Larvae of *Galbella acaciae* and *G. felix* with notes on the systematic position of *Galbella* (Coleoptera: Buprestidae: Galbellinae)

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Abstract. A redescription of the larva of *Galbella acaciae* Descarpentries et Mateu, 1965, the first description of the larva of *G. felix* (Marseul, 1866), their diagnoses and comparison with other buprestid larvae are presented. The taxonomic position of *Galbella* Westwood, 1848 based on both larval and adult characters is discussed. An analysis of larval and some adult characters shows that *Galbella* belongs to the buprestoid instead of agriloid phyletic lineage and supports its separation as a distinct subfamily Galbellinae.

Taxonomy, classification, larval morphology, Coleoptera, Buprestidae, Galbellinae, *Galbella*, Palaearctic region

INTRODUCTION

The genus *Galbella* (type species *G. violacea* Westwood, 1848, by monotypy) was established by Westwood (1848) in Eucnemidae, although the name of its junior synonym, *Janthe* Marseul, 1865 (type species *J. felix* Marseul, 1866, by monotypy), has been most commonly used. The taxonomic history of *Galbella* was discussed in detail by Holynski (1985), Bellamy & Holm (1986) and Bellamy (1995) and is not repeated here. Until now, *Galbella* has been attributed to the subfamily Trachyinae (Cobos 1979) despite the fact that Reitter (1911) established the subfamily Galbellinae. Mistakenly, the authorship of Galbellinae was credited to Cobos (Bellamy 1985; Bellamy & Holm 1986) who made no reference to Reitter's authorship although the citation of Reitter (1911) was presented in bibliography of Cobos (1986); moreover Cobos (1986) wrote about Galbellinae as a new subfamily (1986, "En esta alternativa se incluye la nueva subfamilia Galbellinae, ...", p. 69, footnote 2). Subsequently, Reitter's authorship of Galbellinae was only recently rediscovered (Bellamy, 1995; Kolibáč, 2000). Despite of the fact that Galbellinae was regarded by Cobos as a distinct subfamily, Holynski (1993) placed *Galbella* in subtribe Galbellina of the tribe Trachydini of Agrilinae. Kolibáč (2000), in his recently published classification and phylogeny of Buprestoidea based on cladistic analysis, placed the Galbellinae, in which he also included Mastogeniini and the trachyoid genera *Leiopleura* Deyrolle, 1864, *Pachyschelus* Solier, 1833, *Brachys* Solier, 1833 and "their relatives" in the Agriline lineage which comprised Sphenopterinae and Agrilinae (including Cylindromorphinae and part of Trachyinae). These conclusions are very amazing to any specialist in Buprestidae and cast much doubt; some remarks concerning this work are presented below in the "Discussion". Because the taxonomic position and relations of *Galbella* based on adult characters remain controversial, it was supposed that larval characters would contribute greatly to clarification of these problems.

The first larval description of *Galbella* species, *G. acaciae* Descarpentries et Mateu, 1965, which included not only larval habitus but also mouthpart structures, was published by Mateu

(1972). At that time *Galbella* was regarded as a member of Trachyinae (Obenberger 1937) while the larva described by Mateu had nothing in common with known trachyine larvae being much more similar to that of *Ptosima* Solier, 1833, Mateu himself doubted that it actually belonged to *Galbella*. Later Cobos (1986), using Mateu's description, put *Galbella* in the key to the larvae of higher taxa of Buprestidae and reproduced the picture of the larval habitus of *G. acaciae* from Mateu (1972).

A single larva of *G. acaciae* extracted from *Acacia* wood in Algeria was kindly presented to the authors by Vít Kubáň. Later, a few larvae of another *Galbella* species, *G. felix*, were collected by M. Volkovitsh inside the twig of *Phillyrea latifolia* in Israel. Examination of these larvae confirmed that Mateu (1972) had actually described the larva of *G. acaciae*. Its redescription, the first description of the larva of *G. felix*, their diagnoses, comparison and discussion on the taxonomic position of *Galbella* are presented below.

SYSTEMATICS

Larval descriptions

Galbella acaciae Descarpentries et Mateu, 1965
(Figs 1–11)

DESCRIPTION. Length of larval body 6.9 mm. Larva (Fig. 1) is of the usual buprestid type corresponding to the 2nd morphoecological type of *Acmaeoderella* Cobos, 1955 larvae (Volkovitsh 1979). Body slightly yellowish-white, with brown mouthparts, prothoracic grooves and spiracles; nearly glabrous, without supporting processes on the last abdominal segment. Prothorax slightly enlarged, 1.27 times wider than long; mesothorax of the same width as prothorax, 2.18 times wider than long; metathorax distinctly narrower than mesothorax, 1.93 times as wide as long; abdominal segment 1st slightly narrower than metathorax and following abdominal segments, 1.5 times wider than long; abdominal segments 2–7th strongly elongated, 1.17–1.36 times longer than wide; segment 8th shorter, 1.25 times wider than long; segment 9th round, 1.31 times wider than long; segment 10th short, almost as wide as long, bearing feebly sclerotized, longitudinal anal slit.

Head and mouthparts. Epistome (Fig. 6): broad, 4.80 times as wide as long; anterior margin slightly arcuately bisinuate between mandibular condyles; posterior margin distinctly bisinuate; latero-posterior corners rounded, markedly projecting outwards; lateral margins with deep antennal incision. Epistome bearing single pair of campaniform epistomal sensillae (Fig. 6, es) arranged linearly in front of the middle of epistomal length. Clypeus (Fig. 6) narrow, membraneous and glabrous.

