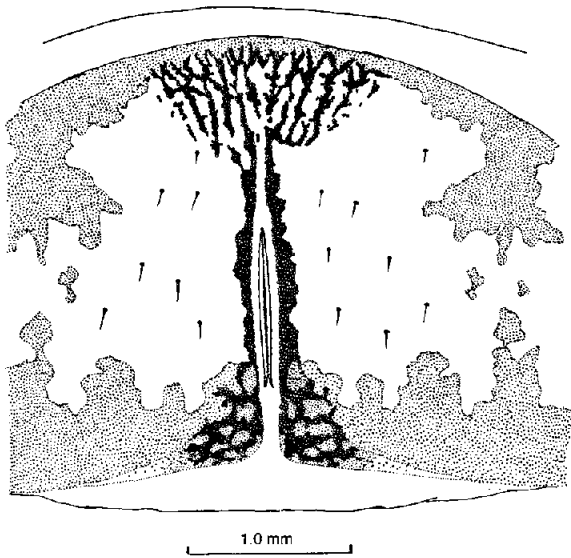


Fig. 9. *Prosppheres aurantiopicta* (Laporte and Gory). Prosternal plate showing the groove, zones of micro-teeth (dotted), bristles, and asperities along the groove. (Illustration: M. G. Volkovitsh).

elongate microspinulae and two long, sharp spinae on internal margin near apex; structures resembling „galea“ of *Acmaeoderella* larvae (VOLKOVITSH 1979, Fig. 28) or „lacinia“ of *Ptosima* larvae (BÍLY 1972) are absent; similar structures were also found in *Chrysophana* and all known larvae of Thrincopyginae, Polycestinae and Acmaeoderinae. Labium (Fig. 7): slightly transverse; prementum (prelabium according to LEVEY 1978) (Fig. 7, pre) about 1.6 times wider than long, deeply emarginate in middle, anterior margin scarcely bisinuate, lateral sides straight, strongly

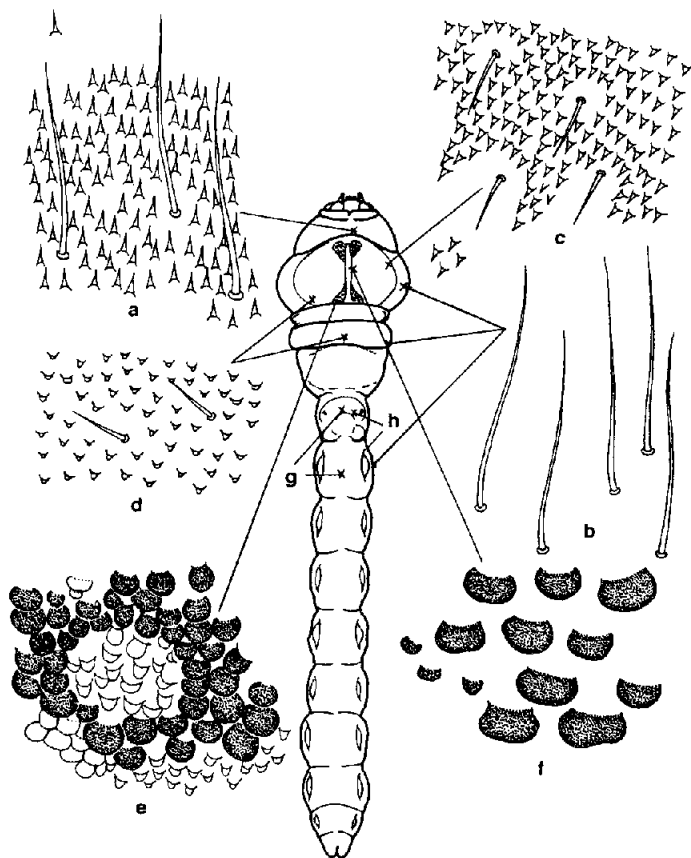


Fig. 10. *Prospheres aurantiopicta* (Laporte and Gory). Ventral view of larvae according to LEVEY (1978, Fig. 9), modified, showing microspinulae and long bristles on the anterior prothoracic membrane (a), long bristles at the sides of the thoracic and abdominal segments (b), microteeth and shorter bristles on the anterior-lateral part of the prothoracic plate (c), reduced microteeth arising from tubercles and shorter bristles on the posterior-lateral part of the prothoracic plates and the middle of the mesothorax (d), unevenly sclerotized asperities at the base of the prothoracic grooves (e), unevenly sclerotized asperities at the middle part of the prothoracic grooves (f), microspinulae on the lateral parts (h), and unsclerotized microteeth on the central part (g). (Illustration: M. G. Volkovitch).

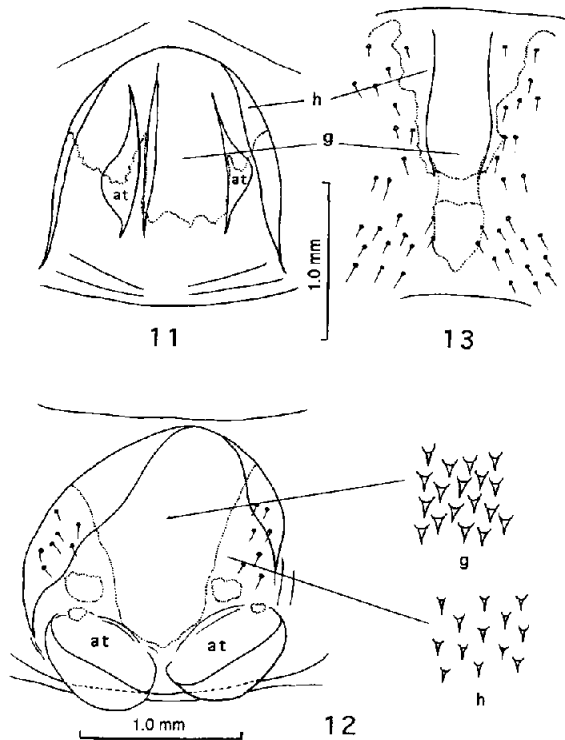
converging to base with maximum width in anterior  $\frac{1}{4}$ ; maxillary mala concealed by anterior-lateral lobes. External surface of prementum with a narrow transverse band of long, dense microsetae along entire anterior margin of labium, changing to microspinulae arising from membranous tubercles posteriorly in the apical  $\frac{1}{4}$ ; posterior margin of this zone slightly curved; remaining area of prementum glabrous except for two small, isolated, longitudinally curved (lunate) microspinulate areas in middle (such zones are characteristic of many Buprestinae and Chalcophorinae); base of prementum with two corner sclerites (labial palpi according to LEVEY 1978) (Fig. 7, cs) each bearing one long, sharp seta almost reaching anterior margin, and five small campaniform sensillae; internal surface of prementum with dense microsetae on anterior corners, changing to microspinulae along lateral sides and forming a complicated pattern. Postmentum (postlabium according to LEVEY 1978) (Fig. 7, psm) with two long, sharp setae extending to base of isolated microspinulate zones on prementum. [Structurally, the mouthparts of *Prospheres* are rather similar to those of higher Buprestinae and Chalcophorinae].

