

MORPHOLOGY OF LYCIDAE WITH SOME CONSIDERATIONS ON EVOLUTION OF THE COLEOPTERA

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ABSTRACT

Morphology of Lycidae with some considerations on evolution of the Coleoptera.

External and internal morphology of the family Lycidae and allied taxa is studied and analyzed. A cladistic analysis of the group is carried out. An evolution scenario of the lineage is discussed and a phylogenetic tree and a key to subfamilies are proposed. Dexoridae Kleine stat. n. is raised to the family level. Lyropaeinae Bocák & Bocáková **stat. n.** and Miniduliticolinae Kazantsev **stat. n.** are raised to the subfamily level within the Lycidae. *Thilmanus* Baudi is transferred from Drilidae to Thilmaninae subfam. n. within the Lycidae. Platerodrilini tr. n. is described. The Lycidae are hypothesized to consist of seven subfamilies, Lyropaeinae **stat. n.**, Leptolycinae, Ateliinae, Thilmaninae, **subfam. n.**, Miniduliticolinae, **stat. n.**, Lycinae and Calochrominae. Lyponiina Bocák & Bocáková is transferred from Platerodini to Calochrominae incertae sedis. Phylogeny of the Coleoptera is discussed. The Coleoptera is hypothesized to be a polyphyletic taxon, not including the common ancestor of its two major lineages, the Polyphaga and the Archostemata-Adephaga-Myxophaga.

Key words: Coleoptera, Lycidae, morphology, phylogeny, taxonomy.

INTRODUCTION

It would not be exaggeration to say that the Lycidae, as many other Coleopterous insects, are fairly little known in many important aspects, including their morphology. Studies on the family have always been exclusively concentrated on external characters; perhaps, the only papers that contributed to the knowledge of their inner structures were those of Rosenberg (1943) who provided some detail on larval mandibular and trochanteral structures and Bocák & Bocáková (1990) who illustrated the internal female genitalia of several taxa.

The present study targeted both external and internal sclerotized structures of the Lycidae. In its course a number of characters demonstrating a considerable range of conditions rarely matched within the Coleoptera have been revealed, which significantly widen the morphological delineation of the family. The mouth parts, the endoskeletal structures, including the tentorium and metendosternite, the spiracular structure, the metathoracic wing venation, the structure of tarsi, the male and female genitalia are among such characters. The new morphological data necessitated a reanalysis of phylogeny of the Lycidae, which required determining of a proper outgroup.

While larval Coleoptera are known to be hardly distinguishable from many other insect orders (Crowson, 1981), the adult beetle is readily separated from all other adult pterygotes by the presence of a protective specifically organized and sclerotized mesothoracic wing, the elytron, covering the accordingly folded metathoracic wing, and the adequate transformation of the mesothorax, in the first place, whatever its plesiomorphies or further apomorphies might be. Therefore, it would be natural to expect that the earliest beetles possessed mesothoracic structures transitional between the ancestral hexapod stock and the Coleopterans, i.e. dehiscent or overlapping elytra with simple, not dove-tailed suture margins, with absent elytral epipleures and locking flanges. Their elytra would inevitably be little coadapted with the rest of the body and not significantly different from the hind wing in terms of length, breadth and venation, their apices would not be jointly rounded and the mesoscutum would not yet be organized to lock the elytra and protect the median notch at their base. The first beetles would have minimal folding of the metathoracic wing. Additionally, the number of their abdominal segments would be close to its maximal condition (i.e. 10 or 11 segments), like that in the ancestral stock. And as the degree of overall sclerotization and hardness in beetles has a marked natural tendency to increase, the first Coleoptera would apparently be more or less soft-bodied. In the earliest known fossils of the Coleoptera, belonging in the suborder Archostemata, however, all these characters are in the opposite, derived condition (Ponomarenko, 1969; Crowson, 1981). The earliest Archostemata are Permian (Ponomarenko, 1969; 1995), hence, allowing, no doubt, many million years to have the above mentioned structures developed to the derived condition they are in in the Archostemata, we should expect the order to have emerged at least in the Carboniferous or, still more probably, in the Devonian. Devonian, on the other hand, is the period when the first terrestrial Hexapoda have been found to occur. This consideration suggests redefining certain criteria of primitiveness in beetles, also because quite a number of possible symplesiomorphies with other insect lineages, such as the hypognathous head, presence of cervical sclerites, absence of postlabial structures, two pairs of functional thoracic spiracles and absence of the closing apparatus, absence of sternal articulation of pro- and mesocoxae, to name but a few, are typically deemed homoplasies/»secondary developments» in the Coleoptera (Crowson, 1981). While it is possible that some of these modifications in certain Coleopteran lineages may be secondary, regarding the opposite condition as primitive for beetles, when it is not supported other than by its occurrence in the Archostemata or Adephaga, seems unreasonable.

Besides, in the course of this study quite a number of new characters have been found that had not been reported before for the Coleoptera. They include the tripartite structure of the larval mandible with presence of a distinct stipes and conspicuous hypopharyngeal lobes and suspensoria, division of the larval trochanter into trochanter 1 and trochanter 2, alveolate cuticle in all sclerites of adult beetles, absent gula of adults, conspicuous trochantinal and meral sclerites of the imaginal metacoxae, etc. Some of them, appearing plesiomorphic from the insect evolution standpoint, could have been considered recent secondary modifications if the currently accepted views on the Coleoptera phylogeny had been applied.

In this respect, during the preliminary morphological analysis of the Lycidae the primitiveness and direction of evolution were determined in accordance with the general trends of hexapod development, with the aim to adjust polarities at the final phase of work, if necessary, with due reference to possible evolution scenarios for the Coleoptera and after defining the outgroup(s) for the family.

MATERIAL AND METHODS

The material studied included representatives of all subfamilies and tribes of Lycidae. Specimens were cleared with 10% KOH and dissected for the examination. All sutures, sulci, sclerites and appendages were studied on such KOH-treated specimens.

The following Lycidae taxa were studied:

LYCINAE: LYCINI

Lycus trabeatus Guerin-Meneville, last instar: 100 km N of Grootfontain, Namibia, 7.I.2002, dry bushveld, under bark, M.Picker leg. (one larva reared to the adult stage) (ICM).

Lycostomus praeustus (Fabricius), adult male and female: India, Andhra Pr., 52 km NW Hyderabad, 4.VII.1986, 600 m, Ghorpade B-547 (ICM).

LYCINAE: CALOPTERINI

Calopteron sp., last instar: Peru, Rio Ucayali, Pucalpa, 11.IV.1986, Zakharov leg. (ICM).

Calopteron reticulatum (Fabricius), adult male and female: USA, TN, Great Smoky Mountains N.P., env. Cosby Campground, 800 m, 16-21.VII.2003, S.Kazantsev leg. (ICM).

Caenia kirschi Bourgeois, adult female: Costa Rica, Vulcan Poas, 1900 m, 7-12.IV.2003, S.Kazantsev leg. (ICM).

LYCINAE: MACROLYCINI

Macrolycus flabellatus (Motschulsky), adult female: FE Russia, Kurils, Kunashir Is., Severyanka R., 20.VII.1988, O.Kabakov leg. (ICM).

Mesolycus shelfordi (Bourgeois), adult female: «Pontianak, Borneo» (ICM).

Dilophotes depressicornis Pic, adult female: E Sumatra, Riau Prov., Bukit Tigapuluh N.P., 0°50'S 102°26'E, 18-25.I.2000, D.Hauck leg. (ICM).

EROTINAE: EROTINI

Platycis minuta (Fabricius), adult male and female: Russia, Moscow Reg., Lopasnya R., env. Davidova Pustyn', 30.VIII.2000, S.Kazantsev leg. (ICM).

EROTINAE: DICTYOPTERINI

Dictyoptera aurora (Herbst), adult male and female: FE Russia, Kunashir Is., Mendeleevo, VI.1985, S.Saluk leg. (ICM).

Helcophorus miniatus Fairmaire, adult male: Sind R. Valley, Sonomarg, 8.VI.1912, A.Jacobson (A.N.Avinov Expn.) (ZIN); adult female: Kashmir, Pahalgam, 2200-3100 m, 7.VII.1976, W.Wittmer (ICM).

EROTINAE: TAPHINI

Taphes brevicollis Waterhouse, adult female: Vietnam, Gialai-Contum, Buen-Loi, trop. forest, 18-19.I.1990, O.Gorbunov leg. (ICM).

EROTINAE: AFEROTINI

Aferos sp., adult female: Congo belge: P.N.A., Nyakibumba (pres Kikere), 2250 m, 5.VII.1934, G.F. de Witte: 474 (ICM).

CALOCHROMINAE: CALOCHROMINI

Lygisterus sanguineus (Linnaeus), last instar: FE Russia, Maritime Terr., Chuguevskij distr., Lesogorje, in cedar red-rotten log, l = 6 m, w = 0.8 m, 22.VI.1990, A.Antipin leg. (ICM).

Calochromus glaucopterus (Guerin-Meneville), adult male: Muffin Bay, Dutch N. Guinea, VI.(19)44, E.S.Ross coll. (ICM).

PLATERODINAE: PLATERODINI

Plateros flavoscutellatus Blatchley, adult female: FLA., Highlands Co., Archerbold Biol. Sta., 10-11.V.1980, insect flight trap, H.V.Weems, Jr. & F.E. Lohrer (ICM).

METRIORRHYNCHINAE: METRIORRHYNCHINI

Metriorrhynchus thoracicus (Fabricius), adult female: S Sulawesi, nr. Bantimurung, 700 m, 11.V.(19)97, S.Kurbatov leg. (ICM).

METRIORRHYNCHINAE: CONDERINI

Conderis signicollis (Kirsch), adult female: Vietnam, Dongnai Prov., Ma-Da Forest, 1.XI.1990, S.Murzin (ICM).

ATELIINAE: ATELIINI

Scarelus umbrosus Kleine, adult male: W Malaysia, Pahang, Fraser's Hill, 1000-1200 m, 28-31.I.1999, S.Kazantsev leg. (ICM).

LEPTOLYCINAE: LEPTOPYCINI

Ceratoprion sp., adult male: Costa Rica, Guanac. Pr., 9 km S Santa Cecilia, Estac. Pitilla, 700 m, Malaise Tp., 1988, GNP Biod. Survey, 330200, 380200 (ICM).

Lycinella parvula Gorham, adult male: Costa Rica, Vulcan Poas, 7-12.IV.2003, S.Kazantsev (ICM).

LEPTOLYCINAE: LYROPAEINI

Lyroneces optabilis (Kleine), adult male: W Malaysia, Perak, NE Taiping, Bukit Larut (Maxwell's Hill), 1100-1450 m, 7-9.II.1999, S.Kazantsev leg. (ICM).

LEPTOLYCINAE: DEXORINI

Dexoris tessmani Bocák & Bocáková, adult male: Akurennam, Guinea Espanola, Dr. L.Baguena (ICM).

MINIDULITICOLINAE, stat. n.: PLATERODRILINI, tr. n.

Platerodrilus paradoxus (Mjöberg), last instar, NE Sarawak, Bario, 1200-1400 m, IX.25-X.7.2001, S.Kurbatov leg. (ICM).

Platerodrilus sp., adult male, E Malaysia, Sabah, km 52 Rd Kota-Kinabalu-Tambunan, 1700-1800 m, 3-8.VII.2002, S.Kurbatov & S.Zimina leg. (ICM).

Additionally, specimens from the following taxa of Coleoptera, including Cupedidae, Oedemeridae and certain Cantharoidea families, such as Lampyridae, Phengodidae, Cantharidae and Drilidae, were also KOH treated and examined for comparative purposes:

ARCHOSTEMATA: CUPEDIDAE

Tenomerga moultoni (Gestro), adult female: Brunei, Kuala Belalong, 13-17.VI.1995, A.Wong leg. (ICM).

POLYPHAGA: OEDEMERIDAE

Xanthochroa sp., adult male: Costa Rica, Monteverde, 1500 m, 15-20.IV.2003, S.Kazantsev (ICM).

POLYPHAGA: LAMPYRIDAE: LAMPYRINAE

Pyractomena sp., last instar, USA: NC, Great Smoky Mountains N.P., Kophart Prong Tr., 800 m, 20.VII.2003, crawling on *Rhododendron* leaves at ca. 1 m above ground at noon, sunny, S.Kazantsev (ICM).

Lampyrus sp., adult male, Greece: Camp Dimitri Mitropolous, 11 km W of Vitina (Peloponisos) (ICM).

POLYPHAGA: PHENGODIDAE: PHENGODINAE

Phengodes sp., adult male: Costa Rica, Vulcan Poas, 2100 m, 7-12.IV.2003, S.Kazantsev (ICM).

POLYPHAGA: CANTHARIDAE: CANTHARINAE: CANTHARINI

Cantharis fusca Linnaeus, adult male: France, La Balme Sur Cerden, 7 km S of Nantua (Jura), 4.VI.1975, Boris Malkin (ICM).

POLYPHAGA: DRILIDAE

Thilmanus obscurus (Baudi), adult male: Corsica (ICM).

Certain divergent lycid genera, such as *Leptolycus* Leng & Mutchler, *Lampyrolycus* Burgeon, *Mimolibnetis* Pic, *Autaphes* Kazantsev, *Miniduliticola* Kazantsev, *Alyculus* Kazantsev, *Proteros* Kazantsev, etc., known by very few or unique specimens, were also examined, but, as this material could not be KOH treated for further dissection, only selected clearly seen external characters of these taxa, including the hind wing structures, were used for the purpose of this study.