Labrum (Figs 6, 7): distinctly transverse, 2.70 times as wide as long; anterior margin broadly arcuate between irregularly rounded anterolateral corners, without lateral lobes. Palatine sclerite (Fig. 7, ps) well defined, transverse and sclerotized, complete, not divided on medial and lateral branches (terminology according to Volkovitsh & Hawkeswood 1995, 1999, Bílý & Volkovitsh 1996, Volkovitsh & Bílý 1997), with median part stronger sclerotized. Anterior margin of palatine sclerite bearing 6 long setae (trichosensillae) with their bases arranged in arcuate line; base of palatine sclerite bears 4 campaniform sensillae. Based on their disposition it can be supposed that one pair of medialmost setae and both pairs of campaniform sensillae constitute the group of medial sensillae of labrum (Fig. 7, msl) while two pairs of lateral setae as well as 1 seta and 1 campaniform sensilla
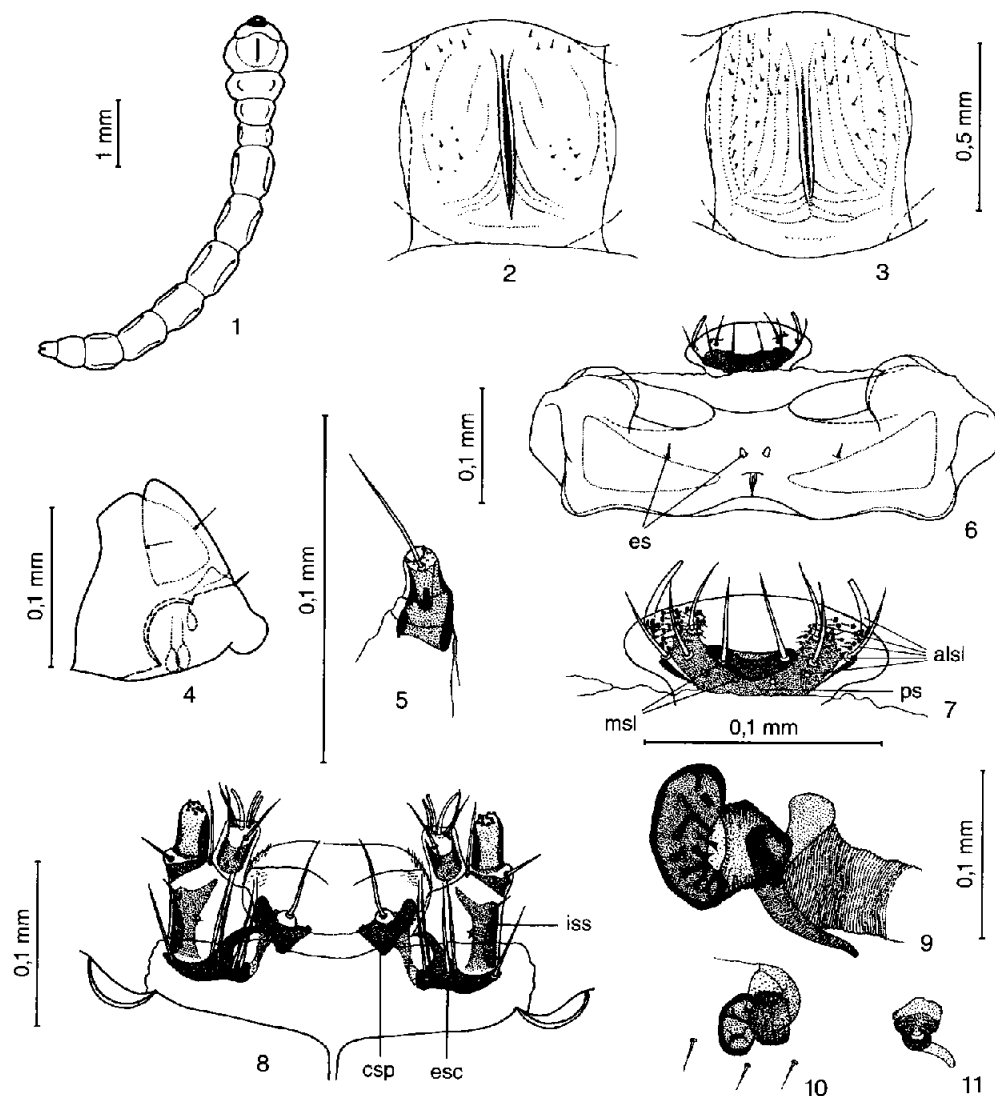
Figs 1–11. Larva of *Galbella acaciae* Descarpantries et Mateu. 1 – larva, dorsal view; 2 – pronotal plate; 3 – prosternal plate; 4 – right mandible, ventral view (arrow shows anterior margin of lateral apical ridge); 5 – left antenna; 6 – labrum, clypeus and epistome (es – epistomal sensillae); 7 – labrum and clypeus (alsl – anterolateral sensillae of labrum, msl – medial sensillae of labrum, ps – palatine sclerite); 8 – labiomaxillary complex (csp – corner sclerite of prementum, isc – isolated sclerite of maxillary cardo, iss – internal sclerite of maxillary stipes); 9 – right mesothoracic spiracle; 10 – 1st abdominal spiracle, right; 11 – 3rd abdominal spiracle, left.

positioned on the membrane in front of anterolateral corners of palatine sclerite on each side externally and 1 blunted seta at lateral margin internally belong to the group of anterolateral sensillae of labrum (Fig. 7, alsl). Internal surface of labrum (epipharynx) mainly glabrous with sparse indistinct microspinulae laterally.

Antennae (Fig. 5): 2-segmented, situated in the deep lateral depression of epistome; articular membrane glabrous. 1st segment is half sunk in the articular membrane, strongly sclerotized, cylindrical, obliquely truncated apically; about as long as wide and 1.06 times as long as segment 2; anterior margin glabrous; campaniform sensillae invisible. Second segment cylindrical, about 1.13 times as long as wide with poorly defined inner sclerites; anterior margin nearly glabrous, with a few inconspicuous microspinulae; apical cavity bearing long trichosensilla near the apex which is as long as whole antenna, and sensory appendage whose base situated on the level of the middle of 1st segment, palmate sensillae invisible. Based upon their disposition and structure larval antennae of Galbella acaciae are very similar to those of Anthaxiini, for example, Chalcogenia Saunders, 1871 (Volkovitsh & Bílý 1997: fig. 16).

Mandibles (Fig. 4): strongly sclerotized, peculiarly in anterior half of their length, triangular, almost as wide as long; without "prostheca" at inner margin, with one short seta externally. Upper cutting edge almost straight with small apical tooth and two lateral ridges with straight anterior margins. Mandibular base with three distinct small glandules.

Hypostome: slightly sclerotized excepting anterior margin, bearing sparse short setae and campaniform sensillae; with well defined ocelli at anterolateral corners near pleurostome (see Fig. 14, oc).