Thorax (Figs. 8–10). Pronotal (Fig. 8) and prosternal (Fig. 9) plates poorly developed, unsclerotized, unevenly covered with fields and isolated areas of scarcely visible, unsclerotized

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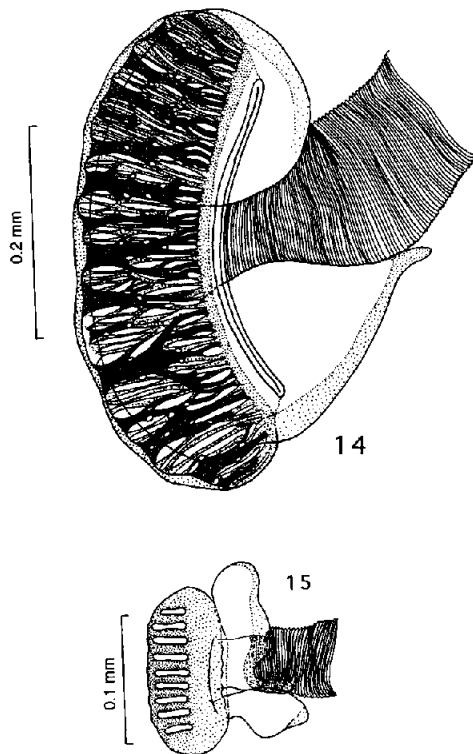
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Figs. 11–13. *Prospheres aurantiopicta* (Laporte and Gory). Dorsal ambulatory pad of the 1<sup>st</sup> abdominal segment, showing additional tubercles (at), microspinulae on the lateral parts (h), and unsclerotized microteeth on the central part (g); 12: Ventral ambulatory pad of the 1<sup>st</sup> abdominal segment, showing additional tubercles (at), microspinulae on the lateral parts (h), and unsclerotized microteeth on the central part (g); 13: Dorsal ambulatory pad of the 2<sup>nd</sup> abdominal segment, showing microspinulae on the lateral parts (h), and unsclerotized microteeth on the central part (g). (Illustrations: M. G. Volkovitch).

tubercles and microteeth (Fig. 10, c, d); pronotal plate (Fig. 8) with glabrous zones around anterior part of groove and on sides; posternal plate (Fig. 9) glabrous in the middle, with fields of microteeth mainly along the base, anterior and anterior-lateral margins; in zones adjacent to grooves of both thoracic plates, microteeth become reduced while tubercles become enlarged and partly sclerotized, changing to grain-like, unequal asperities of differing sizes around grooves (Fig. 10, e.) and forming a complicated, tree-like pattern on the plates (Figs. 8–10); [these asperities are characteristic of some Buprestinae, i.e. *Capnodis*, *Dicerca*, *Diadoxus*, *Eurythrea* (VOLKOVITSH & HAWKESWOOD 1994), but they have never been discovered before in Polycestinae]. Prothoracic plates also with sparse, short bristles (Figs. 8, 9, 10, c, d), which are more common on prosternal plate (Fig. 9); anterior prothoracic membrane with microspinulae and long, sparse bristles (Fig. 10a) on anterior margin and dense, long bristles (Fig. 10, b) at sides; anterior-lateral regions of prothorax also with zones of microspinulae (Fig. 10, a, 12, h) which change to microteeth (Fig. 10c) on plates. Prothoracic grooves (Figs. 8–10) unsclerotized and colourless, visible only because of presence of surrounding asperities; pronotal groove (Fig. 8) uniramous, stripe-like, slightly narrowing at base and apex; zone of asperities (Fig. 10, f) surrounding groove enlarged at base, then narrowed toward middle and enlarged towards apex, forming oblique, curved branches on anterior portion of pronotal plate; asperities forming a net-like pattern in posterior half resulting from uneven sclerotization and differing size (Fig 10, e). Prosternal groove (Fig. 9) uniramous, spindle-shaped, slightly narrowed at base and markedly narrowed in anterior  $\frac{1}{3}$ , with distinct lon-



Figs. 14–15. *Prospheres aurantiopicta* (Laporte and Gory). 14: Thoracic spiracle; 15: abdominal spiracle. (Illustrations: M. G. Volkovitsh).

gitudinal stripe bearing sclerotized median line in posterior half; zone of asperities surrounding the groove broadly enlarged at base, forming a net-like pattern as on the pronotum and gradually fusing with adjacent areas of microteeth, then forming irregular, longitudinal bands along central part of groove and broadly enlarged toward apex in anterior  $\frac{1}{4}$  giving rise to obliquely curved branches as on the pronotum, but forming a sharper angle. Meso- and metathorax nearly completely covered with fields of microteeth and tubercles, sparse short bristles (Figs. 10, c, d, g, h) on both dorsal and ventral surfaces and long bristles on lateral margins (Fig. 10, b), with only small glabrous areas. [LEVEY (1978: 724) noted the presence of rudimentary legs on all thoracic segments, but none were found on the specimen studied]. Thoracic spiracles (Fig. 14) weakly sclerotized, reniform, elongated, about 3.7 times longer than wide, with dense, strongly branched trabeculae.

Abdomen (Figs. 10–13). Abdominal segments (Fig. 10) almost as long as wide, flattened, with darkened, longitudinal, depressed zones laterally; 1<sup>st</sup> segment much narrower than metathorax and other abdominal segments, with markedly developed ambulatory pads on both surfaces, which are clearly visible on the prepared slides (Figs. 11, 12); dorsal pad bearing two small, additional tubercles laterally (Fig. 11, at), ventral pad bearing two small additional tubercles at base (Fig. 12, at; LEVEY 1978, Fig. 9); most of surface of ambulatory pads covered with microspinulae (Fig. 12, h), changing to microteeth (Fig. 12, g); additional tubercles glabrous, zones surrounding tubercles with long bristles (Fig. 10, b); abdominal segments 2–7 of about similar size, markedly wider than 1<sup>st</sup> segment, bearing longitudinal ambulatory pads in anterior half on both dorsal (Fig. 13) and ventral surfaces, surrounded anteriorly with fields of microspinulae (Fig. 12, h) which from longitudinal bands in posterior half of abdominal segments and change to microteeth (Fig. 12, g) on the pads, remaining surface covered in long bristles (Fig. 10, b); abdominal segment 8 without distinct ambulatory pads, with only a vast field of microspinulae which occupies all

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P. por  
dera  
pallid

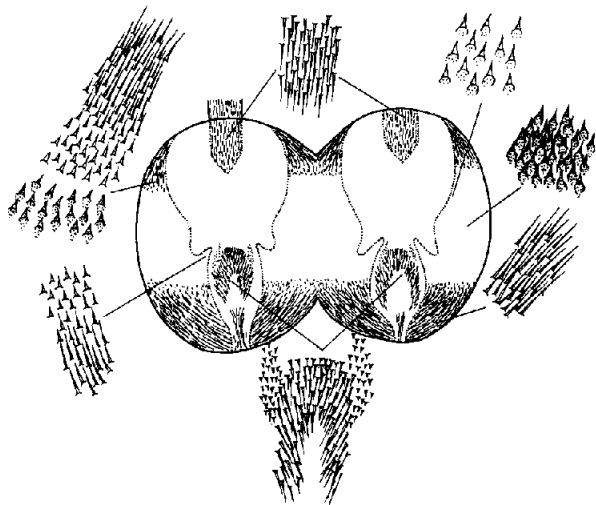


Fig. 16. *Prospheres aurantiopicta* (Laporte and Gory). 16: Armature of proventriculus. (Illustration: M. G. Volkovitsh).

middle portion of segment on both surfaces; abdominal segments 9–10 covered mainly in bristles, with only small zones of microspinulae. Abdominal spiracles (Fig. 15) very variable, oval, reniform or irregular in shape, weakly sclerotized, nearly 2.3 times longer than wide, without any inner trabeculae, with a markedly developed, cancellate peritreme, with almost parallel narrow slits as has been found in *Neocuris* and *Paratassa* larvae.

Proventriculus (Fig. 16). Morphology of fields and their armature is rather complicated, which is characteristic of those species feeding on hard, woody, fibrous organic material; armature includes hairs and well developed, sclerotized microteeth situated singly on apices of simple, sclerotized tubercles in central portion; microteeth denser and larger in middle of main fields, sparser and smaller near the margins; changing to microspinulae anteriorly and posteriorly, and then to setae; in posterior half of proventriculus, hairs and microteeth form additional small fields on both surfaces.