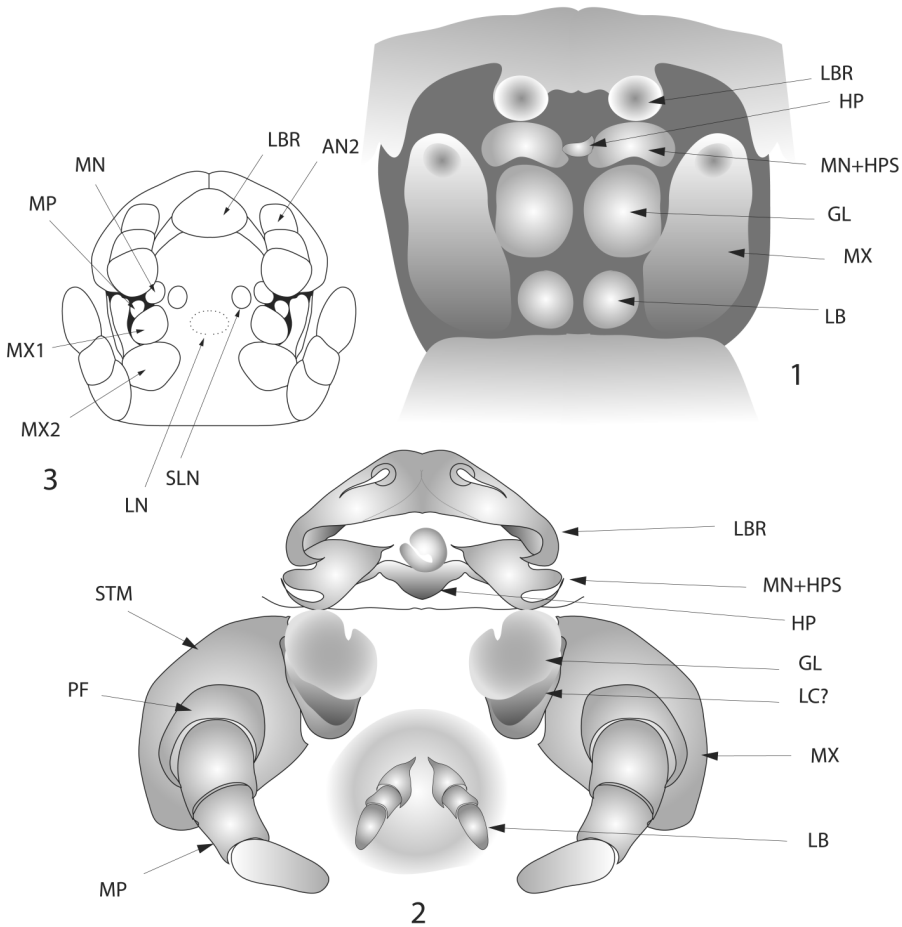
Hexapoda taxonomy is given in accordance with its most recent revision by Kluge (2000), where applicable. Terminology follows Snodgrass (1935) and Chapman (1998); the hind wing terminology follows Kukulova-Peck & Lawrence (1993) modified according to Kluge, 2000 and Fedorenko, 2002.

MORPHOLOGY**IMMATURES STAGES****EGG/EMBRYO**

The egg is oval (*Lopheros*, *Xylobanellus*, Burakowski, 1988; 1990) or round (*Platerodrilus*, Wong, 1996).

- Primitive condition unknown.

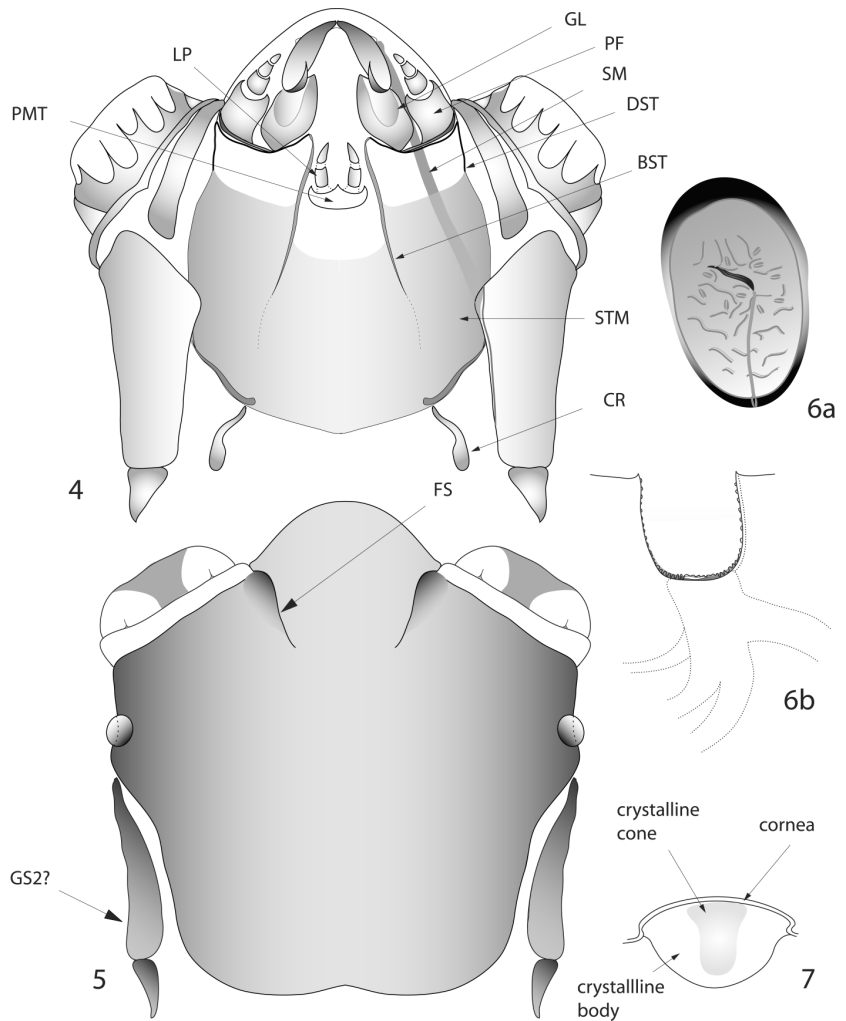
The embryonic stages of *Calopteron* were studied by Cicero (1994) (Figs 1-2): the prekatatrepsis embryo has much in common with the embryo of *Anurida* (Entognatha) (Fig. 3), having the same set of mouth organs: labrum, mandibles, galea, maxillae and labium. Unlike in *Anurida*, however, each of the mouthparts in *Calopteron* is a distinct paired structure (Fig. 1), including the segment hypothesized



Figs 1-3: Embryonic structures: *Calopteron terminale* (Say), prekatatrepsis embryo, mouthparts, ventral view, after Cicero, 1994 (1); same, postkatatrepsis embryo, after Cicero, 1994 (2); *Anurida maritima* (Poda) (Entognatha), head, ventral view, after Folsom, 1900 (3).

AN2 - antenna 2; GL - galea; HP - hypopharynx; HPS - hypopharyngeal suspensorium; LB - labium; LBR - labrum; LC - lacinia; LN - lingua; MN - mandible; MP - maxillary palps; MX - maxilla; MX1 - maxilla 1; MX2 - maxilla 2; PF - palpifer; SLN - superlingua; STM - stipes of maxilla.

to be the labrum. The postkatatrepsis embryo differs by the maxillae subdivided into stipes, palpifer and segmented palps, the labium subdivided into a palpiger and segmented palps and the labrum seemingly constituting one sclerite (Fig. 2). The postkatatrepsis structures are actually the same as in the larval condition, with the exception of the labrum. The fact that in the larvae the labrum is divided again (Figs 47, 50) may be accounted for by the peculiarities of the scanning microscopy process and/or preparation of the embryo therefor, when certain structures could be pictured uniform, even though their cuticle may be of different types, consisting of different number of layers, etc. (as is the case with the larval labral sclerites).

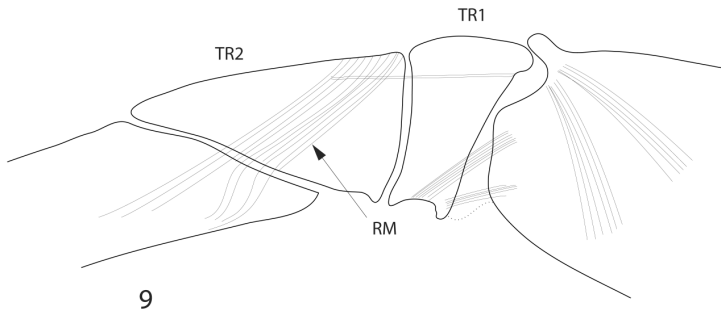
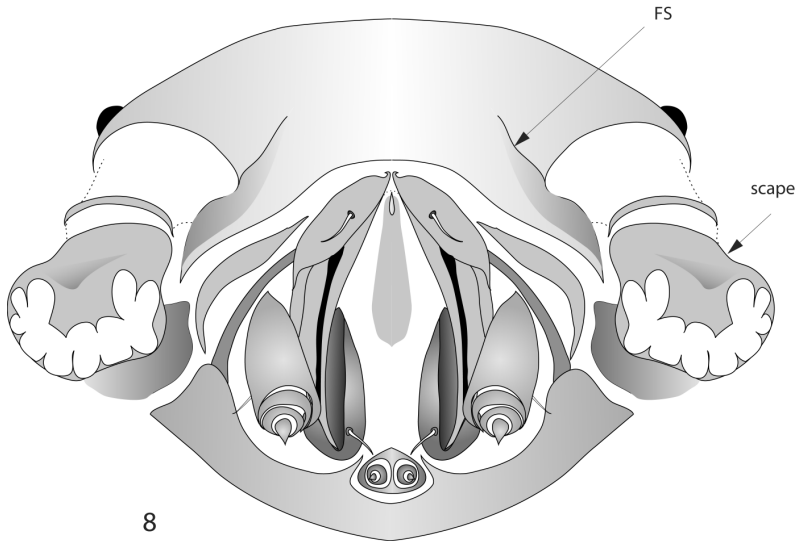


Figs 4-7: Larval structures: *Platerodrilus paradoxus* (Mjöberg), head, ventral view (4); head, dorsal view (5); abdominal spiracle (6a); same, transverse section (6b); stemma, transverse section (7).

BST - basistipes; CR - cardo; DST - dististipes; FS - frontal suture; GL - galea; LP - labial palps; PF - palpifer; PMN - prementum; SM - stipes of mandible; STM - stipes of maxilla.

LARVAE

Cuticle: The larval cuticle is uniformly finely alveolate with roundish alveoli (*Calopteron*, Costa *et al.*, 1988: Fig. 10; *Platerodrilus*); or finely alveolate with the head cuticle tuberculate (*Lycus*); or alveolate on peripheral regions of the head sclerites and thoracic and abdominal segments, as in *Lygisterus*. The Lampyridae larva was found to have alveolate cuticle with the head and tibial cuticle clear (*Pyrractomena*).



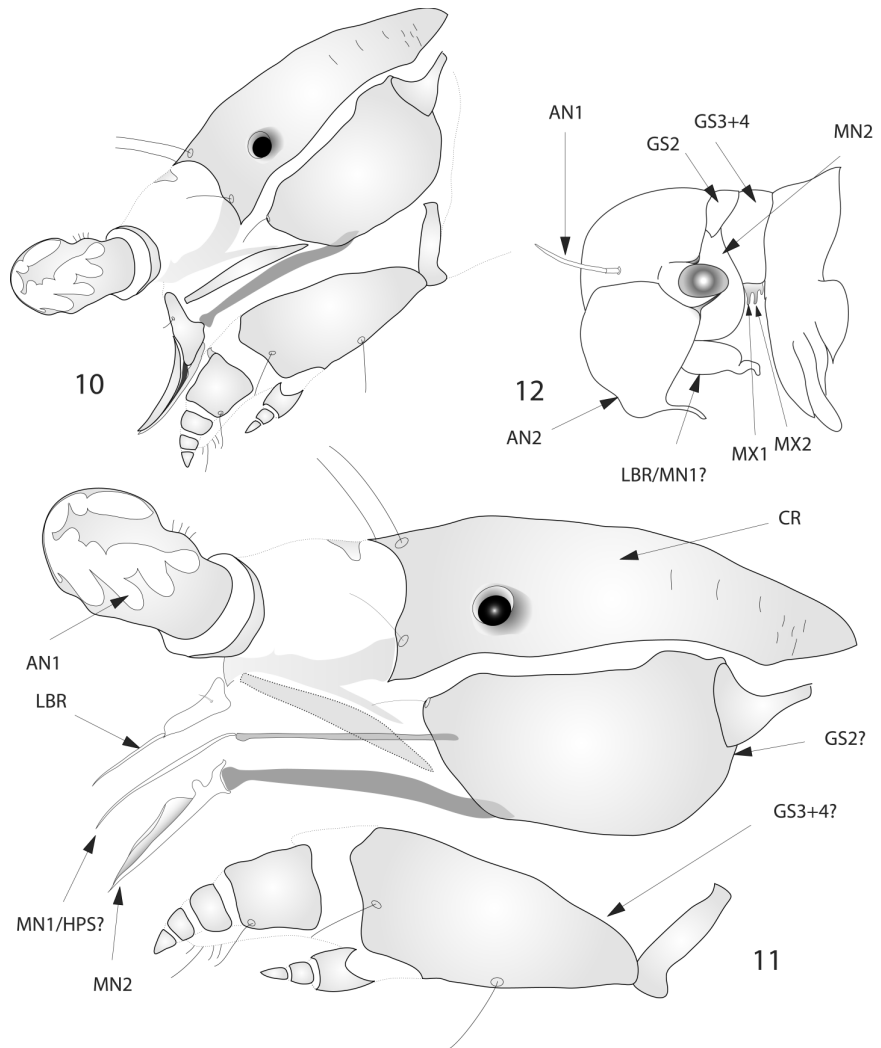
Figs 8-9: Larval structures: *Platerodrilus paradoxus* (Mjöberg), head, anterior view (8); *Platerodrilus* sp., trochanter, after Rosenberg, 1943 (9).