Labiomaxillary complex (Fig. 8). Maxillae: maxillar cardo membraneous, glabrous, transverse, with very large, well defined, intricate inner sclerite (Fig. 8, isc) connected to corner sclerites of prementum (Fig. 8, csp). Each of these sclerites bears five long setae (trichosensillae) of which four medianmost ones arranged in pairs, near the base of single lateral seta one pair of campaniform sensillae is disposed. It can be supposed that these sclerites are homologous to strongly or sometimes completely reduced isolated sclerites of cardo in other buprestid larvae that usually situated at its laterobasal corners and bear two (rarely more) setae and one (or more) campaniform sensillae (Bílý & Volkovitsh 1996: fig. 37, isc; Volkovitsh & Bílý 1997: fig. 17). Stipes with inner sclerite (Fig. 8, iss) moderately sclerotized and bearing one campaniform sensilla at the middle, one short seta closer to external margin, and one long seta between the bases of maxillar palpus and mala; anterior margin of stipes with a few inconspicuous microspinulae. Basal segment of maxillar palpus short, triangular; external margin bearing one campaniform sensilla at the base and long trichosensilla near the apex which is as long as the second segment; long curved sensilla extending along internal margin of 2nd segment arise from the apex of 1st segment. Second segment elongated, 1.70 times as long as wide, slightly sclerotized and besides curved sensilla bearing one campaniform sensilla at the middle of external margin and about 10 conical sensillae at the regularly rounded apex. Mala elongated, nearly rectangular, 1.91 times as long as wide and as long as 2nd segment of maxillar palpus; with well defined inner sclerite, without an additional projection like that in polycestine larvae; bearing one campaniform sensillae near the base, three thick external and 3–4 internal trichosensillae apically, and inconspicuous microspinulae along inner margin. Labium (Fig. 8): prementum transverse, 1.63 times as wide as long, with anterior margin nearly straight and lateral margins regularly arcuated, externally glabrous besides small groups of inconspicuous microspinulae at anterolateral corners; internally with sparse microspinulae on the sides. Corner sclerites of prementum (Fig. 8, csp) short, connected to inner sclerites of cardo; each bearing one apical long seta extending just beyond anterior margin of prementum and four campaniform sensillae. Postmentum distinctly separated from prementum, glabrous.
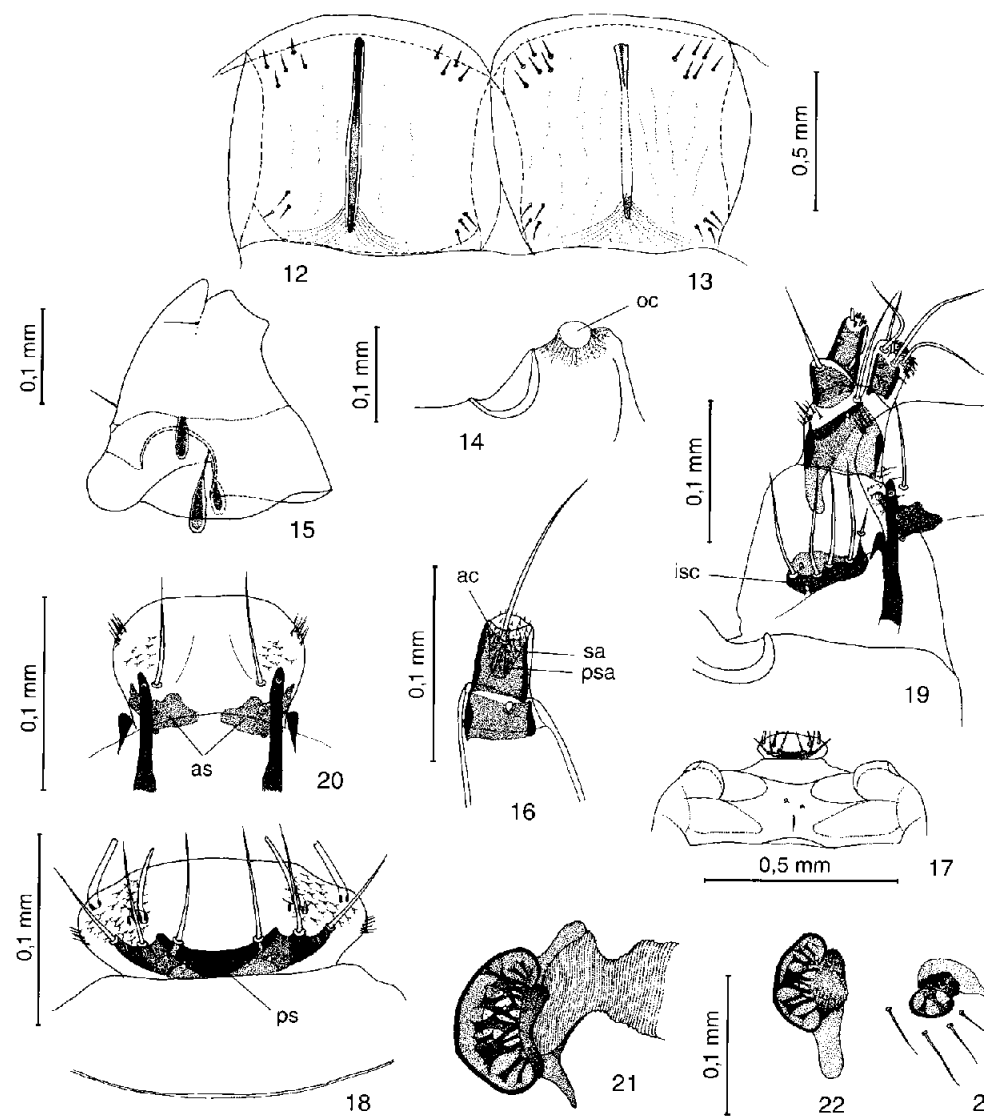
Figs 12–23. Larva of Galbella felix (Marseul). 12 – pronotal plate; 13– prosternal plate; 14 – left par hypostome (oc – ocelli); 15 – right mandible, dorsal view (arrow shows anterior margin of lateral apical ridge) – right antenna (ac – apical cavity of the 2nd segment, psa – palmate sensillae, sa – sensory appendage); labrum, clypeus and epistome; 18 – labrum and clypeus (ps – palatine sclerite); 19 – left maxilla(isc – isol sclerite of maxillary cardo); 20 – labium (as – additional sclerotization); 21 – right mesothoracic spiracle; 22 – abdominal spiracle, left; 11 – 3rd abdominal spiracle, right.

138
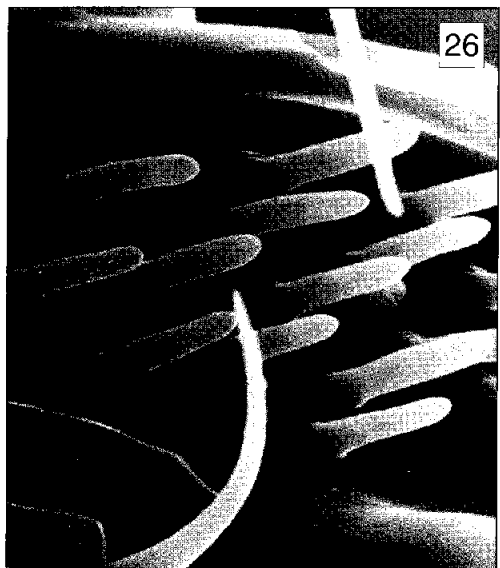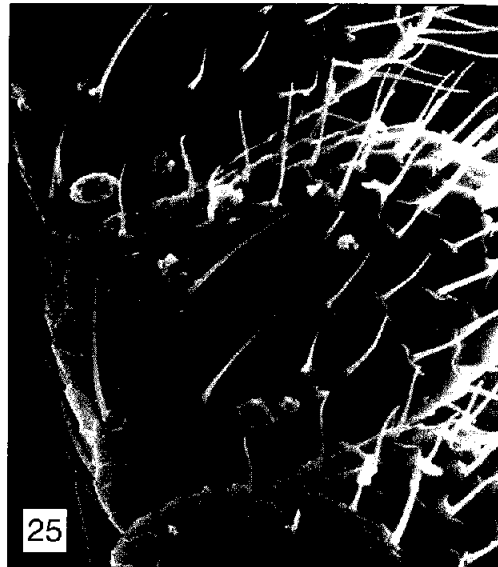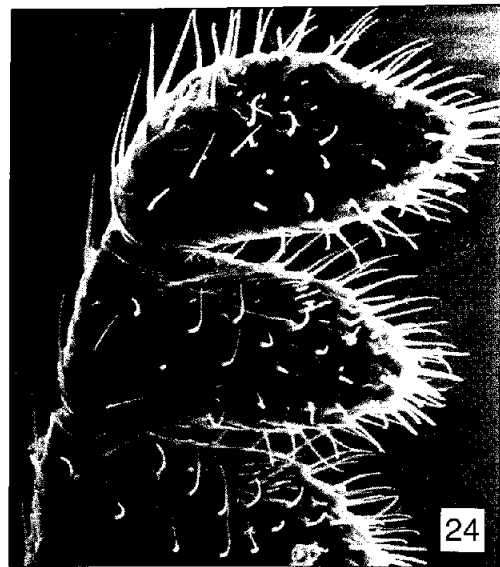
Figs 24–27. *Galbella* spp., antennal structures. 24 – *G. acaciae* Descarpantries et Mateu,?male, 8–11 segments, internal view, ×400; 25 – the same, 8 10 segments, external view, ×600; 26 – the same, 9th segment, apical depression, internal view, ×4000; 27 – *G.* sp., ?female, 5–6 segments, internal view, ×450.