Material examined: Single larva (presumably last instar) from log billets of *Araucaria cunninghamii* D. Don. (Araucariaceae), 13 April 1972, Imbil State Forest, Queensland, collector R. A. Yule. (Specimen lodged in the collections of the Zoological Institute, St. Petersburg, Russia).

### Discussion

#### (a) General comments on *Prospheres* larva and its comparison with other buprestid taxa

The larva of *Prospheres aurantiopicta* (Laporte & Gory) is easily distinguished from all known Australian taxa with the exception of *Strigoptera* and Agriloid genera, in having a single (uniramous) pronotal groove. The differences between *Prospheres* and *Strigoptera* are shown in Table 1. The Agriloid taxa which also possess the single pronotal groove are distinguished in having spiracles of a circular type, by the presence of mandibular prosteca, and by the absence of a sclerotized proventriculus (VOLKOVITSH & HAWKESWOOD 1990). In order to compare the larva of *P. aurantiopicta* with those of other Polycestoid taxa, the larvae of the following tribes and genera were examined: Thrincopygini: *Thrincopyge alacris* LeConte, *T. ambiens* (LeConte) (?); Polyctesini: *Polyctesis rhois* Marscul, *Chrysophana conicola* Van Dyke; Tylauchenini: *Neocypetes* sp.; Tyn-darini: *Tyndaris* sp.; Polycestini: *Strigoptera bimaculata* (Linnaeus), *Polycesta cortezi* Thomson, *P. porcata* (Fabricius); Ptosimini: *Ptosima undecimmaculata* (Herbst); Acmaeoderini: *Acmaeodera* (s.str.) *chalcithorax* Obenberger, A. (*Palaeotethya*) *bipunctata* (Oliver), A. (*Acmaeotethya*) *pallidepicta* (Reitter), A. (*Cobosiella*) *chotanica* (Semenov), A. (*Ptychomus*) *polita* (Klug), *Xan-*

*theremia* (s.str.) *koenigi* (Ganglbauer), *Acmaeoderella* (*Carininota*) *flavofasciata* (Piller & Mitterpacher), *A. (Omphalothorax) adpersula* (Illiger), *A. (s.str.) nivetecta* Volkovitsh, *A. (Euacmaeoderella) alepidota* Volkovitsh, Paratrachyini: *Paratrachys hederiae* Saunders. The results of our morphological analyses and comparison of Polycestoid larvae are shown in Table 1.

The main diagnostic characters of *Prospheres* larva which allow it to be clearly distinguished from all other known Polycestoid larvae are as follows: (a) maxillary stipes with only one projection (mala), without any trace of an additional non-sclerotized projection (galea?) (Fig. 6); (b) prementum of labium with additional areas of microspinulae on external surface in centre (Fig. 7); (c) articular membrane of antennae with area of microspinulae along the anterior-lateral margin externally (Fig. 4); and (d) prothoracic grooves surrounded by large sclerotized asperities (Figs. 8–10). The first feature is characteristic of Buprestoid and Agriloid taxa; the others sometimes also occur among Buprestoid larvae but have never been found among Polycestoid taxa.

Additional diagnostic characters of *P. aurantiopicta* not found in all the other known Polycestoid larvae are as follows: (a) very poorly sclerotized mouthparts which are yellowish in colour; (b) anterior margin of epistome which completely covers the mandibular condyles (Fig. 1); (c) 2<sup>nd</sup> antennal segment which lacks a distinct apical cavity but has a disk-like membranous extension (Fig. 4); (d) strongly elongated, poorly sclerotized mandibles, with 5 sharp teeth apically (Figs. 2, 3); (e) 1<sup>st</sup> abdominal segment which bears 2 additional lateral ambulatory pads dorsally (Fig. 11) and 2 basal ones ventrally (Fig. 12); (f) abdominal segments 2–7 which have elongated pads on both surfaces (Fig. 13); and (g) abdominal spiracles which have a markedly developed cancellate peritreme which bears a few interstices arranged parallel to each other, and which have no trace of inner trabeculae (Fig. 15); this type of spiracle (both thoracic and abdominal) has been found also in *Paratassa* larvae (BÍLY & VOLKOVITSH 1996).

Apart from these main diagnostic characters, the larva of *Prospheres* differs from other Australian Polycestoid larvae (e.g. *Stringoptera*) in some other characters (Table 1). *Prospheres* differs from *Stringoptera* by the following: (a) labrum which bears microsetae along the anterior margin (Fig. 5); (b) median and lateral branches of palatine sclerite which are isolated (Fig. 5); (c) median sensillae of labrum which consists of 1 trichoid and 2 campaniform ones (Fig. 5); (d) anterolateral sensillae of labrum which comprises 3 blunt setae internally (Fig. 5); (e) 1<sup>st</sup> segment of antennae which is markedly elongate (Fig. 4); (f) anterior margin of 1<sup>st</sup> antennal segment which is microspinulate (Fig. 4); (g) lateral sclerite of maxillary cardo which bears 2 setae and one campaniform sensilla (Fig. 6); (h) 1<sup>st</sup> segment of maxillary palpi which is markedly elongate (Fig. 6); (i) prementum of labium which has microsetae along anterior margin externally (Fig. 7); (j) postmentum of labium which has 2 long setae (Fig. 7); (k) thoracic plates which are covered with microteeth and, prothoracic ones which bear asperities along the grooves (Figs. 8–10); and (l) abdominal spiracles which are without inner trabeculae (Fig. 15). *Stringoptera* also differs from *Prospheres* in having additional campaniform sensillae on the maxillary stipes and the corner sclerites of the labium (these are characteristic of all known Polycestini), in the presence of fine, longitudinal rugosities on the prothoracic plates, and the presence of a very strong, well sclerotized armature of the proventriculus.

*Paratrachys* is another Polycestoid genus whose larva was described by BÍLY (1989), and which was recently reported to be found in Australia (BELLAMY & WILLIAMS 1995). It differs significantly from *Prospheres* and from all other known Polycestoid taxa in having profound modifications of its characters (Table 1), including the development of a trachyoid body, which has obviously resulted from its leaf-mining habit.

#### (b) Comments on larval characteristics of the Polycestoid complex.

At present there are two main conceptions on the classifications of the presumably primitive taxa which are regarded here as the Polycestoid complex. The first (traditional) one treats them as belonging to the subfamily Polycestinae (sensu lato) or to the complex of independent subfamilies (i.e. Polycestinae, Acmaeoderinae, Thrincopyginae and Mastogeninae); this conception was generalized by BELLAMY (1985). Another, non-traditional viewpoint on the status, taxonomic position and relationships of Polycestoid taxa, was recently presented by HOLYNSKI (1993), who proclaimed that Polycestinae were not a natural group but formed part of the subfamily

Buprestinae. HOLYNSKI (1993) established three tribes within the subfamily Buprestinae, viz. Acmaeoderini, Thrincopygini [including the subtribes Nothomorphina (to which he also attributed *Xyroscelis*), Paratrachydina, Ptosimina], Thrincopygina, Polyctesina, and others], and Tyndarini (including the subtribes Tyndarina, Tylauchenina, Prospherina, and others); Polycestini Lac. together with the Australian genus *Microcastalia* were attributed to Buprestini as a subtribe. Both of these above-mentioned conceptions were exclusively based on adult characters.