FS - frontal suture; RM - reductor muscle; TR1 - trochanter 1; TR2 - trochanter 2.

The alveolate larval cuticle is also reported in *Dytiscus* (Dytiscidae) and *Lucanus* (Lucanidae) (Kapzov, 1911), whereas the clear cuticular structure of the adult beetles of the same taxa is considered more complex and derived (Snodgrass, 1935).

- The alveolate cuticle structure, uniform in all body sclerites, including the head, is deemed primitive.

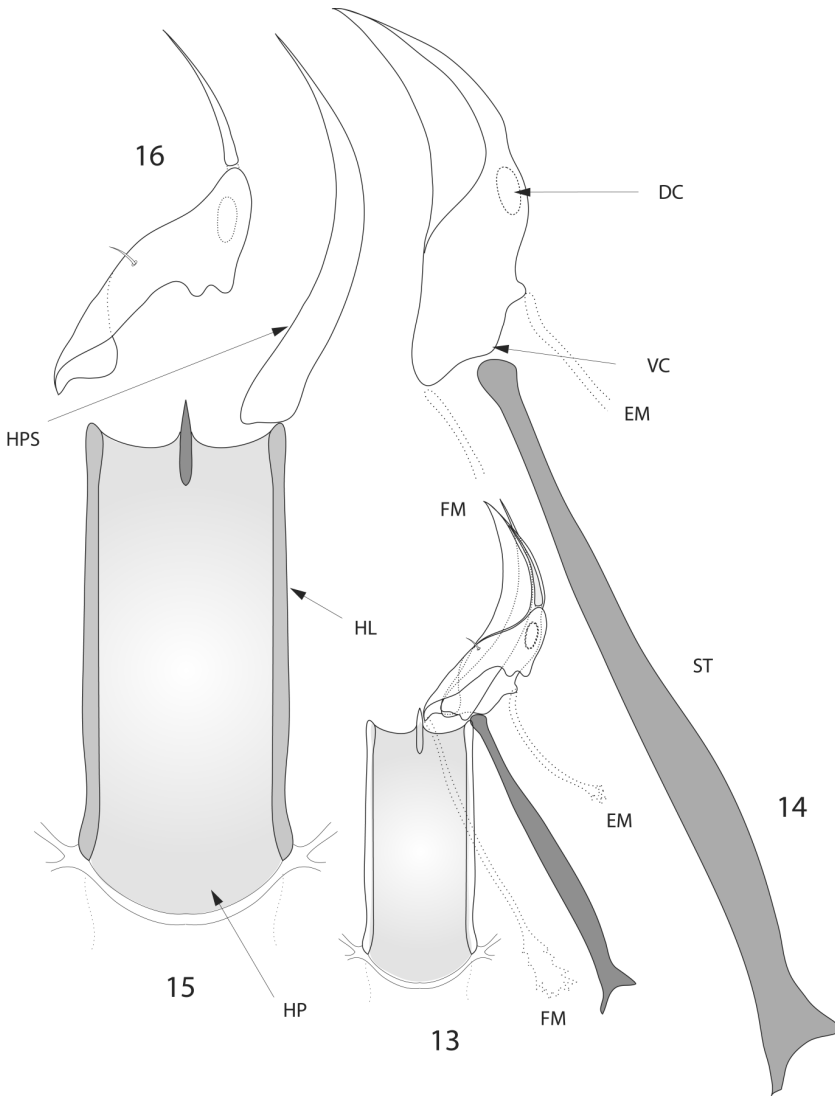
Head: The head is often transverse (e.g. *Lygistopterus*, *Cautires*, Figs 40, 54), sometimes square (*Lycus*, *Calopteron*, *Platerodrilus*, Figs 4-5, 23-24, 47), rarely elongate (*Lycostomus*, Bocák & Matsuda, 2003), completely (e.g. in *Lycostomus*, *Platerodrilus*) or partially retractable into pronotum. Head capsule is open ventrally, consisting typically of three (e.g. *Lycus*, *Pyropterus*, *Cautires*, *Lopheros*, *Plateros*, Figs 23-25, 60, 61; *Xylobanus*, Potoskaya, 1981; *Lyponia*, Bocák & Matsuda, 2003) or five (*Platerodrilus*, Figs 4, 5, 8, 10, 11) sclerites. The three sclerites are: the



Figs 10-12: Larval structures: *Platerodrilus paradoxus* (Mjöberg), head, lateral view (10); same, mandibular sclerites separated (11); *Eubranchypus* (Eucrustacea), head laterally, after Snodgrass, 1935 (12).

AN1 - antenna 1; AN2 - antenna 2; GS2 - gnathal segment 2; GS3+4 - gnathal segment 3+4; HPS - hypopharyngeal suspensorium; LBR - labrum; MN1 - mandible 1; MN2 - mandible 2; MX1 - maxilla 1; MX2 - maxilla 2.

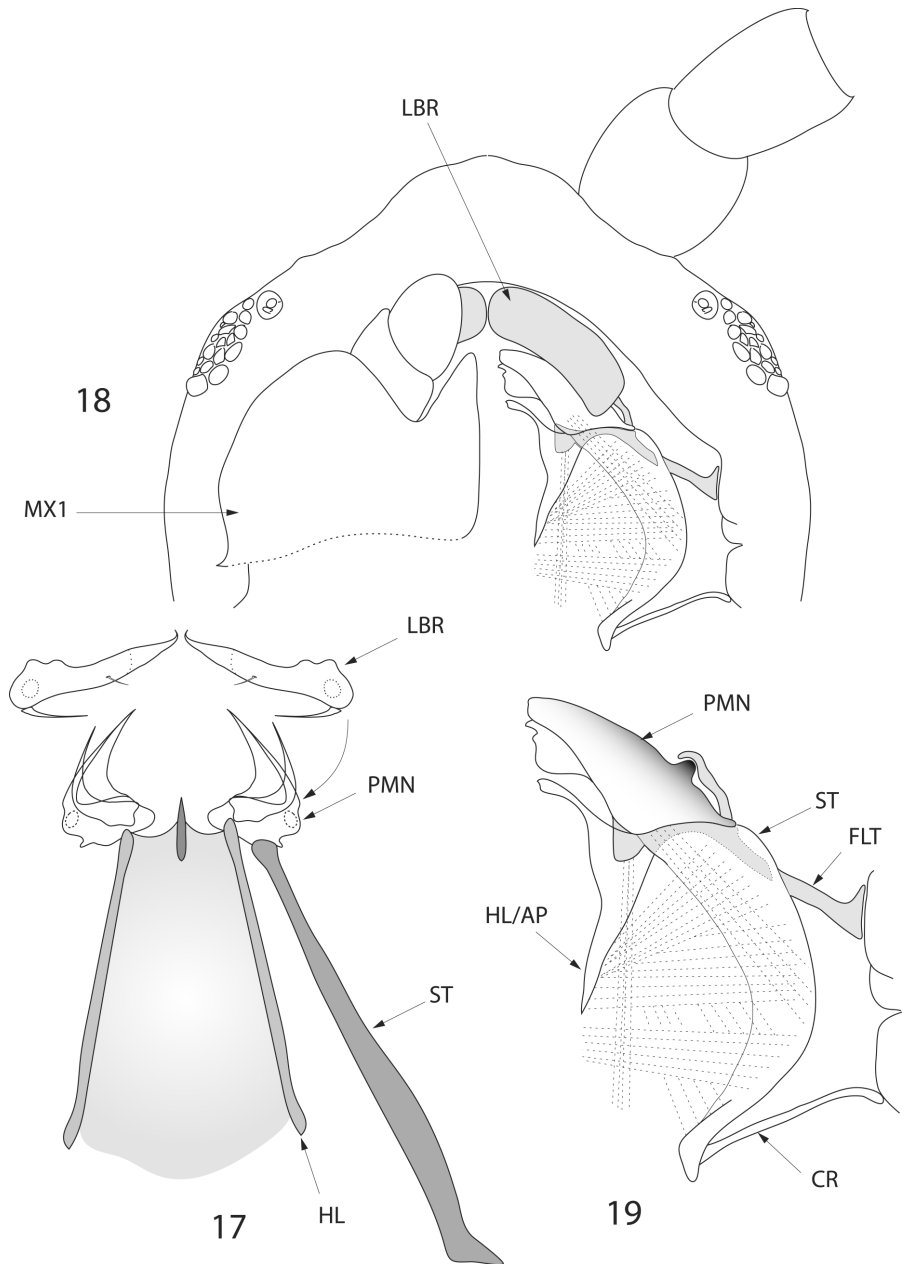
cranium, covering the head dorsally, and a pair of lateral sclerites, presumably gnathal segments II constituting lateral wall, sometimes well visible from above (e.g. *Platerodrilus*, *Lycus*, Figs 5, 11, 24). In *Platerodrilus* an additional pair of narrow anterolateral sclerites is found, possibly related to labrum (Figs 4, 8, 10, 11). The lateral gnathal sclerites are effectively fused to the cranium in *Lygistopterus*, *Calopteron* (Figs 40, 46, 47), *Eros*, *Pseudosynchonnus*, *Metriorrhynchus* and *Porrostoma* and partly fused in *Xylobanellus* (Bocák & Matsuda, 2003). In



Figs 13-16: Larval structures: *Platerodrilus paradoxus* (Mjöberg), mandibular structure, dorsal view (13); same, premandible and stipes of mandible (14); same, stiletto and hypopharyngeal parts (15); same, shutter/labral parts (16).

EM - extension muscle; FM - flexing muscle; HP - hypopharynx; HL - hypopharyngeal lobe; HPS - hypopharyngeal suspensorium; ST - stipes.

Pyractomena the lateral sclerites are also fused to the cranium, with the weaker and lighter sclerotization possibly in place of the former separation (Fig. 71). Miller (1997) considered the membranous stripes separating cranial plates in *Plateros* larva to be ecdysial lines, but Bocák and Matsuda (2003) demonstrated that these stripes have no role in the ecdysis.



Figs 17-19: *Platerodrilus paradoxus* (Mjöberg), larval mandibular structure, dorso-posterior view (17); *Lithobius* sp. (Chilopoda), head ventrally, without maxillae 2 and left maxilla 1, after Kluge, 2000 (18); same, premandible and stipes of mandible, after Kluge, 2000 (19).

AP - apodeme; CR - cardo; FLT - fultura; HL - hypopharyngeal lobe; LBR - labrum; MX1 - maxilla 1; PMN - premandible; ST - stipes.

Ventrally the lycid head is protected by a ventral plate with variant degree of sclerotization, presumably representing fused maxillary stipites (Figs 4, 23, 40, 47). There is a possibility that the maxillary stipite is homologous with gnathal segment III+IV, their two appendages being maxillary and labial structures (e.g. in *Platerodrilus*, Fig. 11), as, for example, in *Eubranchypus* (Eucrustacea) (Fig. 12). Hypotheses considering the postlabial structures secondary derivations (Snodgrass, 1935) seem to conform to this assumption.

Frontal sutures/sulci may be present (e.g. *Lycus*, *Platerodrilus*, Figs 5, 24), while the coronal suture is absent in all studied Lycidae taxa, being complete in *Pyractomena* (Fig. 71). In the latter taxon the frontal sulci that enforce dorsal condyles, to which the mandibles are articulated, and the coronal suture are separate from each other (Fig. 71). The frontal sutures/sulci in *Lycus* and *Platerodrilus* emerge from the antennal suture, while those of *Pyractomena* emerge from the dorsal condyles, and the two do not seem homologous; however, as the «mandibles» of lycid larvae are articulated medially, while those of Lampyridae have their dorsal articulation laterally, near the antennal bases (Fig. 71), it appears that the more prominent frontal sulci in Lampyridae is a result of combination of antennal and mandibular, whatever they are, functions of the sulcus. *Lygisterus* does not have frontal sutures/sulci. Occipital and postoccipital sutures are absent in all studied Lycidae taxa.

- Crowson (1981) considers ventrally open (i.e. with no sclerotized bridge behind the labium) head capsule as a basic type structure for a beetle larva. There is no reason to disagree with this opinion.

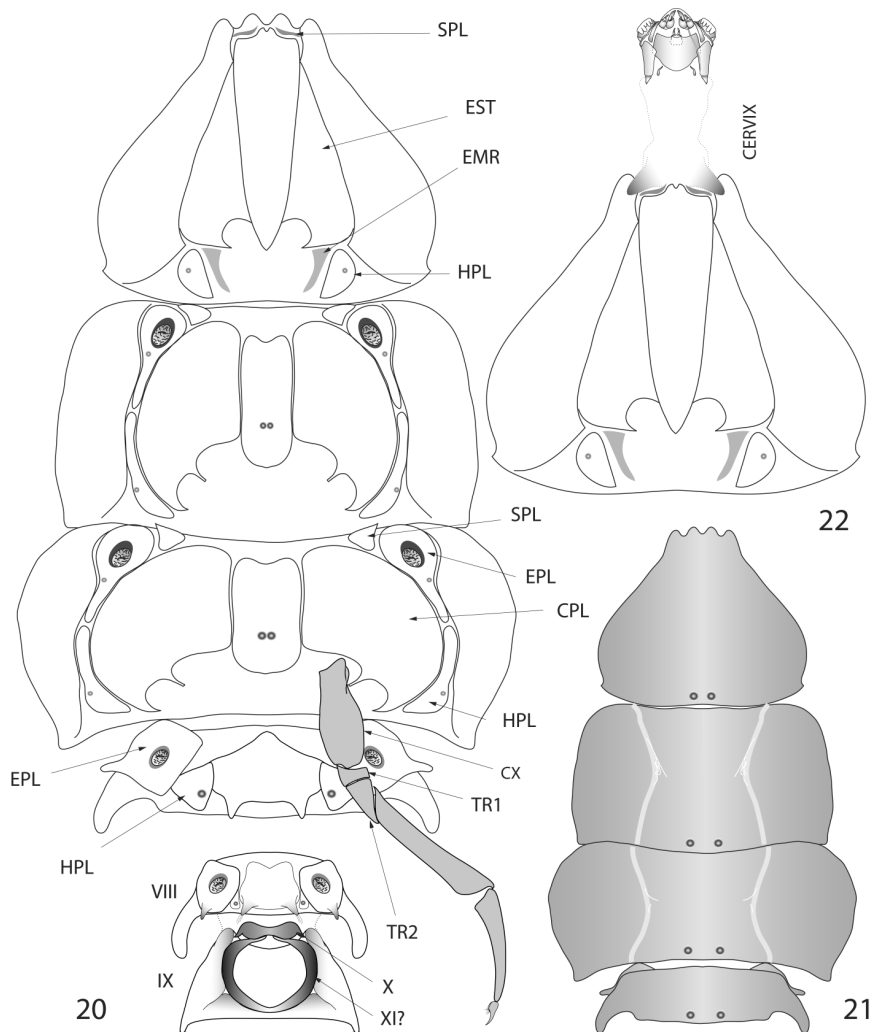
- Division of the cranium into sclerites is considered primitive.
- Division of the cranium into 5 (vs. 3) sclerites is considered primitive.
- As the development of the epicranial/coronal sutures/sulci seems to be related to the development of chewing mandibles, providing rigidity of the frame to which the mandibular muscles are attached in the absence of tentorium, and as the chewing mandibles and tentorium in the Euarthropoda are a derived condition of mouth organs and endoskeletal head structures, absence of the epicranial/coronal suture in forms without tentorium may prove plesiomorphic.