Thorax (Figs 2, 3). Pronotal (Fig. 2) and prosternal (Fig. 3) plates poorly defined, unsclerotized and colourless, glabrous, bearing very fine, inconspicuous rugosity and sparse, short setae which are densest on prosternum, prothoracic sides and anterior margins. Both pronotal and prosternal grooves are single, nearly uniform, distinct in both fixed larvae and slides, fusiform with sclerotized, brown median stripe. Meso- and metathorax without distinct ambulatory pads, glabrous, bearing sparse short setae.

Abdomen (Fig. 1): without distinct ambulatory pads, covered with setae which are denser and longer than those on the thorax. Last segment without terminal supporting processes or sclerotization.

Spiracles (Figs 9–11). Thoracic spiracles (Fig. 9) of multiphorous buprestoid type, reniform; left and right thoracic spiracles differ in shape, size and a number of trabeculae, the biggest one about 2.14 times as long as wide; with well defined but not cancellate peritreme and numerous unbranching inner trabeculae; the atrium and closing apparatus of spiracles sclerotized, brownish. Abdominal spiracles (Figs 10, 11) also greatly variable in shape and size from uniphorous without trabeculae to multiphorous and similar to thoracic spiracles but with lesser number of trabeculae, atrium rather sclerotized.

BIONOMY. The single studied larval tunnel of *G. acaciae* was found in the dead twig of *Acacia raddiana* (diameter about 5 mm); only terminal 10 cm of the tunnel was well preserved and suitable for study. The rest of relatively long twig was nearly completely eaten by various species of buprestids (*Anthaxia* Eschscholtz, 1829, *Acmaeodera* Eschscholtz, 1829, *Xantheremia* Volkovitsh, 1979, *Chrysobothris* Eschscholtz, 1829, *Agrilus* Curtis, 1825). The tunnel was rounded in diameter, parallel with the axis of the twig, situated in sapwood and filled with a mixture of free sawdust and larval feaces resembling a fine sand; this material resembles that of some xylophagous catapillars. The distal portion of the tunnel was widely enlarged, this enlarged part was prolonged towards the surface of wood, without any sawdust containing a pupa which was fixed from both sides by thin, non-transparent and white, membraneous lids.

Galbella felix (Marseul, 1866)
(Figs 12–23)

MATERIAL EXAMINED. Three larvae of different instars and one pupa: "Israel, Carmel Ridge, Nahal Me'arot, Loc. 25, ex twigs of *Phillyrea latifolia*, 21.07.1996, M. Volkovitsh leg." Specimens deposited in Zoological Institute, St. Petersburg, Russia.

DESCRIPTION. Head and mouthparts. Epistome (Fig. 17) of the same structure as that of *G. acaciae*, 4.36 times as wide as long, with posterior margin only slightly bisinuate; epistomal sensillae arranged asymmetrically closer to anterior margin; clypeus wider than in *G. acaciae*.

Labrum (Fig. 18) with better defined but also complete palatine sclerite (Fig. 18, ps); its anterior margin nearly straight, sides almost regularly angularly rounded. The number and arrangement of medial and anterolateral sensillae of labrum and microspinulae on internal surface are the same as in *G. acaciae*.

Antennae (Fig. 16): 1st segment very short, 1.64 times as wide as long, well sclerotized, with one campaniform sensilla on the internal surface closer to anterior margin. 2nd segment cylindrical, strongly elongated, 1.57 times as long as wide and 1.75 times longer than 1st segment; well sclerotized, with only a few inconspicuous microspinulae apically; apical cavity (Fig. 16, ac) with very long sensory appendage (Fig. 16, sa) whose apex extending anterior margin of cavity and with two hardly visible palmate sensillae at each side of sensory appendage base (Fig. 16, psa); long trichosensilla which is longer than the total antennal length arises at near the anterior margin of apical cavity; inner surface of cavity covered with very fine inconspicuous microspinulae.

Mandibles (Fig. 15) are very similar to those of *G. acaciae* but with apical lateral ridges of cutting edge slightly emarginated. Hypostome is of the same structure with well defined ocelli (Fig. 14, oc).

Labiomaxillary complex (Figs 19, 20). Maxillae (Fig. 19): maxillar cardo nearly as long as wide. Inner sclerites of cardo (Fig. 19, isc) partly reduced, have no certain shape, with different number of setae and campaniform sensillae on each side: right sclerite with four long setae and three campaniform sensillae while left one bearing additional short medial seta and two campaniform sensillae arranged one above another. Stipes and maxillary palpus stronger sclerotized but their shape and armament are similar to those in *G. acaciae*. Mala of the same shape but its internal apical margin bearing numerous microsetae. Labium (Fig. 20): prementum sligthly transverse, 1.58 times as wide as long, with lateral sides broadly irregularly rounded. Corner sclerites of prementum long, with well defined transverse additional sclerotization just behind apicies (Fig. 20, as), otherwise their structure is the same as in previous species.

Thorax. Prothoracic plates (Figs 12, 13) are similar to those in *G. acaciae* but pronotal groove (Fig. 12) longer and stronger sclerotized along its whole length while prosternal one (Fig. 13) in contrast very feebly sclerotized at apical part only. Thoracic and abdominal segments with denser and longer setae.

Spiracles (Figs 21–23). Prothoracic spiracles (Fig. 21) more transverse and with repeatedly branching trabeculae, in many respects resembling those of Buprestinae. 1st pair of abdominal spiracles (Fig. 22) of the same shape and structure as thoracic ones being smaller and having lesser number of trabeculae; spiracles on the other abdominal segments (Fig. 23) fluctuated greatly in their shape and presence or absence of trabeculae.

DIFFERENTIAL DIAGNOSES

Larvae of *Galbella acacia* and *G. felix* can be distinguished as follows:

Galbella acaciae
Epistome (Fig. 6) 4.80 times as wide as long, with posterior margin distinctly bisinuate, epistomal sensillae (Fig. 6, es) arranged linearly in front of the middle of epistomal length.

Labrum (Fig. 7) 2.70 times as wide as long, with anterior margin broadly arcuate and sides irregularly rounded.

1st segment of antennae (Fig. 5) nearly as long as wide and 1.06 times as long as segment 2; 2nd segment short, 1.13 times as long as wide; the bottom of apical cavity and base of sensory appendage situated at the level of the middle of 1st segment, apex of appendage extends as far as posterior 1/3 of segment 2; cavity nearly glabrous, without microspinulae internally.