Some larval characters of Thrincopygini, Acmaeoderini and Polycestini (including *Polycesta*, *Ptosima*, and *Paratrachys*) were briefly discussed by BÍLY (1989), however, the shortage of material for comparison did not allow him to evaluate their taxonomic value. Unfortunately, the larvae of many Polycestoid taxa remain unknown up to now (viz. *Astraeusini*<sup>1)</sup>), *Acherusini*, *Pseudacherusini*, *Xyroscelini*, *Perucolini*, *Nothomorphini*, *Bulisini*, *Mastogeninae*) or are known by single or only a few species what makes it difficult to establish the reliable and diagnostic and taxonomic characters and to evaluate their range of variation. Nonetheless, the study of numerous species of Acmaeoderini larvae by the senior author (VOLKOVITSH 1979; VOLKOVITSH & DANILEVSKY 1987; unpublished data) makes it possible to select those larval characters which might be used for classification in contrast to those which can serve only for distinguishing species or species-groups. As a rule, the first group of characters are inadapative while the second are adaptive, although there are no rigid boundaries between both character categories (VOLKOVITSH 1996).

The characters shown in Table 1 may be divided into the following categories:

- (1) presumably inadapative characters: the sclerotization, colour, and shape of the anterior margin of the epistome and the number of epistomal sensillae (characters 2–4) (Table 1); the shape of the palatine sclerite and the number of median and antero-lateral sensillae (6–8); the armature of the articular membrane of the antennae (9); the shape and armature of antennae and the structure and sensillae composition of the apical cavity (10–12); the structure and sensillar composition of the lateral sclerite of the maxillary cardo (14); the shape and armature of the maxillary palpi (15); the presence or absence of an additional projection (galea?) on the maxillary stipes (16); the armature of the postmentum (19); the general shape of the pronotal groove (21); and the general type of spiracles (25, 26). As a rule, the characters comprising this category are practically invariable within the genera and higher taxa and are basically determined by common ancestry, being of the highest value for phylogeny.
- (2) characters, undoubtedly have adaptive nature with a low taxonomic weight: morpho-ecological type of larval body (1), the structure of mandibles (but the absence or presence of prosteca is a inadapative character) (13), the shape of the prementum (17), the presence of undifferentiated (i.e. lacking special inner structures) ambulatory pads and armature of the abdominal segments (23, 24), and the armature of the proventriculus (27). The states of these characters mainly depend on the biological specialization of the larvae, the rigidity of food substrate or the mode of larval movement (SOLDATOVA 1973; VOLKOVITSH 1979, 1996). Since these characters vary widely within genera they may be applied for diagnostics only.
- (3) characters of unclear nature which may be both adaptive and inadapative: the armature of the external surface of the labrum and labium (5, 18), [which may be correlated with the peculiarities of feeding and correlated with the structure of mandibles, the shape of the prementum and the armature of the proventriculus]; the size of the mala (16) which may be correlated with the development of an additional projection (galea?); the development of microteeth and asperities on the thoracic and abdominal segments as well as the differentiated (i.e. having inner structures) ambulatory pads (20, 22), which may be correlated with movement inside the food substrate; the structure (but not the general type) of spiracles (25, 26), which may be correlated with body size, and is often subjected to reduction and variation on the different sides of the same segment. It is possible that the states of some characters partly depend upon the larval instar and physiological condition of the larvae. These characters are only limitedly variable inside the superspecific taxa and may be applied both for diagnostics and phylogeny.

<sup>1)</sup> The larva of *Astraeus crassus* Van De Poll was recently illustrated by TURNER & HAWKESWOOD (1996), but no description was provided. The single but most important character of the *Astraeus* larva which might be taken into account from this illustration is the uniramous pronotal groove.

The characters belonging to the 1<sup>st</sup> and 3<sup>rd</sup> groups above are of a high taxonomic value and may be applied for taxonomy, classification and phylogeny. Some of these characters are discussed here as follows:

(1). The uniramous pronotal groove is the main character shared by almost all of the Polycestoid taxa, except for *Paratrachys*. Although BÍLY (1989, Fig. 10) shows the pronotal groove in *Paratrachys* larva, we failed to find it on the slides. The absence of a pronotal groove and almost complete reduction of the prosternal one has obviously resulted from the complete sclerotization of the prothoracic plates, so that the loss of the pronotal groove in *Paratrachys* represents a secondary state. All of the representatives of the subfamilies Chalcophorinae and Buprestinae, without any known exceptions, have biramous pronotal grooves, in contrast to Agrilinae and Trachyinae whose larvae possess uniramous or biramous ones. The peculiar condition of the pronotal groove consisting of two parallel sclerotized stripes divided by median, unsclerotized line, is found in *Tyndaris*. Some species of some genera of the Polycestoid complex have the pronotal groove bifurcate at the base. It may be concluded then, that the uniramous grooves correspond to the plesiomorphic state and the biramous grooves to the apomorphic one. The prothoracic grooves of *Prospheres* also differ from those of all other Polycestoid taxa in being unsclerotized and barely visible, mainly due to the surrounding sclerotized asperities; such a state also occurs in Buprestini (*Buprestis*, *Eurythyrea*), Epistomentini (*Diadoxus*), Dicerini (*Dicerca*), and some others. We regard the state of pronotal groove in *Prospheres* as most advanced among the Polycestoid complex.

(2). The presence of an additional unsclerotized projection bearing microspinulae on the maxillary stipes is the second important character of all the Polycestoid taxa excepting *Prospheres*; this projection is usually regarded as lacinia (BÍLY 1972, 1986, 1989; COBOS 1986) or galea (VOLKOVITSH 1979). The homology of this projection is unclear: it lacks inner sclerotization and setae which are characteristic of true galea, but it may be the rudiment of the latter; on other hand, it might be a secondary projection of the stipes. The representatives of both Buprestoid and Agriloid complexes, as well as *Prospheres*, have a single projection known as the mala, which is believed to have arisen as a result of the fusion of the lacinia and the galea; some structures resembling the additional projection fused with the mala were found in *Anilara* (VOLKOVITSH & HAWKESWOOD 1993) and *Melobasis* larvae (VOLKOVITSH & HAWKESWOOD 1994). As a rule, the size and shape of the mala are correlated with those of the additional projection and in association with these, the distance from the mala. It might be concluded that the absence of the additional projection and the well-developed, large mala, is an apomorphic state, while their presence is plesiomorphic. Therefore, based on these characters, the larva of *Prospheres* can be regarded as advanced. The intermediate condition has been found in a *Thrincopyge* species which has an elongated mala and a long additional projection almost fused with it, but in the larva of *T. alacris*<sup>2)</sup> described by BÍLY (1986), this projection is clearly separated from the mala might be transformation from a poorly developed mala to a large mala might be demonstrated in the following series:

<sup>2)</sup> There are significant differences between the larvae of *T. alacris* as described by BÍLY (1986) from Texas (Val Verde Co., near Sanderson, 2 July 1972, R. L. Westcott, ex *Dasyllirion* sp.) and those collected in Mexico (Puebla, Chila env., 5 July 1992, S. Bíly & M. Volkovitsh, ex *Dasyllirion* sp.). According to NELSON (1980) both *T. alacris* and *T. ambiens* occur in Texas, developing in *Dasyllirion* spp.; the author noted that three larvae described later in detail by Bíly „are possibly *T. alacris*“ as they differ from the larvae of *T. ambiens* described by BURKE (1917) by „lack (of) the brown spots on thoracic segments 2 and 3“. Since only *T. alacris* is known from Puebla and the adults of this species were collected on *Dasyllirion* in the same place, we suppose that the larvae collected in Puebla belong to *T. alacris* and those mentioned by NELSON (1980) and described by BÍLY (1986) belong to *T. ambiens*. The differences between these larvae are as follows: *T. alacris* (Mexico, Puebla): labrum and prementum with microsetae or microspinulae along the whole anterior margin externally; additional projection situated on inner surface of mala; thoracic and abdominal spiracles with cancellate peritreme and numerous inner trabeculae, *T. ambiens*? (U.S.A., Texas): labrum and prementum glabrous externally; additional projection isolated from mala (this character might be an artifact); thoracic and abdominal spiracles multiloculate, without any trabeculae. There are also some differences in the structure of the prothoracic grooves and armature of the proventriculus, but the above mentioned ones are most important. It is possible that such clear-cut differences in morphology we have observed within the same genus have resulted from the peculiar feeding habits of the larvae, but the biology of both species is poorly known.