Antenna: Antennae prominent, retractable, 2-segmented, located anterolaterally. The scape is represented by a narrow annuliform sclerite located on the membranous retractable tube (e.g. *Platerodrilus*, Figs 10, 11). The apical membranous slit of the pedicel may be bilobed (*Lycus*, *Lygisterus*, *Calopteron*, *Cautires*, *Platycis*, *Lopheros*, *Plateros*, Figs 23-25, 47, 54, 58, 59) or multi-lobed formed by 6 petals ventrally and two pairs of petals dorsally (*Platerodrilus*, Figs 8, 11). The bilobed slit may be small (e.g. in *Lygisterus*, Fig. 40) or relatively large (e.g. *Lycus*, *Calopteron*, Figs 23-25, 47).

In the Lampyridae the antenna has 3 segments, with the basal mostly non-sclerotized retractable section; the apical antennomere may be provided with a pair of small denticles (e.g. *Pyractomena*, Figs 70-71).

The origin of antennal muscles in lycid larvae is cranial, as well as in Lampyridae, *Drilus* (Drilidae), *Cantharis* and a vast majority of Elateriformia and Scarabaeiformia (Beutel, 1995), condition observed also in chilopods and considered primitive (Snodgrass, 1935), as opposed to their attachment on the tentorium.

- Primitive condition of the number of antennomeres (3 vs. 2) and of the slit of the pedicel (bilobed vs. multi-lobed) is unknown.
- The cranial origin of antennal muscles is deemed plesiomorphic.

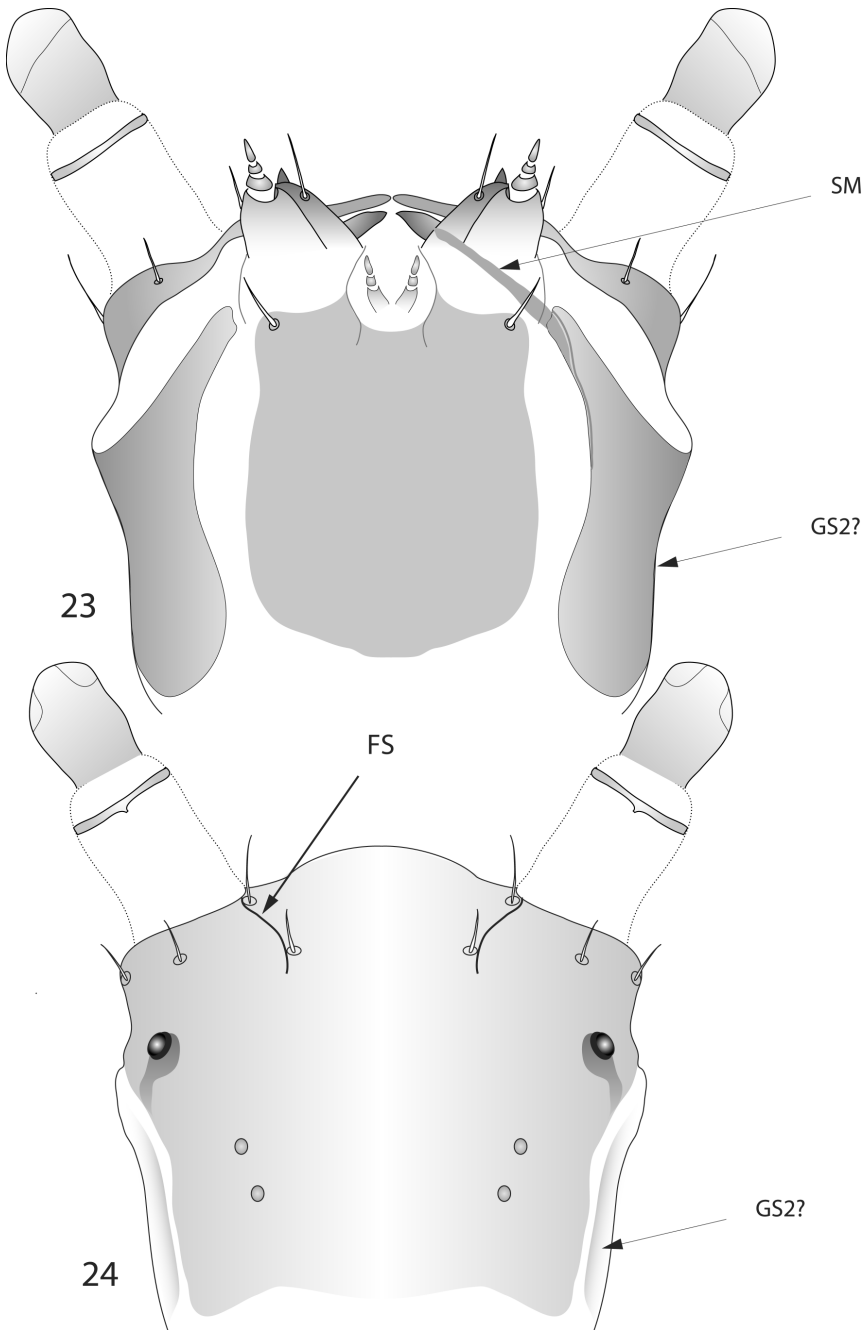


Figs 20-22: Larval structures: *Platerodrilus paradoxus* (Mjöberg), thorax and abdominal segments I and VIII-XI, ventral view (17); same, thorax and abdominal segment I, dorsal view (18); same, head and thoracic segment I, ventral view (19).

CPL - coxopleurite; EPL - epipleurite; EMR - epimeron; EST - episternum; HPL - hypopleurite; SPL - sternopleurite; TR1 - trochanter 1; TR2 - trochanter 2.

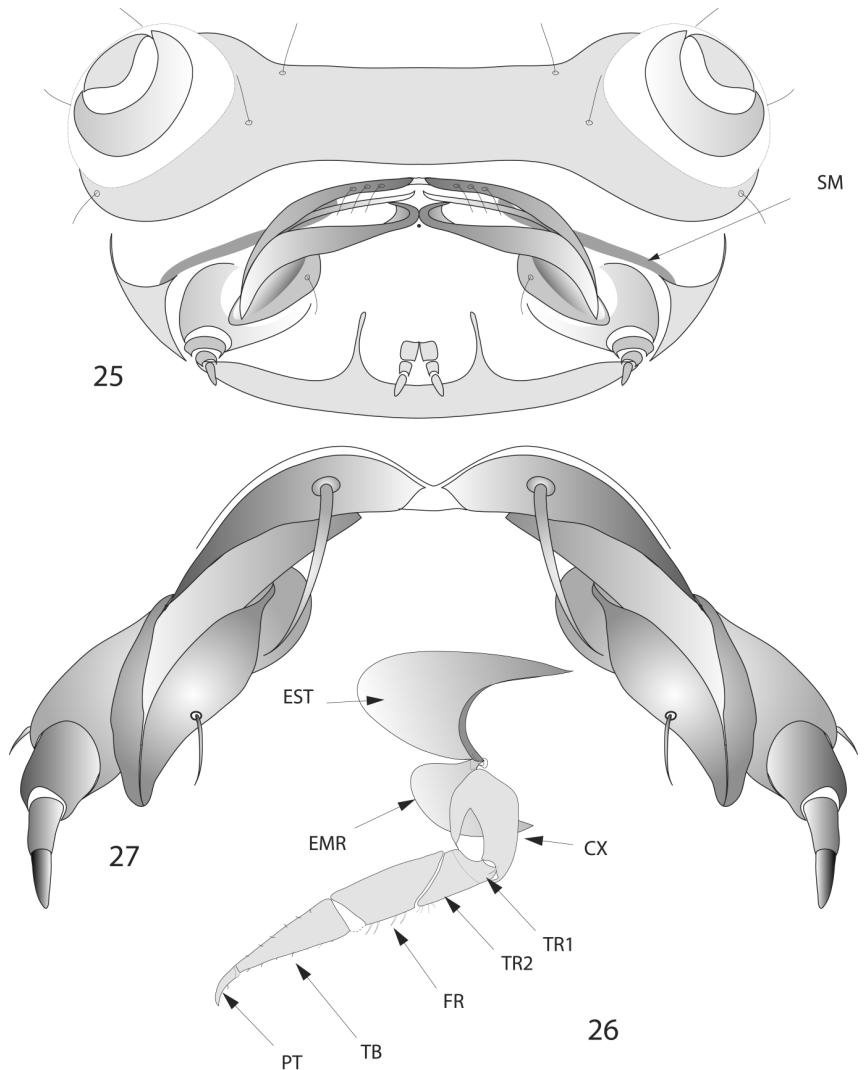
Eye: The larvae of Lycidae have one pair of lateral stemmata located at lateral edges of the cranium posteriad of the antennae (*Lycus*, *Platerodrilus*, Figs 10, 11, 24, 47). The stemma of *Platerodrilus* larva is remarkable in having large crystalline body with a crystalline cone continuous with it (Fig. 7). Bocák & Matsuda (2003) report blind larva in *Plateros*.

- Primitive condition of stemma (with large crystalline body vs. small) is unknown.



Figs 23-24: Larval structures: *Lycus trabeatus* (Guerin-Meneville), head, ventral view (23); same, dorsal view (24).

FS - frontal suture; GS - gnathal segment; SM - stipes of mandible.

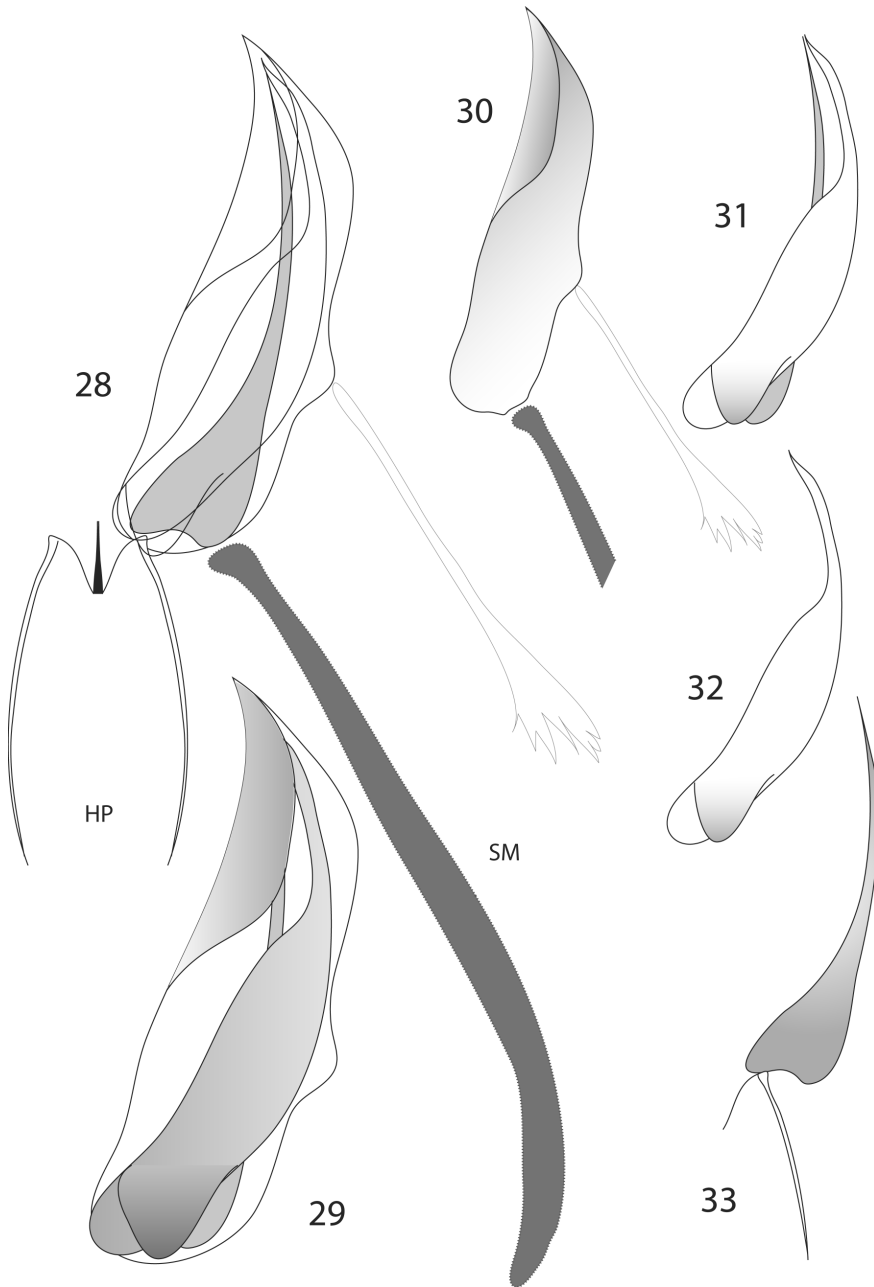


Figs 25-27: Larval structures: *Lycus trabeatus* (Guerin-Meneville), head, anterior view (25); same, leg (26); *Lycus sanguineus* Gorham, mandibular and maxillary structures, frontal view, after Cicero, 1994 (27).