Apical cutting ridges of mandibles with almost straight anterior margins (Fig. 4).

Maxillary cardo (Fig. 8) transverse, distinctly wider than long; internal sclerite (Fig. 8, isc) on each side bearing 5 long setae arranged in pairs.

Mala (Fig. 8) with only inconspicuous microspinulae along internal margin.

Prementum (Fig. 8) 1.63 times as wide as long with lateral sides regularly arcuated.

Corner sclerites of prementum (Fig. 8, csp) with poorly defined additional sclerotization apically.

Pronotal and prosternal grooves (Figs 2, 3) nearly similar, evenly sclerotized along their length.

Mesothoracic spiracles (Fig. 9) with unbranched inner trabeculae.

Galbella felix
Epistome (Fig. 17) 4.36 times as wide as long, with posterior margin weakly bisinuate, epistomal sensillae arranged asymmetrically in anterior 1/3 of epistomal length.
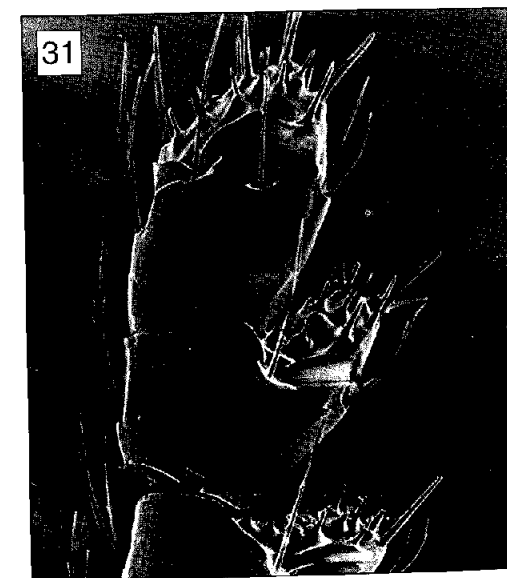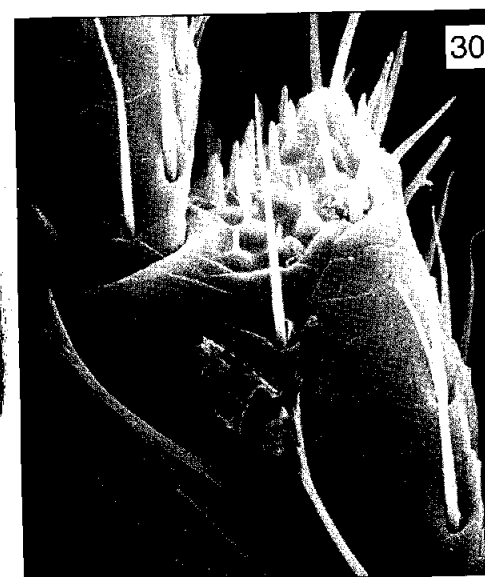
Figs 28–31. Antennal structures. 28 – *Mastogenius cyaneus* Fisher, female, 10–11 segments, internal view, ×700; 29 – *Ptosima undecimmaculata* (Herbst), ?male, 10th segment, internal view, ×450; 30 - *Sponsor* (s. str.) *emmae* Descarpentries, 8th segment, internal view, ×800; 31 – *Paratrachys hederae* Saunders, 9–11 segments, internal view, ×700.
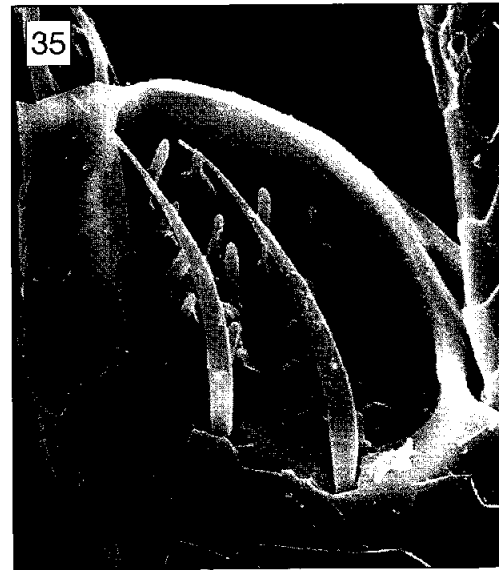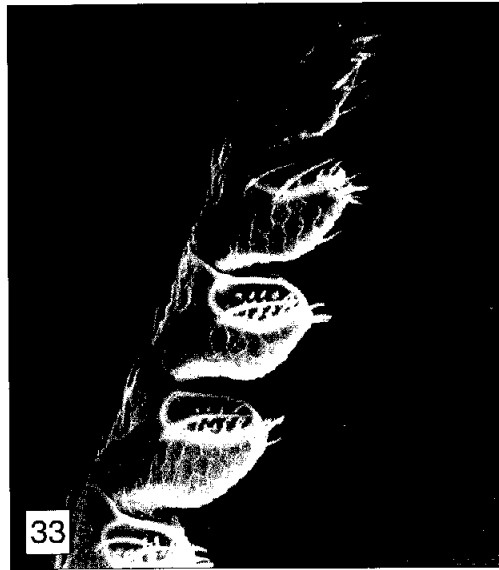
Figs 32-35. Antennal structures.32 – *Leiopleura plaumanni* Obenberger, 10–11 segments, internal view, ×1300; 33 – *Brachys ovata* (Weber), 7–11 segments, internal view, ×250; 34 – *Trachys turanica* Semenov, 7 segment, internal view, ×3000; 35 – *Taphrocerus volitans* Gory, 10th segment, internal view, ×1700.

Labrum (Fig. 18) 2.50 times as wide as long, with anterior margin nearly straight and sides regularly angularly rounded.

1st segment of antennae (Fig. 16) very short, 1.64 times as wide as long; 2nd segment elongated, 1.57 times as long as wide and 1.75 times as long as segment 1; the bottom of apical cavity and base of sensory appendage situated at posterior 1/3 of 2nd segment, apex of appendage (Fig. 16, sa) extends the aperture of apical cavity (though it may be that the bottom of cavity has no fixed position and can move forth and back in live larva); apical cavity (Fig. 16, ac) with fine, inconspicuous microspinulae internally.

Apical cutting ridges of mandibles with slightly emarginated anterior margins (Fig. 15).

Maxillary cardo (Fig. 19) as long as wide; internal sclerite (Fig. 19, isc) on each side bearing 4 long setae and, sometimes, rudimentary 5th seta.

Mala (Fig. 19) bearing numerous microsetae at the apical part of internal margin.

Prementum (Fig. 20) 1.58 times as wide as long with lateral sides irregularly arcuated.

Corner sclerites of prementum (Fig. 20, csp) with well defined additional sclerotization apically (Fig. 20, as).

Pronotal and prosternal grooves (Figs 12, 13) differing in length and sclerotization.

Mesothoracic spiracles (Fig. 21) with distinctly branching inner trabeculae.