[*Chrysophana*, *Neocypetes*, Polycestini, *Ptosima*, Acmaeoderini (mala reduced, short, transverse)] –

[*Tyndaris* (mala as long as wide)] –

[*Polyctesis* (mala slightly longer than wide)] –

[*Thrincopyge* (mala well developed, elongate)] –

[*Prospheres* (mala well developed, elongate, without additional projection)]. *Paratrachys* has a well developed, slightly modified, elongate mala.

(3). The external armature of labrum and prementum allows us to divide the Polycestoid complex (excepting *Thrincopyge*) into two groups. The first group, with these organs externally glabrous, includes *Thrincopyge* (partly, *T. ambiens* ?), *Chrysophana*, *Neocypetes*, *Tyndaris*, Polycestini, and Acmaeoderini; the second group, which bear microsetae or microspinulae along the anterior margin of the labrum and prementum, includes *Prospheres*, *Thrincopyge* (partly, *T. alacris*) and *Polyctesis*. This character has an intermediate state in *Ptosima* and *Paratrachys*: labrum glabrous, prementum with isolated zones of microspinulae laterally (*Ptosima*) or with a well developed zone along the anterior margin (*Paratrachys*). We suppose that the externally glabrous labrum and prementum represents the plesiomorphic state and that the labrum and prementum with microsetae and microspinulae represents the apomorphic state. The morphocline of these characters from the primitive to most advanced state may be traced in the following series:

[*Thrincopyge* (partly, *T. ambiens* ?), *Chrysophana*, *Neocypetes*, *Tyndaris*, Polycestini, Acmaeoderini (both labrum and prementum glabrous externally)] –

[*Ptosima* (labrum glabrous, prementum with isolated zones of microspinulae laterally)] –

[*Paratrachys* (labrum glabrous, prementum with well developed zone of microspinulae along the anterior margin)] –

[*Polyctesis* (labrum with a poorly developed microspinulate zone along the anterior margin)] –

[*Thrincopyge* (partly, *T. alacris*) (labrum with well developed microspinulate zone along the anterior margin)] –

[*Prospheres* (prementum with microspinulae along the anterior margin and additional microspinulate zone in the middle, Fig. 7)].

(4). The armature of thoracic (prothoracic plates in the first place) and abdominal segments also allows us to divide the Polycestoid complex into two groups: (1) those taxa having prothoracic plates and other body surfaces mainly glabrous (except for bristles and indistinct microspinulate zones on some abdominal segments), and (2) those taxa covered with distinct microspinulae, microteeth and asperities. We suppose that the glabrous surface is the primitive state (found also in Anthaxiini) and that the presence of microarmature (i.e. tubercles, spinulae, teeth, asperities) corresponds to the advanced state (found in the majority of buprestid taxa). We have indicated (VOLKOVITSH & HAWKESWOOD 1994) that asperities on the larval prothoracic plates can originate from microteeth independently in different taxa; conversely, microteeth can arise from microspinulae. We have now observed that, in their turn, microspinulae can arise from cuticular tubercles and scale-like bulges which often form a net-like, cancellate superficial sculpture on the prothoracic plates. In some taxa it may be observed that the transformation from a poorly developed, cancellate sculpture to that of a cancellate-rugose sculpture is accompanied by the formation of a distinct longitudinal rugosity which is often better marked on the pronotal plates. The morphoclines of these characters might be presented as follows:

[*Neocypetes*, *Tyndaris*, Polycestini, Acmaeoderini (partly: subgenera *Acmaeotethya* – *Ptychomus*) (plates and body glabrous, plates with longitudinal rugosity)] –

[*Chrysophana*, *Ptosima*, Acmaeoderini (partly: *Acmaeodera* s. str., *Acmaeoderella*) (plates and body glabrous, plates with cancellate sculpture)] –

[*Polyctesis* (plates with cancellate sculpture surrounded with zones of microspinulae, body with more or less distinct zones of microspinulae)] –

[*Thrincopyge* (plates and body with distinct zones of microteeth, tubercles and microspinulae)] –

[*Prospheres* (plates with extensive microteeth zones and asperities along the grooves, body with vast zones of microteeth and microspinulae)].

*Paratrachys* has an isolated position, having evenly sclerotized plates surrounded with micro-teeth and glabrous zones, body with microspinulate and glabrous, granulate zones, which undoubtedly correspond to an advanced state.

(5). The structure of spiracles has been frequently discussed in our previous papers (VOLKOVITSH 1979; VOLKOVITSH & HAWKESWOOD 1987, 1990, 1993, 1994; BÍLY & VOLKOVITSH 1996). The spiracles of the Polycestoid taxa belong to the buprestoid type in contrast to those attributed to the Agriloid (circular) type (VOLKOVITSH & HAWKESWOOD 1990), but within the Polycestoid complex, a complete morphocline from uniloculate spiracles through to multiloculate ones and to typical buprestoid spiracles with large cancellate peritreme and numerous inner trabeculae can be observed. It should be noted, that the structure of spiracles is a more variable character from the above-mentioned ones; it varies significantly within genera and species groups; it seems to be correlated with body size and larval instar; sometimes one of two thoracic spiracles is/are markedly reduced. We regard uniloculate spiracles as the most primitive state among Buprestidae while the typical buprestoid ones with developed peritreme and inner trabeculae we regard as advanced. Among the Buprestinae and Chalcophorinae, the intermediate state with interstitial peritreme and inner trabeculae lacking have been found only in *Paratassa* (BÍLY & VOLKOVITSH 1996) and *Neocuris* (VOLKOVITSH & HAWKESWOOD 1987); the loculate spiracles have never been observed in these subfamilies. The evolution of spiracular structure might be demonstrated in the following series:

[*Paratrachys* (both prothoracic and abdominal spiracles uniloculate)] –

[*Thrincopyge* (partly: *T. ambiens*?), *Chrysophana*, *Ptosima*, Acmaeoderini (partly) (both prothoracic and abdominal spiracles multiloculate)] –

[Acmaeoderini (partly), *Neocypetes*, Polycestini (partly) (prothoracic spiracles are typically buprestoid, abdominal ones uni- or multiloculate)] –

[*Prospheres* (prothoracic spiracles typically buprestoid, abdominal ones with interstitial peritreme without inner trabeculae)] –

[*Tyndaris*, *Thrincopyge* (partly: *T. alacris*), *Polyctesis*, Polycestini (partly) (both prothoracic and abdominal spiracles of buprestoid type with well developed peritreme and inner trabeculae)].

Although the abdominal spiracles of *Prospheres* do not belong to the most advanced state, they are much closer in structure to those of Buprestinae and Chalcophorinae, than they are to the majority of Polycestoid taxa.

There are also characters shared by some taxa which might be used for taxonomic purposes but their morphocline directions and state are not quite clear. Those are as follows: the presence or absence of setae on the postmentum (Fig. 7), sometimes significantly reduced (this character occur in different subfamilies; among Polycestoid taxa these setae are found only in *Prospheres*, *Thrin-copyge* and *Polyctesis*); the number of epistomal sensillae which is usually 4 (Fig. 1), except for *Tyndaris* (6) and *Paratrachys* (2); the number of antero-lateral sensillae of labrum; and some others.