CX - coxa; EMR - epimeron; EST - episternum; FR - femur; PT - pretarsus; SM - stipules of mandible; TB - tibiotarsus; TR1 - trochanter 1; TR2 - trochanter 2.

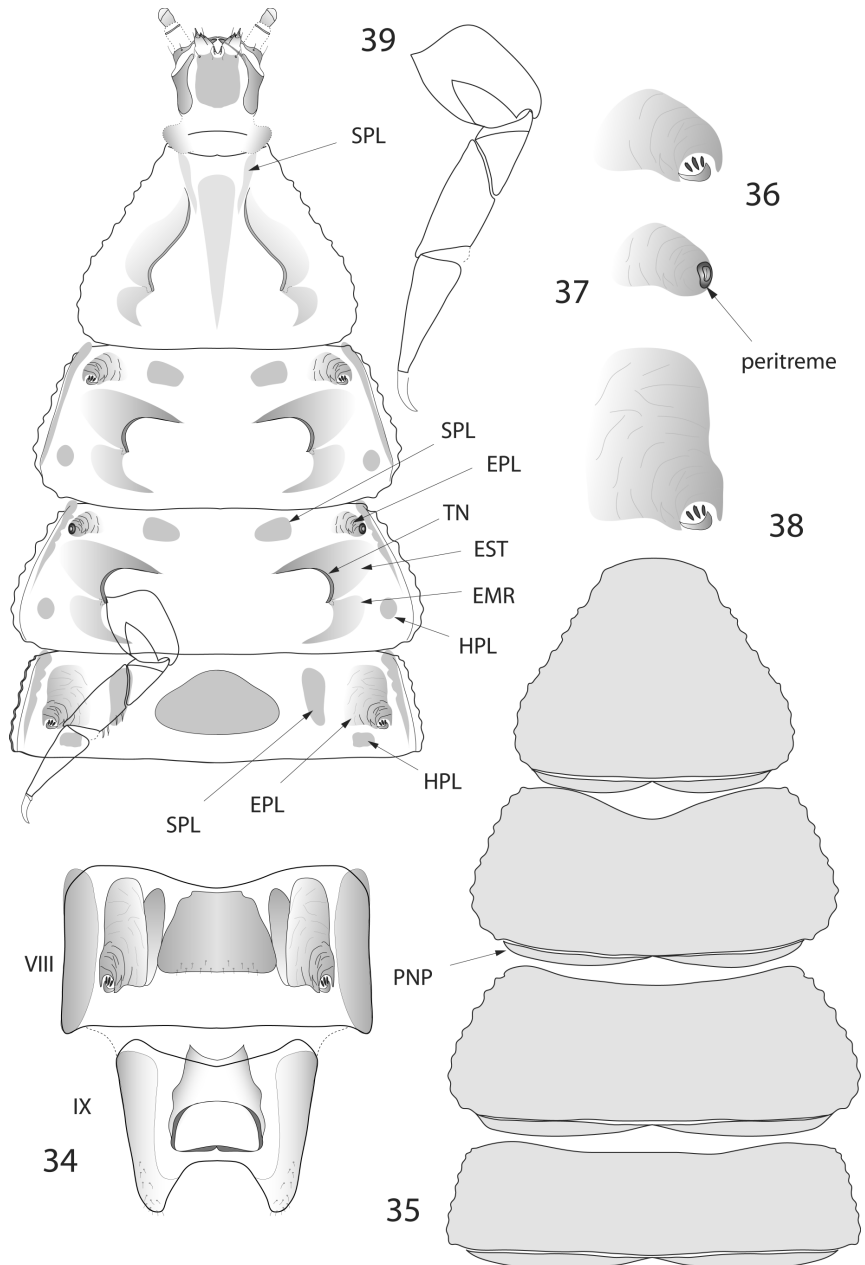
«**Mandibles**»: Mandibular structures are basally approximate and medially attached, apically divergent and non-opposable, at rest often projected slightly backwards proximally and forwards distally, typically resting on galea (Figs 8, 25, 27). Each «mandible» is tripartite (Figs 10-11, 13-16, 28-33, 50-53), consisting of:

a) a sheath, presumed to be the premandible, or the mandible proper, constituting the interior and exterodistal surface of the mandibular structure, bearing



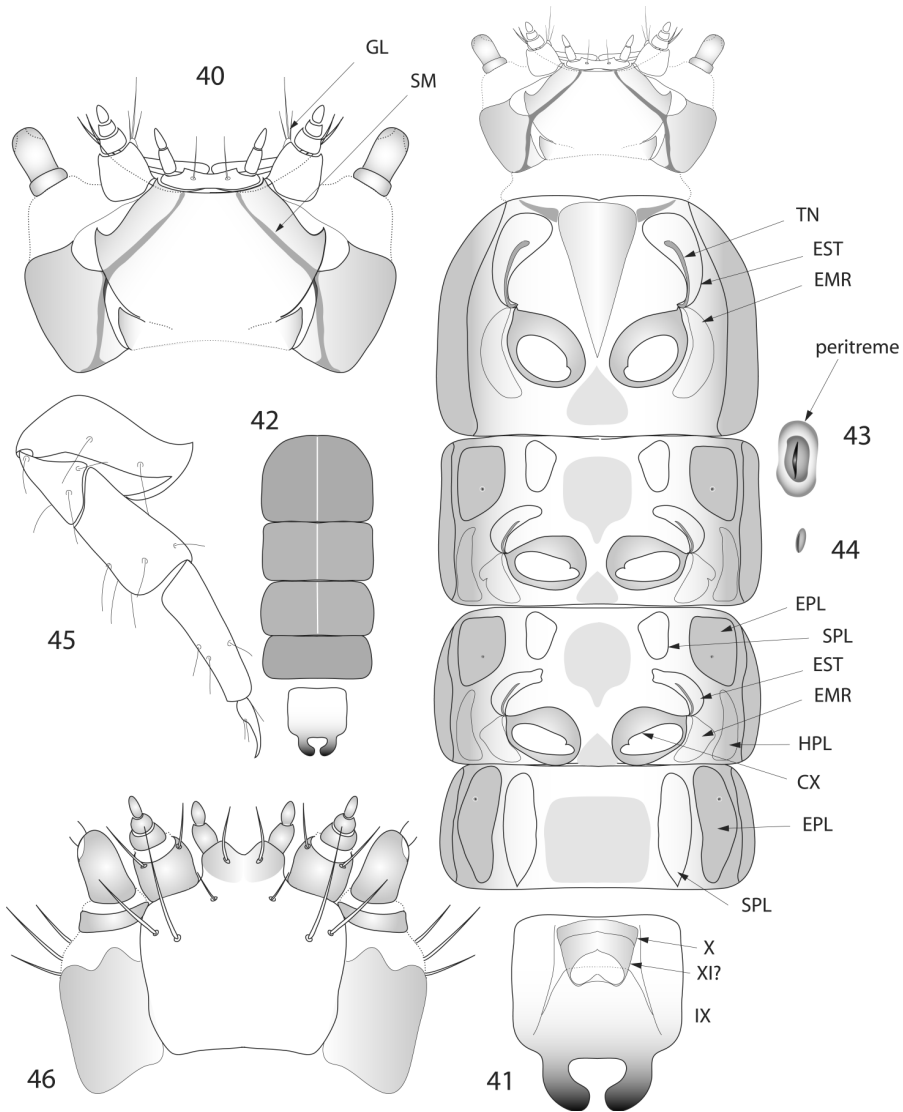
Figs 28-33: Larval structures: *Lycus trabeatus* (Guerin-Meneville), mandibular structure, dorsal view (28); same, anterior sclerites (29); same, premandible (30); same, labral lobe with stiletto (31); same, labral lobe (32); same, stiletto (33).

HP - hypopharynx; SM - stipes of mandible.



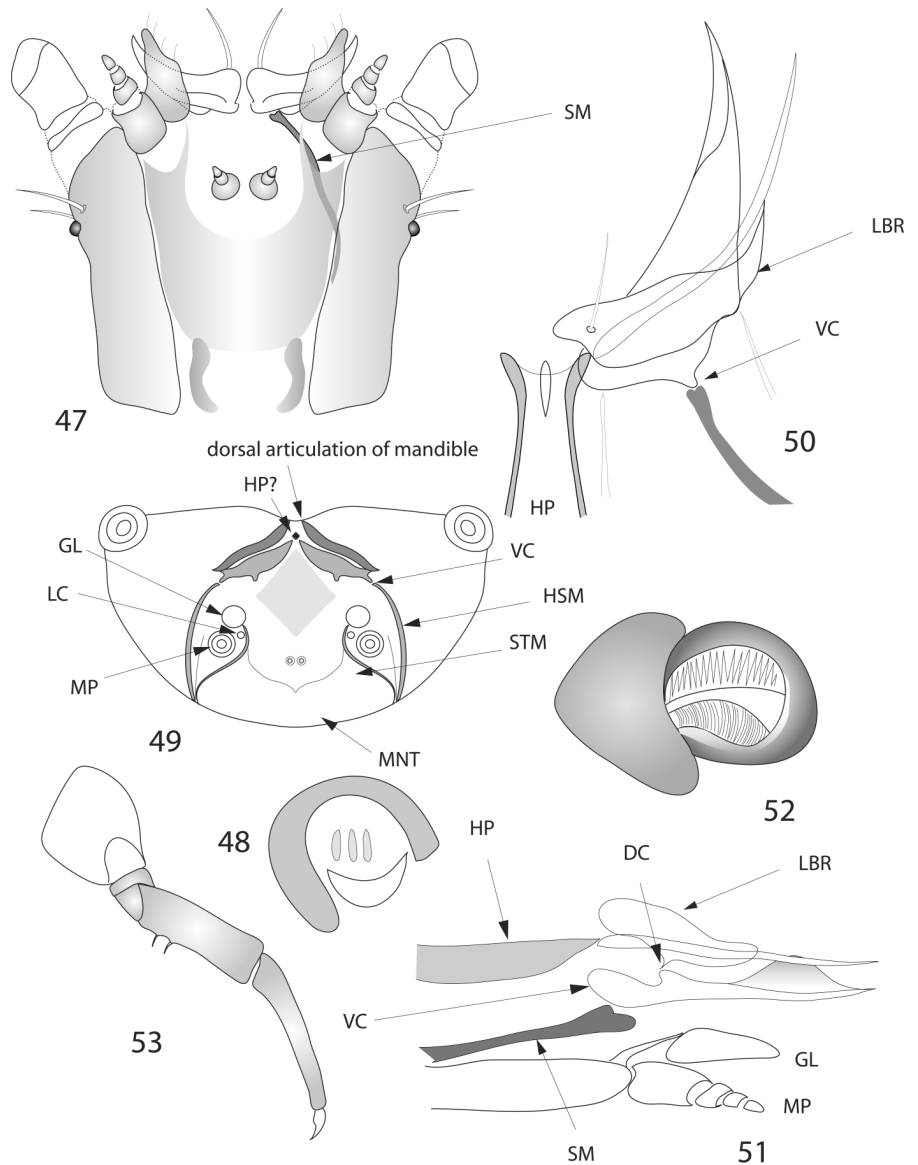
Figs 34-39: Larval structures: *Lycus trabeatus* (Guerin-Meneville), head, thorax and abdominal segments I and VIII-XI, ventral view (34); same, thorax and abdominal segment I, dorsal view (35); same, mesothoracic epipleurite with spiracle (36); same, metathoracic epipleurite with spiracle (37); same, abdominal epipleurite (A1) with spiracle (38); same, metathoracic leg (39).

EMR - epimeron; EPL - epipleurite; EST - episternum; HPL - hypopleurite; PNP - postnotal plate; SPL - sternopleurite; TN - trochantin.



Figs 40-46: Larval structures: *Lygistorpterus sanguineus* (Linnaeus), head, ventral view (40); same, head, thorax and abdominal segments I and IX-XI, ventral view (41); same, thorax and abdominal segment I and IX, dorsal view (42); same, mesothoracic epipleurite with spiracle (43); same, metathoracic epipleurite with spiracle (44); same, metathoracic leg (45); *Macrolygistorpterus* sp., head, ventral view, after Costa et al., 1988 (46).

CX - coxa; EMR - epimeron; EPL - epipleurite; EST - episternum; GL - galea; HPL - hypopleurite; SM - stipes of mandible; SPL - sternopleurite; TN - trochantin.



Figs 47-53: Larval structures: *Calopteron terminale* (Say), head, ventral view, after McCabe & Johnson, 1979b, modified (47); same, abdominal spiracle (48); *Calopteron reticulatum* (Fabricius), head, anterior-ventral view, schematic, after Böving & Craighead, 1931 (49); *Calopteron* sp. (Peru), mandibular structure, dorsal view (50); same, lateral view (51); *Calopteron* sp., thoracic spiracle, after Costa et al., 1988 (52); same, leg (53).