DISCUSSION

Taxonomic position of *Galbella*

As stated above, there are several hypotheses attributing *Galbella* as follows: 1) to monogeneric subfamily Galbellinae (Reitter 1911, Bellamy 1985, Bellamy & Holm 1986, Cobos 1986); 2) to subtribe Galbellina of the tribe Trachydini of the subfamily Agrilinae (Holynski 1993); and 3) to subfamily Galbellinae comprising also Mastogeninae and some trachyine genera and belonging to agriline lineage (Kolibáč 2000). Two latter hypotheses proclaim a close relation of *Galbella* to trachyine taxa of agriloid complex. Since taxonomic position and relationship of *Galbella* remains so far uncertain, our own analysis of larval (Tab. 1) and some adult characters is presented below.

Before proceeding any further we would like to discuss the classification and phylogeny of the Buprestidae suggested by Kolibáč (2000) which is based on a cladistic analysis of eighty seven characters including eleven larval characters. The most objectionable features of his analysis are the assignment of character states (plesiomorphic vs. apomorphic) and the evaluation of the trends of character transformations (polarity) using outgroup comparison and frequency of occurrence. These methods are universally adopted in cladistics but the requirements for outgroup(s) to be a closest sister group(s) and homology of compared structures to be proven while the affinities of Buprestoidea and homologies of many structures, peculiarly larval ones, are rather vague. It is well known that a secondary segmentation is commonly occurring in arthropods and many structures have no homologies in other groups being a secondary or new formations. "Galea" or "lacinia" having no inner sclerites or sensillae in polycestine larvae (Kolibáč 2000, character 40), mandibular "prostheca" and "urogomphi" (supporting processes in our terminology) in agriline larvae (characters 42 and 46) are the examples of such structures. The most interesting case is the presence of larval "urogomphi" (plesiomorphy according to Kolibáč 2000) which certainly are not homologous to real urogomphi in other insect larvae representing the sclerotized prolongations of the last abdominal segment and sometimes having a secondary segmentation; these processes are also found in the buprestine genus *Pterobothris* Fairmaire et Germain, 1858 (see Moore & Cerda 1986; personal observation) and the first-instar larvae of *Buprestis rusticorum* Kirby, 1837 and *B. aurulenta* Linnaeus, 1767 (see Rees 1941, Plate 22, Figs 13, 14, 16) though the latter two lose these

processes during larval development (Rees 1941; personal observation on mature larvae); the larva of *Anocisseis danieli* Bilý, 1997 (Agrilinae: Coraebini) loses supporting processes on prepupal stage (Bilý 1997). Such an occurence of this structure and its secondary loss in some taxa confirms that it may be a plesiomorphy but only for representatives of buprestine and agriline lineages because no traces of these processes are found in first-instar larvae of *Schizopus* Le Conte, 1857 (see Rees 1941, Table 23, Figs 8, 10, 13) or *Julodis* Eschscholtz, 1829 (see Cobos 1986: Figs. 6, 8); there is no evidence of their presence in neonate larvae of *Galbella*, Polycestinae or even all buprestine and agriline taxa. Another example of uncertainty is a homology of sclerites of the male abdominal tergite 9 (proctiger) (Kolibáč 2000: character 2) which is traditionally believed consisting of 9th (paraproct) and 10th (epiproct) tergites (Gardner 1989, Jendek 2001). Earlier stages of formation and complete series of paraproct transformation throughout the prolongation of lateroposterior projections of epiproct (Mastogenini), their separation first as two isolated sclerites and then their fusing into single horse-shoe sclerite connected to epiproct by membrane (*Acmaeodera* s. str., *Galbella*) followed by sclerotization of surrounding membrane resulted in formation of additional sclerite (paraproct) can be easily observed in Polycestinae (Volkovitsh in press) and some other groups (see Kolibáč 2000: figs 297, 307, 295, 294, 298–302); in Agrilinae paraproct formation goes in somewhat different way (Kolibáč 2000: figs 304, 303; Kubáň et al 2000). If Kolibáč's concept of polarity (plesiomorphy – paraproct distinct, apomorphy – that fused with epiproct or reduced) is taken for granted it should be accepted that the most primitive, in many other respects, Polycestinae demonstrate a most advanced state of the proctiger. From our viewpoint, this structure is comprised of the 9th tergite and its derivates exclusively. It is impossible to discuss here all the other characters analyzed by Kolibáč (2000) but these presented examples demonstrate that his results are highly debatable.

Larval characters (Figs 1–23)

In order to compare the larvae of *Galbella* with those of other taxa placed by Kolibáč (2000) to Galbellinae, the following larvae were examined additionally: ?*Mastogenius* sp. (undeterminated larvae, presumably belonging to this genus), *Brachys tesselata* (Fabricius, 1801), *Pachyschelus swartzii* Kerremnans, 1892, *P. panamensis* Fisher, 1922, *Hylaeogena rotundipennis* (Fisher, 1922) (all larvae deposited in Museum of Natural History, Smithsonian Institution, Washington, U.S.A.), and *Trachys turanica* Semenov, 1892 (Zoological Institute, St-Petersburg, Russia). The results of comparison are shown in Tab. 1.

Some other larval characters which are important for analysis of taxonomic position and relations of *Galbella* should be previously discussed here as well: the structure of spiracles (0 – buprestoid, 1 – agriloid), body shape (0 – agriline; 1 – buprestine, 2 – trachyine; 3 – julodine, 4 – schizopine), pronotal groove (0 – I-shaped, 1 – Y-shaped, 2 – V-shaped, 3 – absent, 4 – julodine: wide Y-shaped), proventriculus (0 – present, 1 – absent), and sensory appendage (0 – ejected, 1 – retracted) (Kolibáč 2000: characters 36, 37, 41, 43, 44; 0 = plesiomorphy, 1–6 = apomorphies).

Actually, buprestoid and agriloid spiracles differ greatly in inner structure (Steinke 1919; Volkovitsh 1979) and each type is characteristic of buprestine (also julodine) and agriline lineages correspondingly. The complete series of transformations from "spiracula uniforia" (very small, unilocular spiracles without any trabeculae) to typical buprestoid "spiracula multiforia" can be easily traced throughout Polycestinae, intermediate states are also found in some buprestine taxa (*Paratassa* Marseul,1882; see Bilý & Volkovitsh 1996: figs 39–40). The origin of agriloid spiracles is not so clear. In some trachyine genera abdominal spiracles strongly resemble "spiracula uniforia" with a few inner microspinulae (which may be a secondary reduction). According to Rees (1941), larval spiracles of *Schizopus* belong to type "spiracula biforia" which as supposed also arose from "spiracula uniforia". It can be concluded that "spiracula uniforia" is the most primitive state of buprestid

character	Galbella	?Mastogenius	trachyine genn.
body shape	buprestoid	buprestoid	buprestoid to trachyoid
labrum, palatine sclerite	undivided (Figs 7, 18, ps)	divided on medial and lateral branches	divided on medial and lateral branches, or modified
antennae, apical cavity	present (Figs 5, 16, ac)	present	absent
mandibles, "prostheca"	absent (Figs 4, 15)	absent	present
maxillae, isolated sclerite of cardo	very big, with 4–5 long setae (Figs 8, 19, isc)	completely reduced, with 2 trichosensillae arising from membrane	completely reduced, without any sensillae
maxillae, mala, additional projection	absent (Figs 8, 19)	present, very big	absent
prothoracic plates	with a single medial groove (Figs 2, 3, 12, 13)	with a single, hardly visible, unsclerotized, medial groove	with a single medial groove or sclerotized area
spiracles	buprestoid: uniphorous to multiphorous (Figs 9–11, 21–23)	buprestoid: uniphorous to biphorous	
sclerotized proventriculus	?absent	?absent	absent

spiracles which subsequently gave rise to both buprestoid and agriloid types. At least buprestoid spiracles have never been observed in agriline or trachyine taxa and vice versa. In our opinion buprestoid spiracles are an apomorphy which *Galbella* shares with buprestoid taxa and Julodinae.