It should be noted that the larval characters, despite their obvious value for delineating species, have relatively limited taxonomical implication for higher classification because there is a limited diversity of larval characters suitable for investigation and of these, many are adaptive in nature and display a much lower level of morphological differentiation in comparison to adult characters; moreover the trends of specialization displayed by larval and adult stages of the same taxon may be absolutely different. It appears, that morphological differentiation in the larval stage depends on biological specialization of the species in the first place, revealing itself in the differentiation of morpho-ecological forms, which can be almost similar in systematically unrelated taxa (e.g. the larvae of *Paratrachys* and *Trachys* are distinguishable in only a few inadaptive characters, i.e. general type of spiracles and mandibles, and presence/absence of proventriculus, yet their real systematic position lies within the Polycestoid (*Paratrachys*) and Agriloid (*Trachys*) complexes, respectively). Several related morpho-ecological forms can be found within the same genus (for example, *Acmaeoderella*: VOLKOVITSH 1979); as a result, the larvae belonging to different morpho-ecological forms within the same genus are often distinguished much more clearly from each other than the larvae from closely related genera, attributed to the same forms (VOLKOVITSH 1996).



One more interesting evolutionary aspect associated with different trends and level of specialization in larval and adult stages is that highly specialized, advanced, and recently abundant groups may possess rather primitive, only slightly specialized larvae (i.e. Acmaeoderini) and vice versa (*Thrincopyge*, *Prospheres*). The lower level of morphological differentiation of larval characters which are independent of biological specialization, is a possible reason that we failed to find reliable characters to distinguish close related genera within Acmaeoderini, Polycestini, Anthaxiini (*Anthaxia-Chalcogenia*) and some others. At the same time the larval characters proved to be of great value for separating and delimiting supergeneric taxa, such as subtribes, tribes, and subfamilies, and for the establishment of taxonomic relations of some higher taxa, whose systematic positions were not quite clear.

Based on the analysis of larval characters it is possible to establish a number of groups inside the Polycestoid complex which we believe form natural taxa:

- (1) Acmaeoderini, Ptosimini, Polycestini, Tylauchenini, Tyndarini, *Chrysophana*. Body of buprestoid type; maxillary stipes with an additional projection (galea?); labrum and prementum glabrous or prementum with isolated zones of microspinulae laterally (*Ptosima*); postmentum without setae; prothoracic plates and other body segments glabrous, plates with cancellate or cancellate-rugose structure; structure of spiracles rather variable: prothoracic spiracles are multiloculate to buprestoid type (some Polycestini, *Tyndaris*). Among these taxa Tyndarini and *Chrysophana* have some unique characters which sets them apart: viz. the first with 6 epistomal sensillae, relatively long mala, complicated structure of pronotal groove (Table 1) and a peculiar shape of the mesothorax which is markedly narrower than that of the pro- and meta-thorax; the second with 3 antero-lateral spines on the internal surface of the labrum, peculiar shape of prementum (like *Prospheres*) and strongly elongate 1<sup>st</sup> antennal segment.
- (2) *Polyctesis*, Thrincopygini. Body of buprestoid type; maxillary stipes with additional projection (galea?); labrum and prementum with microsetae or microspinulae along anterior margin (except for *T. ambiens?* which has glabrous labrum and prementum); postmentum bearing 2 setae; prothoracic plates glabrous, surrounded by zones of microspinulae (*Polyctesis*) or covered with microteeth and tubercles except for their central parts (*Thrincopyge*), other body segments with distinct zones of microteeth or microspinulae; both prothoracic and abdominal spiracles of the buprestoid type (except for *T. ambiens?* which has multiloculate spiracles). In spite of the variation in mouthparts armature and structure of spiracles in two known larvae, the other characters shown in Table 1 allows us to place *Thrincopyge* into this group.
- (3) *Prospheres*. Body of buprestoid type; maxillary stipes without additional projection (galea?); labrum and prementum with microsetae or microspinulae along anterior margin and bearing additional zones of microspinulae in the middle of the prementum; postmentum with two long setae; prothoracic plates unevenly covered with microteeth and tubercles except for some glabrous zones on the central surface and asperities along the grooves; other body segments with distinct zones of microteeth or microspinulae; both prothoracic and abdominal spiracles of buprestoid type, but abdominal ones with interstitial peritreme without inner trabecula; other characters are presented in diagnosis and in Table 1 (in pocket).
- (4) *Paratrachys*. Body of trachyoid type; maxillae with additional projection (galea?); labrum glabrous, prementum with a triangular zone of microspinulae along anterior margin; postmentum glabrous; prothoracic plates evenly sclerotized, with pronotal groove absent and prosternal one strongly reduced, surrounded by zones of microteeth and glabrous zones, other body segments with zones of microspinulae; both prothoracic and abdominal spiracles uniloculate; other characters presented in Table 1. *Paratrachys* has the most specialized larva among the Polycestinae which has resulted from its leaf-mining habit.

### Conclusions

The comparative morphological study of the larvae of the Polycestoid taxa has demonstrated some important characters shared by all or nearly all of the groups (i.e. uniramous pronotal groove, additional projection on the maxillary stipes) which allow us to distinguish them easily from Bu-

prestoid larvae. These characters, as well as an agreement between morphoclines of some other ones, testify that the taxa attributed to the Polycestoid complex form a natural monophyletic group which might be regarded as a distinct subfamily. The majority of Polycestoid taxa demonstrate the primitive states of morphoclines and might be thought as the most primitive within the Buprestoid subfamily group (i.e. Polycestinae, Chalcophorinae, Buprestinae), which is in complete agreement with the traditional viewpoint, based on adult morphology. The similar occurrence of some important characters in the larva of *Prospheres* (absence of additional projection of maxillary stipes, the presence of additional zones of microspinulae in the middle of prementum, microspinulate articular membrane of antennae, and the presence of asperities on prothoracic plates), which are the most advanced states among Polycestinae larvae, with the similar states within Buprestinae and Chalcophorinae, is rather the result of parallel evolution in closely related groups rather than the evidence of a transitional/intermediate state. The inclusion of Polycestoid taxa within the Buprestinae and especially the transference of Polycestini to Buprestini next to *Buprestina* (HOLYNSKI 1993) are in complete contradiction to our findings.

The close similarity in larval characters between Acmaeoderini and Polycestini does not support the separation of the first as a distinct subfamily. Larval morphology tends to suggest that the first Acmaeoderini should be regarded as tribe within the Polycestinae, being closely related to Polycestini, Tyndarini, and Tylauchenini. In many respects, the larva of *Ptosima* is much closer to those of the Acmaeoderini, than to those of the Polycestini, only differing from the first in having the deep-scated apical cavity of the 2<sup>nd</sup> antennal segment densely microspinulate along anterior margin, presence of indistinct lateral sclerite of maxillary cardo, isolated zones of microspinulae on the external surface of the prementum, and indistinct zones of microspinulae on the meso- and metathoracic plates. Based on both larval and antennal morphology, we propose that *Ptosima* should be transferred to the Acmaeoderini as a subtribe.

Tyndarini has a most deviant larvae among the Polycestini tribal group, which confirms its tribal status; unfortunately only the larva of a single unidentified species was able to be studied. The amalgamation of Tyndarina, Tylauchenina and Prospherina with Tyndarini (HOLYNSKI 1993) is also not in agreement with our results.

No peculiar diagnostic characters were found in Tylauchenini larva, although it obviously belongs to the Polycestini tribal group. The additional larval study of other genera is badly needed to reveal its relationships, taxonomic position and status.

Significant differences in larval characters between *Chrysophana* and *Polyctesis* (Table 1) indicate that these genera are not closely related and is also confirmed by antennal morphology of the adults. We propose that *Chrysophana*, perhaps together with *Beerelus* Nelson, should be separated within its own tribe or subtribe.

Despite some similarity between the larvae of *Thrincopyge* and *Polyctesis*, based on adult characters, we cannot regard them as closely related genera. The nature of the very strong differences displayed by the larvae of two species of *Thrincopyge* is not clear. We believe both Thrincopygini and Polyctesini are distinct tribes within Polycestinae.