DC - dorsal condyle; GL - galea; HP- hypopharynx; HSM - hypostomal margin; LBR - labrum; LC - lacinia; MNT - mentum; MP - maxillary palps; SM - stipes of mandible; STM - stipes of maxilla; VC - ventral condyle.

a condyle articulated to the fossa on what is assumed to be the stipes of mandible and a dorsal acutabular fossa received by a condyle on the shutter (Figs 13-14, 50-51);

b) a stiletto, hypothesized to be the paired hypopharyngeal suspensorium, which may also prove to be the superlinguae, at rest hidden within the cavity formed by the sheath and the shutter (Figs 13, 15, 28, 31, 33, 50, 51); its surface bears longitudinal cuticular ribs, along with similar ribs on the inner surface of the sheath forming canal; it is articulated distally with apical part of shutter and basally with hypopharyngeal lobe; in some forms (e.g. *Lygisterus*) the distal part of the stiletto is fused with the shutter; and

c) a shutter, presumed to be the labral lobe, sometimes segmented, with a wide basal sclerite constituting basal portion of exterior surface and connected by a condyle to the sheath, with its exterior surface bearing chaeta, and a long and narrow apical sclerite, covering the sheath opening distally (Figs 13, 16, 28-29, 32, 50-51).

The free elongate sclerite articulated distally with the condyle on the premandible and attached proximally to the anteroventral edge of the gnathal segment, is probably homologous with the stipes of mandible characteristic of Myriapoda (Figs 17-19). The stiletto part of the mandibular structure is articulated proximally to the hypopharyngeal lobe, which may be a prominent (e.g. in *Platerodrilus*, Figs 13-14) or a slender sclerite (e.g. in *Lycus*, *Calopteron*, Figs 28, 50, *Lygisterus*, etc.). The presence of the hypopharyngeal lobes, as well as the superlinguae is also known in some Entognatha and Myriapoda. At the same time the broadly separated condyles of the mandible proper, with the anterior/lateral one positioned on the dorsal surface is typical for Ephemeroptera, Entognatha, Myriapoda and Eucrustacea, all of these structures considered lost in other taxa of the Metapterygota (Kluge, 2000).

Rosenberg (1943) interprets the shutter as clypeus (basal segment) and labrum (apical segment). Cicero (1994) basing on his *Lycus* and *Calopteron* embryonic and larval studies comes to a conclusion that the shutter is labrum, considering it to be continuous with transfrontal region. It does seem continuous on the photograph (Fig. 3), but in fact the pair of labral sclerites is independent both from the transfrontal region and each other, the cuticle connecting them less sclerotized and obviously not constituting their part. It indeed seems plausible to interpret the shutter as a lobe of the divided labrum. The presence of a mandibular canal in lampyrid larvae and the general similarity of their mandible to the lycid larval composite mandible might suggest it is a fused version thereof, with the shutter participating in forming the dorsal surface of the definitive mandible and the stiletto separating the channel from the chamber (e.g. in *Pyraclomena*, Fig. 76), but studies on embryonic development in fireflies suggest that their labrum is not divided in early stages and does not participate in forming the mandible (Cicero, 1994). This conclusion likewise suggests, despite the widespread presence of a conspicuous mandibular canal in adult Lycidae (e.g. *Dictyoptera*, Fig. 166), that mandibular structure of the adult Lycidae is not homologous with that of their larvae, i.e. the imaginal mandible is not formed in part by the modified labrum. On the other hand, the definitive pterygote mandible and the adult lycid mandible are never attached to the labrum, whereas the true mandible of the lycid larva, or the sheath of its mandibular structure, is hinged posteriorly to the stipes of mandible, being also articulated with a condyle to the shutter of the same mandibular structure (e.g. Figs 17, 51). In this respect it differs both from the apterygote type, in which the mandible

is hinged by a single point of articulation, and the pterygote type, in which the mandible acquires the second anterior dorsal articulation on the head (Snodgrass, 1935). Similar structure of the mandibular apparatus may appear to occur in Protorrhynchota (incl. Palaedictyoptera), where the dorsal pair of stiletos may prove to be lobes of divided labrum; this taxon is known from the Carboniferous and Permian, with the mouthparts preserved in very few specimens (Kluge, 2000).

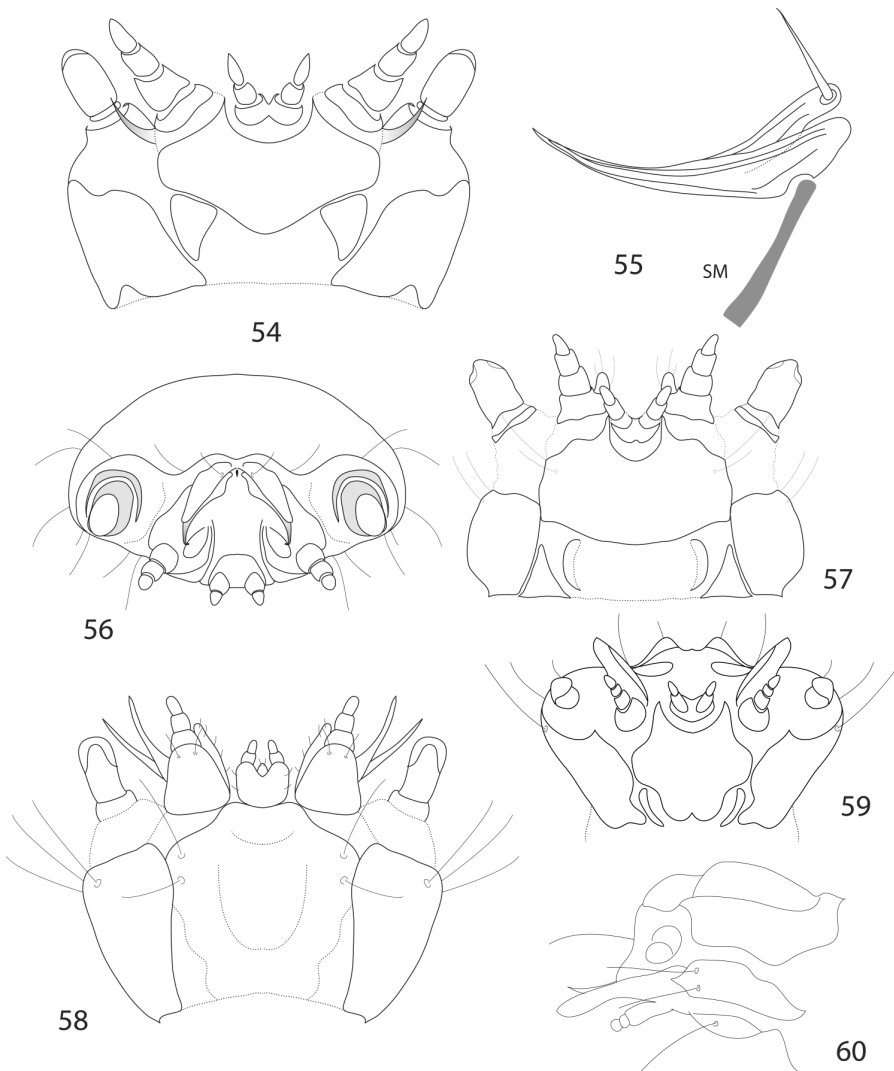
Comparison of the structure of the lycid larval mouthparts with that of a *Lithobius* sp. (Chilopoda) (Figs 18-19) demonstrates that the mandible in both cases is divided into the gnathal lobe («premandible») and stipes; the labrum is similarly represented by a paired sclerite; and the distal suspensoria located dorsad of the mandibles and supported laterally by fultura, have prominent proximal lobes (presumably homologous with hypopharyngeal lobes in the Lycidae). The premandible has a dorsal acutabular fossa on its anterior surface making a joint with the condyle on the labral segment in Lycidae or with the fultura in Chilopoda (Figs 17-19). Due to location of the second/lateral condyle of the true mandible and its articulation the possibility of homology of the presumed labral segment in lycid larvae with the fultura in chilopods should not be ruled out either.

Unlike the mandibular structures in the myriapod hexapods, however, the lycid stipes, both larval and imaginal, does not have musculature and, though conspicuously invaginated, makes part of the cranial wall, being connected to the cranial and maxillary sclerites by thin membrane. The degree of its invagination in some lycid larvae may be fairly inconsiderable, as in *Lygistopterus*, whereas it is completely fused to the cranium in Lampyridae (Fig. 70) and other Cantharoidea. In certain Symphyla (e.g. *Scutigrella* species, Kluge, 2000: Fig. 23) the stipes of the similarly divided mandible is also fused to the cranium, attaining approximately the same condition as in larval Lampyridae and some adult Lycidae with vestigial mandibles, where the hypostomal margin is conspicuously more prominent than other sulci (e.g. *Lycostomus*, *Lyroneces*, Figs 88, 114).

The hypopharyngeal lobes of Lycidae larvae and the proximal lobes of fulturae of Chilopoda, as well as the Collembolan Folsam arms, may be homologous with the anterior arms of tentorium of Amyocerata. The divided labrum serving as the shutter of the lycid mandibular structure, and perhaps the hexapod labrum in general, may also be homologous with antenna 2, a postoral appendage, fully developed in Chelicerata and Eucrustacea, but present as rudimentary lobes only in few adult insects, such as, for instance, Diplura (Snodgrass, 1935).

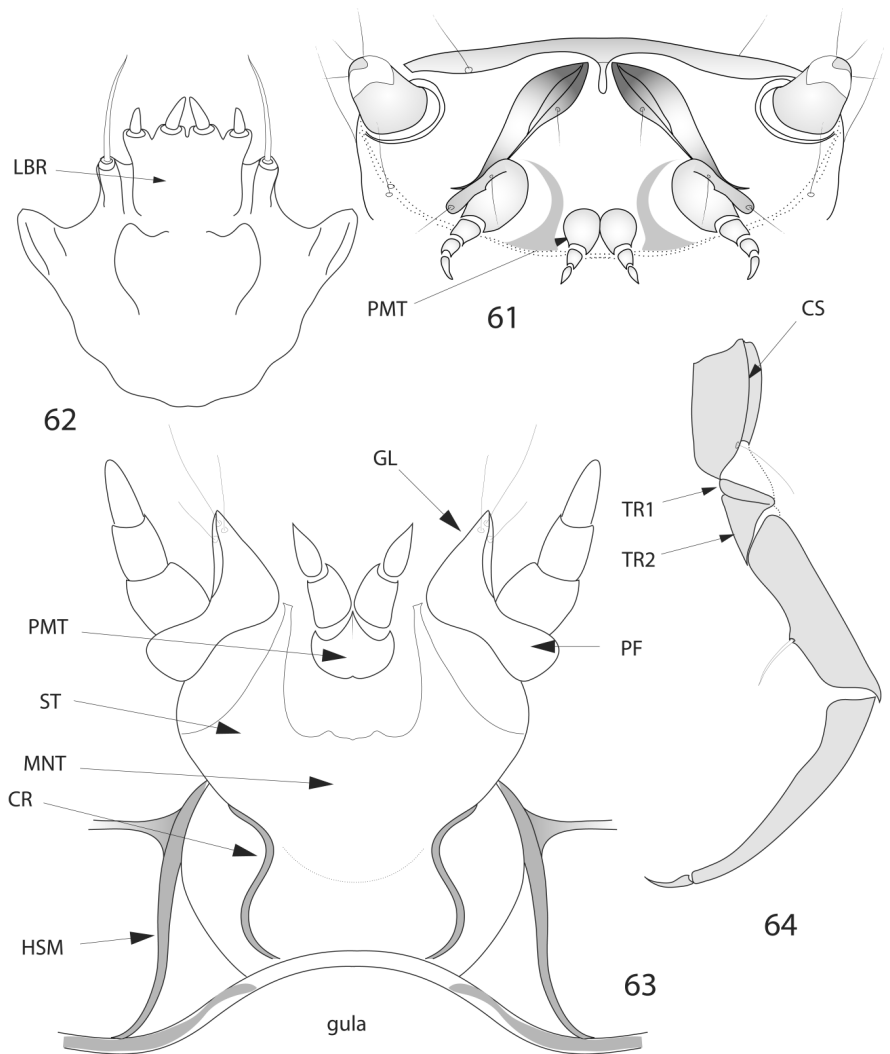
- Composite tripartite mandible is considered primitive.
- Division of the mandible into premandible and stipes is considered plesiomorphic.
- Absence of the dorsal cranial articulation of mandible is considered plesiomorphic.
- Presence of long hypopharyngeal lobes and suspensoria is considered plesiomorphic.
- Primitive labral condition (divided vs. undivided; segmented vs. non-segmented) is unclear.