It is hard to believe that the agriloid body shape is a plesiomorphic state comparing to buprestoid one. In spite of the presence of very strange abdominal appendages ("prolegs") and ventral glands (Rees 1941) the larvae of *Schizopus* are most similar to generalised polyphagous coleopteran larvae with poorly differentiated thoracic and abdominal segments. The buprestoid type is more primitive than the agriloid type because many polycestine, chalcophorine and buprestine larvae exhibit the rudiments of thoracic legs and even prothetelic larvae with quite developed ones are described (Bilý 1972); thoracic segments are, to a variable extent, enlarged. Julodine larvae, in spite of peculiar mandibular shape and the structure of prothoracic plates, can be attributed to the buprestoid type. Agriloid larvae differ from buprestoid larvae mainly by having terminal supporting processes although some agriline larvae have no processes (*Ethonion* Kubáň, 2000) or lose them in later instars. Contrary to Kolibáč (2000), it may be supposed that the agriloid type derived from the buprestoid one. The trachyoid type is undoubtedly the most advanced and specialized. However, a body shape is obviously adaptive character of low phylogenetic value. Different larval types may be found in the same taxa, for example trachyoid type in Polycestinae (*Paratrachys* Saunders,1873), agriloid type in Buprestinae (*Pterobothris* Fairmaire et Germain, 1858), buprestoid type – in Trachyinae (*Hylaeogena* Obenberger, 1934), etc. At least in body shape, *Galbella* is much closer to buprestoid taxa than to any agriloid ones.

We can not also agree with hypothetic transformation series of larval pronotal groove as suggested by Kolibáč (2000, Figs 372–375). We suppose that the absence of defined prothoracic grooves (Schizopodinae and Julodinae) is a plesiomorphic state while well developed and sclero-

tized medial grooves in Galbellinae, Polycestinae and many agriline larvae is an apomorphic state though more primitive than Y, V or II-shaped grooves in buprestine and coraebine larvae. The most advanced state is the sclerotized plates frequently with the traces of the medial groove in leaf mining larvae (*Paratrachys*, many trachyine genera). In the structure of medial grooves and prothoracic plates, *Galbella* much resembles Polycestinae.

The sclerotised proventriculus is the most developed and complicated internal armament-bearing in buprestoid larvae feeding on dead, dry, and solid wood; those feeding on softer tissues or living under the bark have a poorly sclerotized and armed proventriculus (Volkovitsh 1979). The presence of a well developed proventriculus is obviously an adaptive feature and cannot be regarded as the plesiomorphic state. Taking into account the very small size of larvae and the fact that on some larval stages the proventriculus is empty and hardly extractable, the complete lack of this structure in *Galbella* (and ?*Mastogenius* Solier, 1851) cannot be proved in this study.

The presence of an apical cavity containing a sensory appendage, sensillae and, sometimes, microspinulae on the 2nd antennal segment seems a more advanced state than its absence. The apex of the segment around the cavity aperture is frequently enlarged and bears dense microspinulae and microsetae. Some trachyine larvae (*Brachys*) have a very shallow terminal depression though without surrounding microspinulae. The presence of the apical cavity is characteristic of Schizopinae (see Rees 1941) and buprestoid taxa while its absence found in Julodinae (see Bílý 1983) and agriloid taxa.

Our analysis of larval characters testifies that *Galbella* belongs to the Buprestine (Polycestinae, Chalcophorinae, Buprestinae) rather than the agriline lineage (Agrilinae, Trachyinae). Buprestine larvae are characterized by absent mandibular "prostheca"; apical cavity of 2nd antennal segment well developed (sensory appendage retracted according to Kolibáč 2000) (Figs 5, 16) except for *Paratassa* (see Bílý & Volkovitsh 1996: fig. 35) and *Paratrachys* having poorly developed cavity; spiracles of uni- or multiphorous buprestoid type (Figs 9–11, 21–23); sclerotized proventriculus present. Agriline larvae are characterized by mandibular "prostheca" present (Volkovitsh & Hawkeswood 1990: figs 10, 11, 17, 18); 2nd antennal segment without apical cavity with sensory appendage and sensillae sitting openly on its apex (sensory appendage ejected according to Kolibáč 2000) (see Volkovitsh & Hawkeswood 1990: figs 9, 21); spiracles of agriline circular type (see Volkovitsh & Hawkeswood 1990: figs 5, 25, 26); sclerotized proventriculus absent; all these characters are found in examined trachyine larvae (Table 1). For comparison, julodine larvae have no mandibular "prostheca" though mandibles are extremely specialized; 2nd antennal segment without apical cavity with sensory appendage and sensillae sitting openly on its apex (though there are two flat tooth-shaped projections possibly protecting sensory organs); spiracles of multiphorous buprestoid type (though differing from those in buprestoid larvae); sclerotized proventriculus absent (Bílý 1983; Volkovitsh, unpublished date). The unproven absence of a sclerotized proventriculus (plesiomorphy) is a single character which *Galbella* (and ?*Mastogenius*) shares with agriloid taxa and also with Julodinae.

Larvae of *Galbella* demonstrate at least two autapomorphies which are never found in other buprestid larvae, those are the complete palatine sclerite of labrum with linearly arranged medial and partly anterolateral sensillae (Figs 7, 18, ps, msl, alsl), and the very large internal sclerites of the maxillary cardo bearing 4–5 long setae each (Figs 8, 19, isc). Larva of *Tyndaris planata* (Laporte et Gory, 1835) also has large, though greatly reduced, internal sclerites of the maxillary cardo connected to the corner sclerites of the prementum and bearing only two setae and one campaniform sensilla each. These states can be regarded as the most primitive among Buprestidae; further transformation of palatine sclerites in both buprestoid and agriloid lineages leads to the differentiation of the medial and lateral branches followed by partial reduction of one of them, and that of isolated

sclerite of the cardo resulted in its complete reduction (sensillae arise from membrane or also reduce). It can be noted that julodine larvae (Bílý 1983; Volkovitsh, unpublished date) have the palatine sclerite divided on the medial and lateral branches and isolated sclerite of cardo lacking though there are numerous setae arising from the membrane. Among buprestoid taxa, *Galbella* shows a certain similarity in larval characters to Polycestinae, peculiarly to Acmaeoderini, ?*Mastogenius* (single pronotal groove, dispostion and structure of antennae, glabrous mouthparts, but an additional lobe on the mala is absent) and also to Anthaxiini (dispostion and structure of antennae, glabrous mouthparts). Larva of ?*Mastogenius* (Tab. 1) is of typical polycestine structure differing from all other known Polycestoid larvae in the peculiar maxillary palpi.