The larvae of *Prospheres* in many respects is more closely related to those of *Polyctesis* and *Thrincopyge* than to the representatives of the Polycestini tribal group, having the most advanced states of some above-mentioned characters and resembling ones found in the Chalcophorinae and Buprestinae; such that its position within the Polycestoid complex is rather isolated. It is important to study the larvae of *Astraeus* and *Xyroscelis* to elucidate the true relationships and taxonomic position of the Australian Polycestinae. However, the differences between the larvae of *Prospheres* and *Polyctesis* are such that they contradict the assignment of these genera within the same tribe Polyctesini (LEVEY 1978).

Finally, Paratrachyini should be regarded as a distinct, highly specialized group of tribal rank due to its peculiar larval morphology resulting from its leaf-mining habit.

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Table 1. Comparison of the main taxonomic characters among the larvae of Prospherini (*Prospheres*), Thrincopygini (*Thrincopyge*), *Chrysophana*, Polyctesini (*Polyctesis*, *theremia*, *Acmaoderella*) and Paratrachyini (*Paratrachys*).

Character	<i>Prospheres</i>	<i>Thrincopyge</i>	<i>Chrysophana</i>	<i>Polyctesis</i>	<i>Neocypetes</i>
1. Morpho-ecological type	Buprestoid (Fig. 10)	Buprestoid	Buprestoid	Buprestoid	Buprestoid
2. Epistome: sclerotization, colour	Weak, mainly yellowish	Normal, mainly brownish	Normal, mainly brownish	Normal, mainly brownish	Normal, mainly brownish
3. Epistome: mandilubar condyles	Almost concealed by anterior margin (Fig. 1)	Not concealed	Not concealed	Not concealed	Not concealed
4. Epistome: epistomal sensillae	4 (2 trichoid, 2 campaniform) (Fig. 1)	4 (2 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)
5. Labrum: armature of external surface	With microsetae along whole anterior margin (Fig. 5)	With microsetae along whole anterior margin or glabrous	Glabrous	With microsetae along anterior margin	Glabrous
6. Labrum: palantine sclerite	Median branches poorly developed, isolated from lateral ones (Fig. 5)	Median branches poorly developed, joined to lateral ones	Median branches poorly developed, isolated from lateral ones	Both median and lateral branches well developed, joined at base	Both median and lateral branches well developed, joined at base
7. Labrum: median sensillae	1 trichoid, 2 campaniform (Fig. 5)	1 trichoid, 2 campaniform	1 trichoid, 2 campaniform	1 trichoid, 2 campaniform	1 trichoid, 2 campaniform
8. Labrum: anterolateral sensillae (Fig. 5)	$\frac{1t + 2c + 3t - 4t}{1c - 2t + 3t + 4t}$	$\frac{1t + 2c - 3t + 4t}{1c + 2t + 3t + 4t}$	$\frac{1t + 2c + 3t - 4t}{1t + 2t + 3t}$	$\frac{(1t + 2c) - 3t - 4t}{1t + 2t + 3t}$	$\frac{(1c + 2c) + 3t - 4t}{1t + 2t}$
9. Antennae: articular membrane	Microspinulate (Fig. 4)	Glabrous	Glabrous	Glabrous	Glabrous
10. Antennae: 1st segment	Elongate (Fig. 4)	As long as wide	Strongly elongate	As long as wide	As long as wide
11. Antennae: 1st segment: anterior margin	Microspinulate (Fig. 4)	Microspinulate	Glabrous	Microspinulate	Glabrous
12. Antennae: 2nd segment: apical cavity	Poorly developed, covered with a disk-like microspinulate extension (Fig. 4)	Developed, microspinulate along anterior margin	Developed, shallow, microspinulate along anterior margin	Developed, deep, microspinulate along anterior margin	Developed, shallow, scarcely microspinulate along anterior margin
13. Mandibles	Elongate, poorly sclerotized, with 5 sharp teeth apically (Figs. 2, 3)	Weakly elongate, strongly sclerotized with 5 blunt teeth apically	Short, strongly sclerotized with 3 weakly rounded teeth apically	Moderately elongate, strongly sclerotized, with 4 rounded teeth apically	Short, strongly sclerotized, with small apical tooth and 2 ridges at apex
14. Maxillae: cardo: lateral sclerite	Distinct, poorly sclerotized, bearing 2 setae and one campaniform sensilla (Fig. 6)	Distinct, strongly sclerotized, bearing 2 setae and one campaniform sensilla	Distinct, poorly sclerotized, bearing 2 setae and one campaniform sensilla	Distinct, strongly sclerotized, bearing 2 setae and one campaniform sensilla	Lacking, with 2 setae and one campaniform sensilla arising from membrane
15. Maxillae: palpi: 1st segment	Elongate, 1.7 times as long as wide (Fig. 6)	Weakly elongate, approx. 1.3 times as long as wide	Transverse	Transverse	Transverse
16. Maxillae: mala	Well developed, elongate, without additional projection (Fig. 6)	Well developed, elongate, with long, narrow additional projection	Short, transverse with broad additional projection	Slightly longer than wide, with broad additional projection	Short, transverse, with broad additional projection
17. Prementum: shape	Transverse, sharply converging to base (Fig. 7)	Transverse, rectangular	Transverse, sharply converging to base	Rounded, almost as long as wide	Slightly transverse
18. Prementum: armature of external surface	Microspinulate along anterior margin, with additional zones of microspinulae in centre (Fig. 7)	Microspinulate along anterior margin or glabrous, without additional zones of microspinulae	Glabrous	Partly microspinulate along anterior margin, without additional zones of microspinulae	Glabrous

<i>Petes</i>	<i>Tyndaris</i>	Polycestini	<i>Ptosima</i>	Acmaeoderini	<i>Paratrachys</i>
stoid	Buprestoid	Buprestoid	Buprestoid	Buprestoid	Trachyoid
al, mainly ish	Normal, mainly brownish	Normal, mainly brownish	Normal, mainly brownish	Normal, mainly brownish	Normal, mainly brownish
concealed	Not concealed	Not concealed	Not concealed	Not concealed	Partly concealed
choid, paniform)	6 (4 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)	4 (2 trichoid, 2 campaniform)	(2 campaniform only)
ous	Glabrous	Glabrous	Glabrous	Glabrous	Glabrous
median and branches developed, at base	Median branches poorly developed, isolated from lateral ones	Median branches poorly developed, joined to lateral ones at base	Both median and lateral branches well developed, joined at base	Both median and lateral branches well developed, joined at base	Both median and lateral branches well developed, parallel to each other
oid, paniform	1 trichoid, 2 campaniform	1 trichoid, 3> campaniform	1 trichoid, 2 campaniform	1 trichoid, 2 campaniform	1 trichoid, 2 campaniform
$(2c) + 3t - 4t$	$(1t + 2c) - 3t + 4t$	$(1t + 2c) + 3t - 4t$	$(1c + 2c) - 3t - 4t$	$(1c + 2c) + 3t + 4t$	$1c - (2t + 3t) (?)$
	$1t + 2t$	$1c + 2c - 3t + 4t$	$1t + 2t$	$1t + 2t$	$1t + 2t$
ous	Glabrous	Glabrous	Glabrous	Glabrous	Glabrous
g as wide	As long as wide	Slightly transverse	As long as wide	As long as wide	Elongate
ous	Scarcely microspinulate	Glabrous	Glabrous	Glabrous	Glabrous
oped, w, scarcely spinulate along or margin	Developed, shallow, scarcely microspinulate along anterior margin, microspinulate inside	Developed, deep, scarcely microspinulate along anterior margin, microspinulate inside	Developed, deep, densely microspinulate along anterior margin,	Poorly developed, shallow, scarcely microspinulate along anterior margin	Lacking, sensory organs, partly covered with apical projection
strongly sized, with small tooth and 2 at apex	Moderately elongate, strongly sclerotized, with apical tooth and 2 ridges at apex	Short, strongly sclerotized, with small apical tooth and 2 ridges at apex	Weakly elongate, strongly sclerotized, with rounded apical tooth and 2 ridges at apex	Variable in shape, with apical tooth and with 2 pairs of teeth or with 2 ridges at apex	Elongate, evenly sclerotized, with 2 apical teeth and 2 indistinct tubercles
ng, with 2 e and one campaniform sensilla g from membrane	Lacking with 2 setae and one campaniform sensilla arising from membrane	Distinct, strongly sclerotized, bearing 2 setae and 2-4 campaniform sensillae	Indistinct, poorly sclerotized, bearing 2 setae and one campaniform sensilla	Lacking, with 2 setae and one campaniform sensilla arising from membrane	Lacking, without any setae or sensillae
erse	Transverse	Transverse	Transverse	Transverse	Elongate
transverse, broad additional tion	As long as wide, with broad additional projection	Strongly reduced, very short, broad, additional projection	Strongly reduced, with very short, broad, additional projection	Strongly reduced, with very short, broad, additional projection	Elongate, narrow, scarcely visible, with broad, additional projection
y transverse	Rounded, almost as long as wide	Slightly transverse	Rounded, almost as long as wide	Variable, ranging from transverse to rounded	Transverse, rectangular
ous	Glabrous	Glabrous	With isolated zones of microspinulae laterally	Glabrous	With triangular zones of microspinulae along anterior margin
ous	Glabrous	Glabrous	Glabrous	Glabrous	Glabrous