Hypopharynx: The hypopharynx, defined as the median postoral lobe of the ventral wall of the gnathal region of the head anterior to the labium (Snodgrass, 1935), in lycid larvae includes a pair of suspensoria and hypopharyngeal apodemes, or lobes (e.g. *Platerodrilus*, *Lycus*, Figs 15, 28), the suspensoria making part of the composite mandibles. It is also possible that the distal sclerites of the hypopharynx,



Figs 54-60: Larval structures: *Cautires yuasai* Nakane, head, ventral view, after Hayashi (nec *Lyponia quadricollis*), 1954 (54); same, mandibular structure (55); *Platycis sculptilis* (Say), head, anterior view, after McCabe & Johnson, 1979a (56); same, ventral view (57); *Lopheros lineatus* (Gorham), head, ventral view, after Burakowski, 1990 (58); *Plateros floralis* (Melsheimer), head, ventral view, after Miller, 1997(59); same, lateral view (60).
SM - stipes of mandible.

here presumed to be the suspensoria, are in fact the superlinguae, articulated to the hypopharynx, as is the case in some other insects, e.g. in Ephemeroptera (Kluge, 2000: Fig. 50D). Similar presence of the hypopharyngeal suspensoria and apodemes is noted for some Entognatha (e.g. *Heterojapyx*, Snodgrass, 1935: Fig. 61); the participation of the hypopharynx as the stiletto part of the haustellate «rostrum» is also presumed in Protorrhynchota (Kluge, 2000). Snodgrass (1935) points out that the hypopharyngeal apodemes are homologous with the anterior arms of the



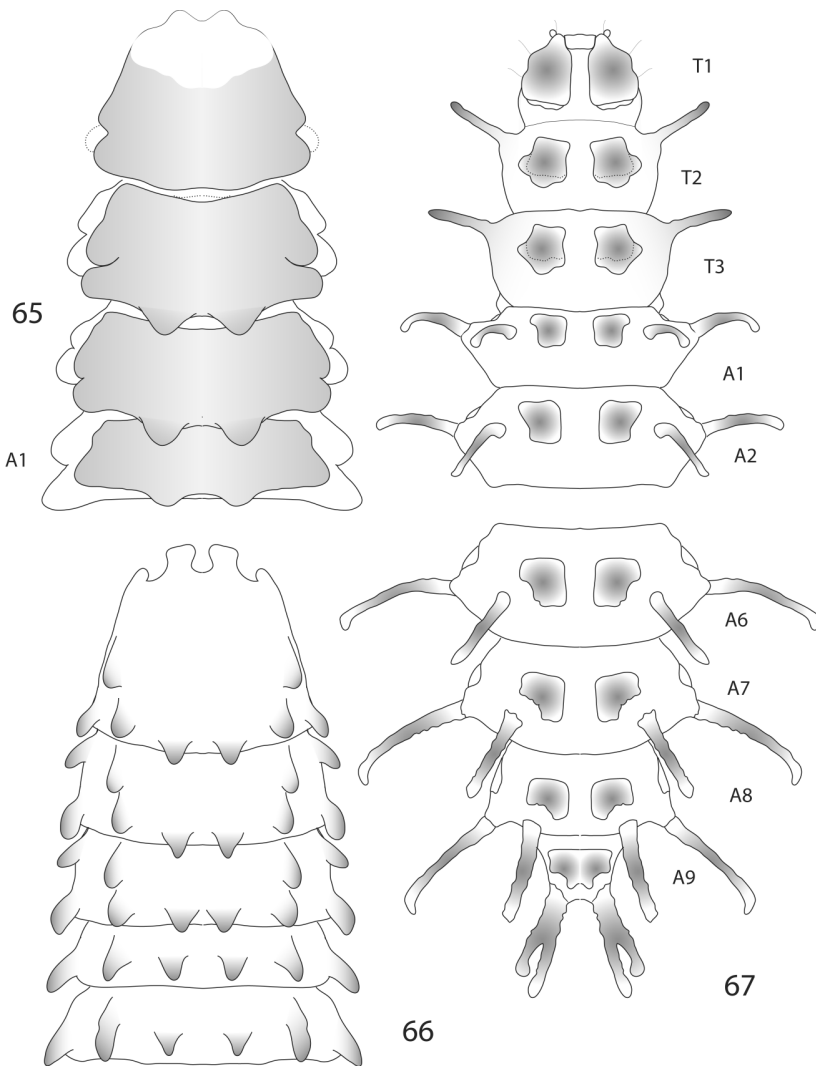
Figs 61-64: Larval structures: *Pyropterus nigroruber* (Degeer), head, anterior view (61); *Brachypsectra lampyroides* Blair, clypeus and labrum, dorsal view, after Blair, 1930 (62); *Eros humeralis* (Fabricius), mouthparts, ventral view, after Böving & Craighead, 1931 (63); *Lyponia* sp., leg, after Bocák & Matsuda, 2003 (64).

CR - cardo; CS - coxal suture; GL - galea; HSM - hypostomal margin; MNT - mentum; PF - palpifer; PMT - prementum; ST - stipes; TR1 - trochanter 2; TR2 - trochanter 1.

tentorium and also suggests that the suspensorial area of the hypopharynx may not be a part of the true hypopharynx, probably representing the venter of the postoral tritocerebral somite of the head.

In *Pyractomena* (Lampyridae) the hypopharyngeal apodemes, or lobes, are fused (Fig. 75).

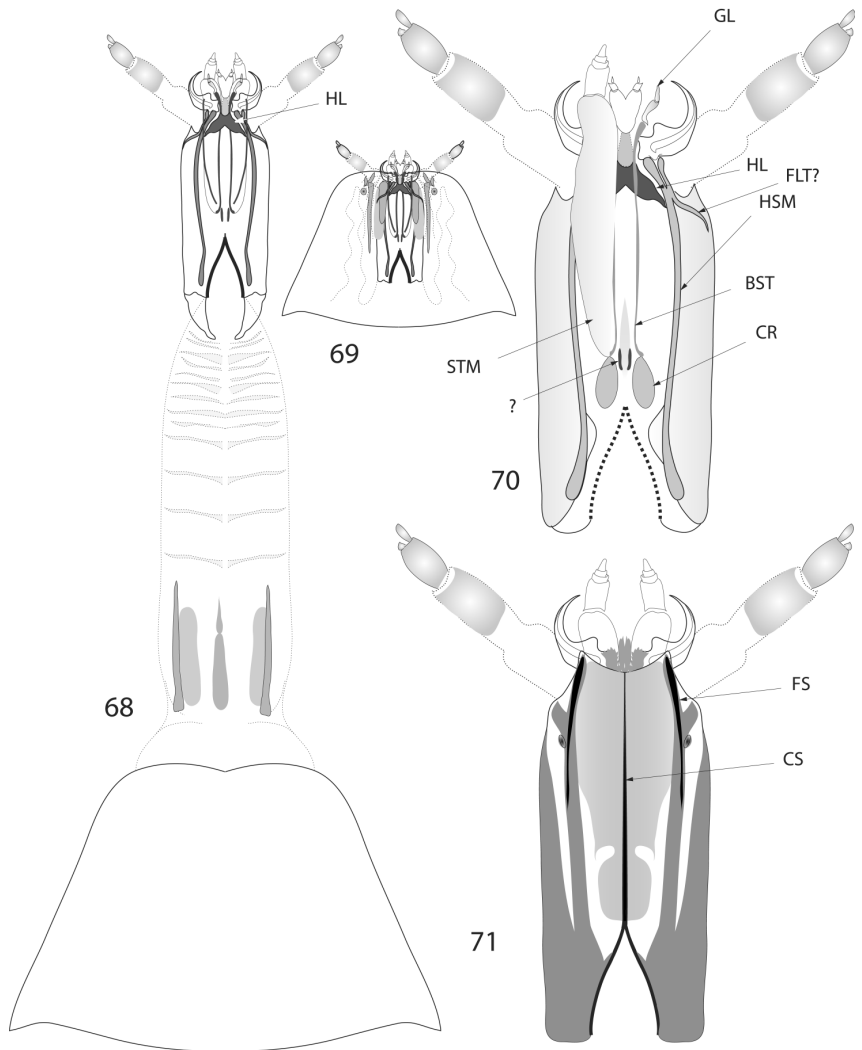
- Prominent paired hypopharyngeal lobes are considered primitive.



Figs 65-67: Larval structures of *Cautires*, after Bocák & Matsuda, 2003: *C. pulcher* Kleine, thorax and abdominal segment I, dorsal view (65); *C. asper* Kleine, thorax and abdominal segments I and II, dorsal view (66); *C. yasai* Nakane, thorax and abdominal segments I, II and VI to IX, dorsal view (67).

A - abdominal segment; T- thoracic segment.

Tentorium: The tentorium, defined as the endoskeletal structure bracing the lower edges of the epicranial walls, is absent in lycid larvae. What is present is typically confined to a pair of elongate sclerites, constituting the lobes of the hypopharynx, that are articulated anteriorly to the base of suspensoria (Figs 15, 17). They are, according to Snodgrass (1935), homologous with the front arms of tentorium. From the functional standpoint, however, a structural analogue of tentorium, as in Entognatha, seems to be the stipes of mandible attached posteriorly

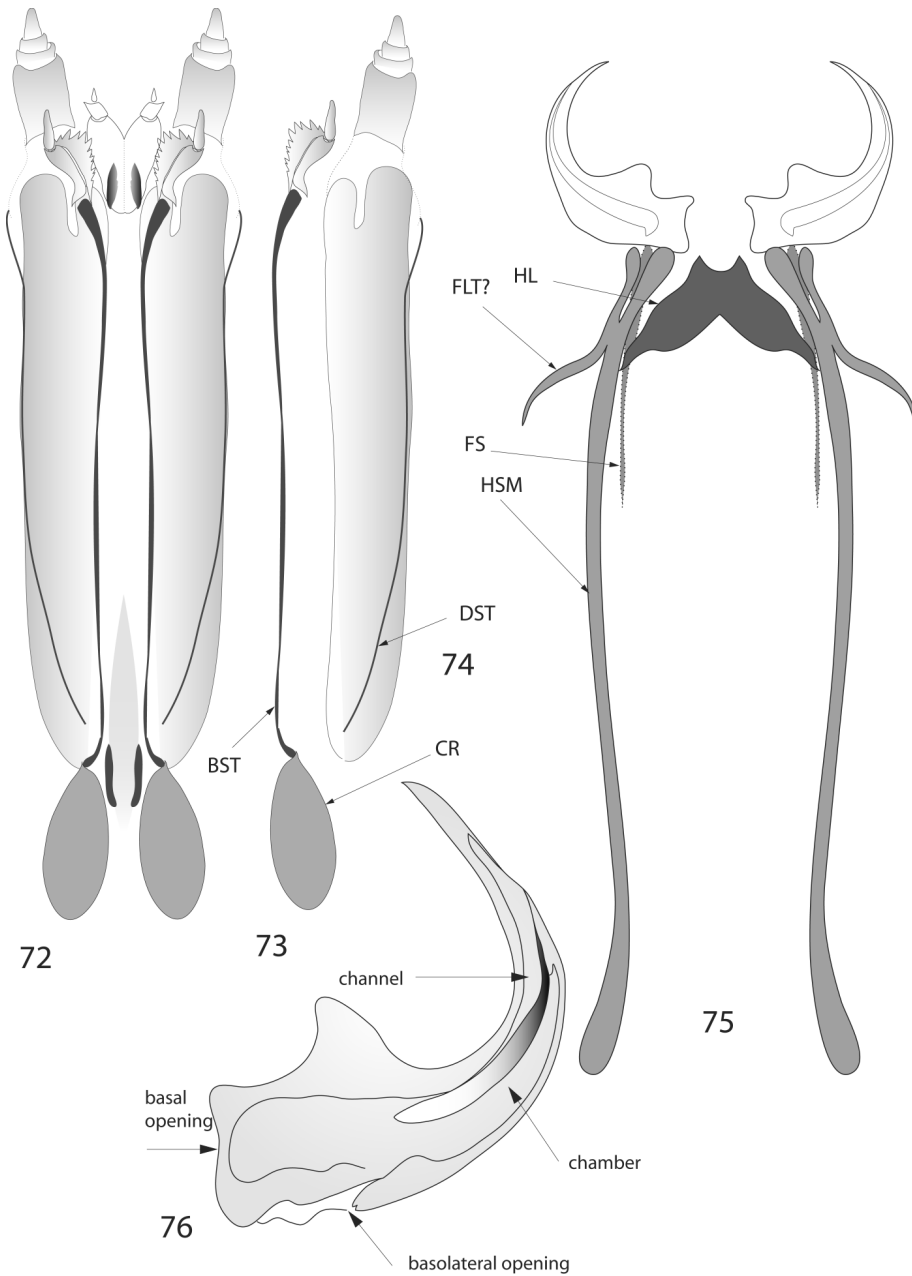


Figs 68-71: Larval structures of *Pyractomena* sp.: head and prothorax, ventral view (68); same, head retracted (69); head, ventral view, without left maxilla (70); same, dorsal view (71).

BST - basistipes; CR - cardo; CRS - coronal suture; LT - fultura; FS - frontal suture; GL - galea; HL - hypopharyngeal lobe; HSM - hypostomal margin.

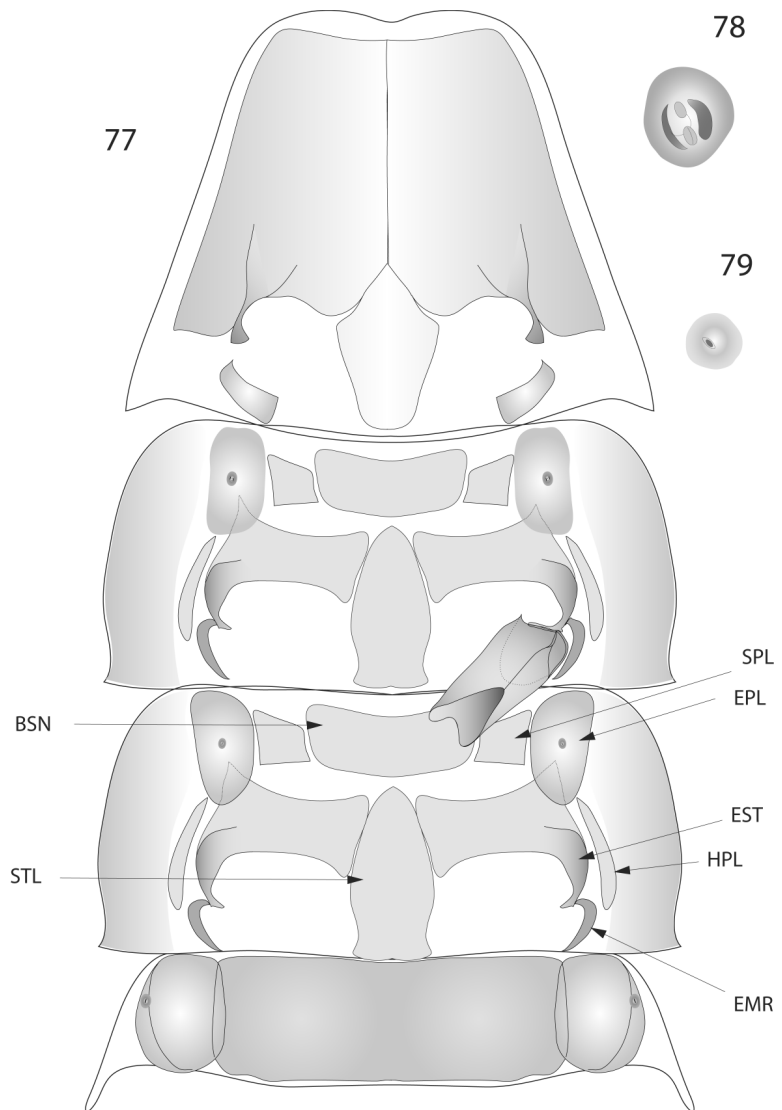
to the anteroventral edge of a sclerite presumed to be gnathal segment II (Figs 4, 11, 23). The posterior arms, as well as the tentorial bridge are equally absent.