Adult characters (Figs 24–35 and Kolibáč 2000: figs 51, 79–80, 96, 112, 128, 144, 174, 189, 277, 292, 307, 334–335, 366–367)

According to Kolibáč (2000) the synapomorphies which *Galbella* shares with Mastogenini and trachyine taxa are as follows: (1) unique shaped premental sclerites, (2) tendency to coalescence of sclerites of maxilary stipes, (3) antennae with inconspicuous sensorial fields (probably secondary reduction), (4) metasternal transversal line absent, and (5) phallus short. Additionally, to prove the affinity of *Mastogenius* to *Galbella* he speculates about the possible origin of hypomeral keel in *Mastogenius* as a result of secondary closing of galbelloid antennal furrow. The affinities to mentioned trachyine genera are supported by following characters: (1) furrow for antennae present, (2) mediostipes strongly widened, palpifer large, rounded, (3) general structure of maxilla galbelline, excepting strong pigmentation of central sclerite, (4) inner side of mandible concave, 2 or 3 apical dentes present, (5) all sternites with incision though only inconspicuous on the last one in *Brachys*.

Comparison of the figures has shown that whole labial structures in *Galbella* and *Mastogenius* are quite different (Kolibáč 2000: figs 103, 112) and the similarity in only premental sclerites may be a convergence; moreover, the shape of these sclerites as well as the structure of stipes varies greatly within at least Coraebini and even within the genus *Coraebus* Laporte et Gory, 1839 (Kubáň et al. 2000: figs 120–150, 92–119). The structure of stipes in *Galbella* (Kolibáč 2000: fig. 96) is unique (big internal lobe of mediostipes) differing greatly from that in *Mastogenius* (Kolibáč 2000: fig. 86) and other buprestid taxa we have studied (Kolibáč 2000: figs 81–96) and may be regarded as autapomorphy; unfortunately, those of *Brachys* and *Pachyschelus* are not illustrated. The metasternal transversal line, though sometimes hardly visible, is found in all studied species of *Galbella*, *Mastogenius*, *Brachys*, *Taphrocerus* Solier, 1839, and *Pachyschelus*. The aedeagus length fluctuates greatly throughout the Buprestidae; among other groups a short aedeagus is found in polycestine genera *Paratrachys* and *Sponsor* Laporte et Gory, 1839. Antennal furrows occur not only in trachyine genera (*Pachyschelus*) but also in *Acmaeodera* (*Cavacmaeodera* Holm et Schoeman, 1999, *Ptychomus* Marseul, 1865). The peculiar structure of the legs with the femora and tibiae flattened and tibiae dorsally excavated for the reception of the tarsi in repose also occurs in *Xyroscelis* Thomson, 1878 (Polycestinae) and *Aphanisticus* Latreille, 1829 (Trachyinae), and similar tendency can be observed throughout Acmaeoderini. Mandibular structure is also rather variable and different types can be found within the same taxa (Kolibáč 2000: figs 52–80; Kubáň et al. 2000: figs 75–91).

The unique antennal structures of *Galbella* (Figs 24–27, see also Volkovitsh in press), being rather primitive (apical sensory organ poorly defined), differ greatly from those of the compared trachyine genera (Figs 32–35) with well developed apical organs but these reveal a certain similarity to Mastogenini (Fig. 28), Acmaeoderini and some other polycestine taxa (Figs 29–31). From the other hand, the sensory organs of *Galbella* also resemble those in the agriline and trachyine genera *Synechocera* Deyrolle, 1864, *Polyonychus* Chevrolat, 1837, *Endelus* Deyrolle, 1864 and *Germarica* Blackburn, 1887. Because the similarity of antennal structures of *Galbella* and other mentioned

taxa based on symplesiomorphy, it does not clarify the relationships of *Galbella* to any phylethic lineage of the Buprestidae.

Kolibáč (2000) also supposed that synapomorphies which Galbellinae shared with Agrilinae are as follows: (1) male tergite 9 (paraproct) not separated from tergite 10, (2) abdominal sternite 1 absent, (3) mesepimeron small with mesepimeron-mesepisternum suture oblique or imperfect. The hypothetical transformation of male tergite 9 was discussed above; in our opinion the paraproct is a secondary sclerite (at least in the Buprestidae) and its absence is a plesiomorphy. Tergite 9 of *Galbella* (Kolibáč 2000: fig. 307) is very similar to that in *Mastogenius* (Kolibáč 2000: fig. 297), some species of *Acmaeodera* s. str., *Paratrachys*, and *Sponsor* (Volkovitsh, unpublished data), and also *Synechocera*, *Ethonion* (see Kubáň et al. 2000, Figs 292, 293), *Cylindromorphus* Théry, 1930, *Trachys* Fabricius, 1801 (Kolibáč 2000: figs 305, 306), and some others. Jendek (2001), in his excellent work, demonstrates that in its general abdominal structure, *Galbella* has more relation to the Buprestine rather than the agriline lineage and confirms the subfamily status of Galbellinae. The most significant character which does not allow to place *Galbella* in agriline lineage is a lack of any trace of sternal groove which is regarded to be an important synapomorphy of agriloid taxa (Jendek 2001).

Galbella sharply differs from *Mastogenius* and other polycestine taxa in having the groups of long setae on paramere apicies (Kolibáč 2000: fig. 334); the latter state is chracteristic of the majority of buprestine and agriline taxa. In the same time in poorly developed dorsal lobe of basal piece of tegmen, penis structure, general structure of genital segments, and the presence of setal patches on abdomen (the similar patches are also found in females of *Acmaeoderella* s. str., both sexes of *Cochinchinula* Volkovitsh, 1996 from Acmaeoderini, and some species of *Polycesta*) it resembles many Polycestinae. Ovipositor of *Galbella* is of short uritiforme type similar to that in *Mastogenius* but this type is widely occurring throught all the groups of the Buprestidae.

CONCLUSIONS

Examination of larval and adult morphology has shown that *Galbella* possesses a unique set of primitive and advanced features. Analysis of both larval (buprestoid body shape, spiracles, mandibles, 2nd segment of maxilary palpi bearing apical cavity) and adult characters (general abdominal structure) has shown that *Galbella* belongs to the Buprestoid rather than the agriloid complex. The relationships of *Galbella* to trachyine taxa as suggested by Holynski (1993) and Kolibáč (2000) are not supported by our results. *Galbella* is most similar to *Mastogenius*, Acmaeoderini, and some other polycestine taxa. *Galbella* also exhibits a number of autapomorhic states (the unique structure of labrum and isolated sclerites of cardo in the larvae, adult antennal and labial structures, maxillae, etc.) which support its isolated position. The results of our analysis confirm that *Galbella* should be placed in separate monogeneric subfamily Galbellinae as was suggested by Reitter (1911) and Cobos (1986) belonging to the Buprestoid complex next to Polycestinae.

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