(Fig. 7)

18. Prementum: armature of external surface	Microspinulate along anterior margin, with additional zones of microspinulae in centre (Fig. 7)	Microspinulate along anterior margin or glabrous, without additional zones of microspinulae	Glabrous	Partly microspinulate along anterior margin, without additional zones of microspinulae	Glabrous
19. Postmentum: armature	With 2 long setae (Fig. 7)	With 2 short setae	Glabrous	With 2 long setae	Glabrous
20. Prothoracic plates: armature	Unevenly covered with microteeth and tubercles, with glabrous zones and asperities along grooves (Figs. 8-10)	Unevenly covered with microteeth and tubercles on the sides, central part glabrous with scarce, short bristles	Glabrous, with scarce, short bristles, surface with net-like sculpture	Glabrous, with scarce, short bristles, surrounded by zones of microspinulae; surface with net-like sculpture	Glabrous, with scarce, short bristles, surface with very fine longitudinal rugosity
21. Prothoracic grooves	Uniramous on both surfaces, unsclerotized, visible due to surrounding asperities (Figs. 8-10)	Uniramous on both surfaces, sclerotized,	Uniramous on both surfaces, unsclerotized, scarcely visible	Uniramous on both surfaces, sclerotized	Uniramous on both surfaces, poorly sclerotized, scarcely visible
22. Meso- and metathorax: armature	Plates covered with microteeth and tubercles, with glabrous zones; sides with bristles (Fig. 10)	Plates covered with microteeth and tubercles, with glabrous zones; sides with bristles	Glabrous, with sparse short bristles on sides	Plates mainly glabrous with zones of microspinulae; sides with bristles	Plates mainly glabrous, metasternum with inconspicuous zones of microspinulae; sides with bristles
23. Abdomen: 1st segment: ambulatory pads	With longitudinal pad and 2 additional ones on the sides dorsally, and rounded pad with 2 additional ones ventrally (Figs. 10-12)	Poorly developed	Poorly developed	Poorly developed	Poorly developed
24. Abdominal segments: armature	With elongate pads on both surfaces and zones of micro-teeth and spinulae (Fig. 13)	Without distinct pads, with zones of microteeth and spinulae	Mainly glabrous, with indistinct zones of inconspicuous microtubercles	Mainly glabrous, with distinct zones of microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae
25. Prothoracic spiracles	With cancellate peritreme and numerous inner trabeculae (Fig. 14)	With cancellate peritreme and numerous inner trabeculae or multiloculate	Multiloculate	With cancellate peritreme and numerous inner trabeculae	With cancellate peritreme and numerous inner trabeculae
26. Abdominal spiracles	With cancellate peritreme, without inner trabeculae (Fig. 15)	With cancellate peritreme, and inner trabeculae or multiloculate	2-3-loculate	With cancellate peritreme, and inner trabeculae	Multiloculate
27. Proventriculus: armature	Main zones with well developed, dense microteeth arising singly from sclerotized tubercles (Fig. 16)	Main zones with well developed, dense microteeth arising singly or in groups from sclerotized tubercles	Main zones with well developed, dense microteeth arising singly from sclerotized tubercles	Main zones with well developed, very dense microteeth arising in groups from sclerotized tubercles	Main zones with well developed, dense microteeth arising in groups from sclerotized tubercles

	as long as wide		as long as wide	from transverse to rounded	
ous	Glabrous	Glabrous	With isolated zones of microspinulae laterally	Glabrous	With triangular zones of microspinulae along anterior margin
ous	Glabrous	Glabrous	Glabrous	Glabrous	Glabrous
ous, with scarce, short bristles, surface very fine longitudinal rugosity	Glabrous, with scarce, short bristles, surface with very fine longitudinal rugosity	Glabrous, with scarce, short bristles, surface with very fine longitudinal rugosity	Glabrous, with scarce, short bristles, surface with net-like sculpture	Glabrous, with scarce, short bristles, surface with very fine, longitudinal rugosity or net-like sculpture	Evenly sclerotized, yellowish, surrounded by microteeth and glabrous zones
ous on both sides, poorly sclerotized, scarcely visible	Uniramous on both surfaces, pronotal one consisting of 2 parallel sclerotized stripes	Uniramous on both surfaces, sclerotized	Uniramous on both surfaces, sclerotized, with complete median line	Uniramous on both surfaces, sclerotization and shape variable	Pronotal one lacking, prosternal one scarcely visible
mainly glabrous, sternum with inconspicuous zones of spinulae; sides with bristles	Plates mainly glabrous with zones of microspinulae; sides with bristles; mesothorax narrower than metathorax	Glabrous, with dense, long bristles on the sides	Plates mainly glabrous with zones of microspinulae and bristles on the sides	Glabrous, with sparse short bristles on the sides	Covered with granulate sculpture, with glabrous zones and zones of microspinulae
y developed	Poorly developed	With distinct pad bearing sclerotized structures dorsally and with adjacent sclerotized rings ventrally	Poorly developed	Poorly developed	With 2 pads on both surfaces
y glabrous, with indistinct zones of conspicuous microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae	Mainly glabrous, with indistinct zones of inconspicuous microspinulae
cancellate peritreme and numerous trabeculae	With poorly developed peritreme and a few inner trabeculae	With cancellate peritreme and numerous inner trabeculae	Multiloculate	With cancellate peritreme and numerous inner trabeculae or multiloculate	1-loculate
loculate	With poorly developed peritreme and a few inner trabeculae	With cancellate peritreme, and inner trabeculae or 2-3-loculate	3-loculate	1-3- or multiloculate	1-loculate
zones with well developed, dense microteeth arising in groups from sclerotized tubercles	Main zones with well developed, very dense microteeth arising in groups from sclerotized tubercles	Main zones with well developed, very dense microsetae arising in groups from sclerotized tubercles	Main zones with well developed, dense microteeth arising in groups from sclerotized tubercles	Variable, main zones with well developed, dense microteeth arising singly or in groups from sclerotized tubercles	Main zones poorly developed, unsclerotized, consisting of sparse, isolated groups of microteeth arising in groups from tubercles