Pyractomena, equipped with strong non-composite mandibles, does not have tentorium either, the rigidity of the mandibular frame being provided, ventrally, by the stipes of mandible, which is fused to the cranial lobe and becomes the hypostomal margin, and the fused hypopharyngeal lobes, and, dorsally, by the frontal sulci arising from the frontal condyles (Figs 70-71, 75).



Figs 72-76: Larval structures of *Pyrractomena* sp.: maxillae and labium, ventral view (72); galea, ventral view (73); maxillae, ventral view (74); mandibular structure, ventral view (75); right mandible, dorsal view, longitudinal section, after Cicero, 1994 (76).

BST - basistipes; CR - cardo; CRS - coronal suture; DST- dististipes; LT - fultura; FS - frontal suture; GL - galea; HL - hypopharyngeal lobe; HSM - hypostomal margin; HP - hypopharynx.



Figs 77-79: Larval structures of *Pyrractomena* sp.: thorax and abdominal segment I, ventral view (77); mesothoracic and abdominal spiracle (78); metathoracic spiracle (79).

EMR - epimeron; EPL - epipleurite; EST - episternum; HPL - hypopleurite; SPL - sternopleurite; STL - sternellum; BSN - basisternum.

- Besides bracing the cranial walls, the tentorium gives attachment to the ventral adductor muscles of the mandibles (Snodgrass, 1935), and in this respect its development is no doubt correlated with development of the mandible. As the mandible in the Lycidae larvae appears to be in the process of formation, their tentorium is adequately undeveloped. Absence of tentorium is considered plesiomorphic.

Stipes of mandible/«Hypostomal margin» sensu Böving & Craighead: The sclerite identified as the «hypostomal margin» by Böving & Craighead (1931) (Fig. 49) would perhaps be more correctly named the stipes of mandible, when referred to structures of the Lycidae larvae (Fig. 47). Being anteriorly articulated to the sheath of the «mandible», it is attached posteriorly to the anteroventral edge of gnathal segment II (*Lycus*, *Platerodrilus*, Figs 4, 23), or to its ventral edge (*Calopteron*, Fig. 47), or is prolonged to its posterior edge, being fused thereto from the point they meet (*Lygistropterus*, *Eros*, Figs 40, 63). The portion of the stipes anterior of the cranial sclerite lies free in the membrane. The lycid stipes of mandible appears to be homologous with the hypostomal margin of other coleopterans fused with the cranium (e.g. *Pyractomena*, Fig. 70).

Clypeus: The clypeus is absent in lycid larvae (Figs 8, 25), though Rosenberg (1943) considers the basal part of the mandibular appendage herein referred to as the labrum to be the clypeus, with its distal segment representing the labrum. In *Brachypsectra*, however, the structure that can be identified as the labrum is similarly bisegmented, while the clypeus is also developed as a separate structure (Fig. 62). It seems more probable, in this respect, that the clypeus, when present, as in *Brachypsectra*, is a secondary derivation of the epistoma.

Labrum: The one- or two-partite shutter, constituting the dorsal surface of the mandibular structure, is here tentatively homologized with the labrum. The labrum in lycid larvae is a paired sclerite consisting of two independent lobes, each lobe sometimes divided into two segments (e.g. *Platerodrilus*, Fig. 16); the lobes are articulated with each other and the cranium with cuticle of lesser degree of sclerotization.

- As there is no clarity with homology of labral sclerites in lycid larvae, its plesiomorphic condition is considered unknown.

Maxilla: The maxilla in Lycidae larvae typically consists of cardo, stipes, palpifer and 3-segmented palps. The stipes are considerably enlarged and almost completely fused, forming the ventral plate, possibly to insure protection of the otherwise open ventrally head. The dististipes and basistipes are relatively inconspicuous and the cardo is represented by a pair of cardines (e.g. *Platerodrilus*, Fig. 4). Galea is always prominent, receiving apices of the mandibular structure when at rest, and may be positioned, with respect to the palps, interoventrally (*Platerodrilus*, Figs 4, 8), interodorsally (*Lycus*, *Calopteron*, *Platycis*, Figs 23, 25, 27, 47, 56-57), dorsally (*Lopheros*, *Plateros*, *Lygistropterus*, Figs 58, 59, 40), or laterodorsally (*Pyropterus*, Fig. 61, *Macrolycus*, Bocák & Matsuda, 2003), being usually proximally fused to the palpifer. In *Eros* the galea, according to Böving & Craighead (1931), is completely fused with the palpifer (Fig. 63). In *Lygistropterus* and *Cautires* it is considerably reduced. Lacinia, when present (e.g. in *Calopteron*, Fig. 47), is significantly less conspicuous than galea. In neither taxon the maxillary segments are attached to the cranium.

In Lampyridae the maxillary structure includes two-segmented galea and separate stipites; its dististipes articulated to maxilla and basistipes articulated to galea are far more conspicuous (e.g. *Pyractomena*, Fig. 73).

- Separate maxillary stipites are considered plesiomorphic.
- The two-segmented galea is considered to be a derived form of a «true galea», to which the flexor muscles are attached (Snodgrass, 1935). This opinion shared, the one-segmented galea is deemed plesiomorphic.

Labium: The labium in Lycidae larvae is composed of a prementum and 2-segmented palps (Figs 4, 47). The prementum, which is homologous with the maxillary stipes (Snodgrass, 1935), is typically undivided (*Platerodrilus*, *Eros*, *Platycis*, *Plateros*, *Lopheros*, *Cautires*, *Lygistropterus*, Figs 4, 40, 54, 57, 63; *Macrolycus*, Bocák & Matsuda, 2003, etc.), but may be divided into two stipites, which may be contiguous (*Pyropterus*, Fig. 61; *Lyponia*, Bocák & Matsuda, 2003) or separated (*Lycus*, *Calopteron*, Figs 23, 47). When the prementum is undivided, it may, nevertheless, have a distal median suture (*Eros*, Fig. 63). The ligula is typically absent, but may be present in certain taxa (e.g. *Lopheros*, Fig. 58; *Plateros*, Hayashi & Takenaka, 1960), appearing both absent and well-developed within *Plateros* (cf. *P. coracinus*, Hayashi & Takenaka, 1960 and *P. floralis*, Fig. 59).

Lawrence (1991) indicates complete or almost complete fusion of the maxillae with the labium in the larvae of Lycidae. However, this condition was not observed in any of the studied taxa: these two structures may at most be somewhat fused proximally, with the maxillary stipites possibly absorbing the mentum, hypothetically in the process of fusing together (Figs 4, 47). However, the presence of a membranous mentum in a number of hexapod taxa and the apparent absence of the true mentum in, for instance, the Neuroptera (Snodgrass, 1935), suggest possible occurrence of a similar condition in other hexapods, including the Lycidae, with, consequently, fusion of the two maxillary stipites not interfering with any labial structure. An opinion that is deemed equally sound (Snodgrass, 1935), which considers all postlabial structures, i.e. related to mentum (and submentum), to be sternal derivatives, being nothing more than secondary sclerotizations, as well as absence of division of the postlabial plate in all Entognatha (Kluge, 2000) also supports this hypothesis; it means that quite possibly no fusion of the maxillae with the labium has ever taken place in the larvae of Lycidae.

- As there is no clarity with respect to homology of the postlabial structures, their primitive condition is considered unknown.
- The divided condition of prementum, in conformity with Snodgrass's (1935) opinion, is deemed primitive.

Cervix: The cervix, a membranous region of the trunk between the head and the prothorax, varies in length in Lycidae from considerably longer than head (e.g. in *Platerodrilus*, Fig. 22) in forms with heads completely retractable inside the prothorax to considerably shorter than head, when heads are only slightly retractable (e.g. *Lycus*, *Lygistropterus*, Figs 34, 41). Proximally the cervix has two weakly sclerotized areas, an annuliform sclerite, and a conical lateral bulge (e.g. *Platerodrilus*, Fig. 22) at each side, which together are presumed to be homologous with the cervical sclerites of the imagines. Both sclerites are located posteriad of the assumed intersegmental line and hardly represent any part of the second maxillary/labial structures, as suggested by Snodgrass (1935). In *Lycus* the annuliform sclerite appears to be absent (Fig. 34).

The Lampyridae larvae usually have long cervix and fully retractable head (e.g. *Pyractomena*, Fig. 68). The proximal part of their cervix may have, in addition to two pairs of sclerotized areas, similar to those of the Lycidae, a feebly sclerotized median stripe (Fig. 68), apparently divided in two parts anteriorly.

Thorax: A thoracic segment in the larval Lycidae consists of a tergum, usually several pleural plates and a sternum, which may also be divided into two sclerites. Some lycid larvae are distinguished by wide thoracic segments (Fig. 21), which

make them appear similar to Trilobitomorpha or larval Protorrhynchota (Kluge, 2000: Fig. 65B).

Thoracic terga: The thoracic terga may be considerably wider than the abdominal tergites, as in *Platerodrilus* (Figs 20, 21), or may not significantly differ from them in width, as in *Lycus* and *Lygistropterus* (Figs 34, 35, 41, 42), or Lampyridae taxa (e.g. *Pyractomena*, Fig. 77). The dorsum of all thoracic terga may be apparently tripartite, as in *Plateros* (Bugnion, 1907; Hayashi & Takenaka, 1960; Miller, 1997; Bocák & Matsuda, 2003) or *Phosphaenus* (Lampyridae) (Korschefsky, 1951), or the two posterior terga may be bearing two longitudinal lines indicating their possible tripartite nature (e.g. *Platerodrilus*, Fig. 21). Sometimes a median separation line or suture may be present in all three or two posterior terga (e.g. *Lygistropterus*, Fig. 42; *Calochromus*, Gardner, 1946|1947; *Dictyoptera*, Korschefsky, 1951; *Xylobanellus*, Burakowski, 1988; *Porrostoma*, *Metriorrhynchus* and *Pyropterus*, Bocák & Matsuda, 2003), or the dorsum of all thoracic terga may lack any conspicuous longitudinal lines (e.g. *Lycus*, Fig. 35; *Lopheros*, Pototskaya, 1981; Burakowski, 1990; *Platycis*, McCabe & Johnson, 1979a; *Eros*, *Lyponia*, *Macrolycus*, *Pseudosynchonnus*, Bocák & Matsuda, 2003). Both divided and undivided tergal plates coexist in *Cautires* (Figs 65-67). *Calopteron* is quite unique among the Lycidae in having in its two posterior thoracic terga both the median line and additional lateral sclerites (McCabe & Johnson, 1979; Costa *et al.*, 1988). *Caenia* and various *Metriorrhynchini* are distinguished by more or less conspicuous lateral processes on all thoracic tergites, whereas *Lyponia* and *Porrostoma* (Bocák & Matsuda, 2003), as well as some *Cautires* (Fig. 66) have four processes at the posterior margin of all thoracic and most abdominal terga.

Unlike in the rest of the studied Lycidae, each of the thoracic terga of *Calopteron* (e.g. Costa *et al.*, 1988) and *Lycus* (Fig. 35) also has a pair of postnotal plates posteriorly, which are similar to the abdominal postnotal plates.

- The primitive condition of terga is not clear, as it has not been demonstrated if the tripartite, bipartite or one-piece tergum preserves the condition characteristic of ancestors of the Polyphaga.
- Presence of postnotal plates in all thoracic segments is deemed plesiomorphic.

Thoracic pleura: The pleuron seems to be typically divided into a coxopleurite, an epipleurite, a hypopleurite and a sternopleurite. The epipleurite and hypopleurite are seemingly the laterotergites, though the hypopleurite (Figs 20, 34, 41) may appear to be homologous with the primitive anapleurite sensu Snodgrass (1935), as lying laterad of the coxopleurite and not being identical with the spiracle-bearing pleurite. The hypopleurite, present in meso- and metathorax of *Lygistropterus*, is absent in its prothorax and abdominal segments (Fig. 41). The coxopleurite may consist of two sclerites, the episternum and the epimeron, as, for example, in *Lycus* or *Lygistropterus* (Figs 34, 41); or the two sclerites may be fused without noticeable suture, as in *Platerodrilus* (Fig. 20). The epimeron is often reduced in size and less sclerotized, in *Platerodrilus* and *Pyractomena* appearing to be separate from the episternum (Figs 20, 77). At the proximal edge the episternum has a more sclerotized elongate plate attached to the base of the suture between the two sclerites, which appears to be the trochantin, not being, however, articulated with the anterior edge of the coxa distally. The sternopleurite is always located in close proximity to the epipleurite. In the more modified prothorax the hypopleurite is always absent (Figs 20, 34, 41), which testifies to its probable relationship to the spiracle-bearing