

function, while the sternopleurite seems to persist (e.g. Figs 20, 34, 41). This spiracle-bearing thoracic epipleurite is apparently homologous with the abdominal epipleurite, also bearing a spiracle. In some lycid taxa the thoracic epipleurite may be equipped with a conspicuous lateral process (e.g. *Metriorrhynchus*, Bocák & Matsuda, 2003).

In *Pyractomena* the trochantin is attached distally to the coxa (Fig. 77).

- Presence of a hypopleurite and a sternopleurite in the thoracic pleural area is deemed primitive.
- In conformity with Snodgrass's opinion (1935) the trochantin not attached distally to the coxa is deemed primitive.

Thoracic sterna: The sternum in lycid larvae is typically not or weakly sclerotized. When sclerotized, it may be divided into the anterior sclerite, or basisternum, and the posterior sternellum (*Lygisterus*, Fig. 41). It may equally lack any sclerotic areas (e.g. *Lycus*, Fig. 34). An example of a more sclerotized sternum is found in the prothorax of *Platerodrilus* (Fig. 20), which serves as the ventral half of the tube accepting the retractable head.

In *Pyractomena* the sternum is divided into the basisternum and sternellum, the basisternum of the prothorax divided into two parts by a median suture (Fig. 77).

- Primitive condition of the thoracic sterna is not clear.

Thoracic spiracles: In Lycidae, unlike in most of the Coleoptera (Crowson, 1981), there are often two pairs of functional thoracic spiracles in the larvae (*Lycus*, *Platerodrilus*, Figs 20, 34; *Lyponia*, *Pseudosynchonus*, Bocák & Matsuda, 2003). Absent metathoracic spiracles have been signaled in *Lopheros* and several other lycid genera, including *Lygisterus* (Bocák & Matsuda, 2003), but this needs confirmation, as in the latter genus the rudimentary non-functional metathoracic spiracles are present. In the latter study the non-functional rudimentary spiracles of the metathorax are also indicated for *Calopteron*, *Lycostomus* and *Plateros*. The thoracic spiracle may be located at the posterior margin of the epipleurite, as in *Lycus* (Fig. 34), or may lie in its middle (e.g. *Platerodrilus*, Fig. 20). They may be lip-type (e.g. *Platerodrilus*, Figs 6a, 20), annuliform (e.g. metaspiracles of *Lycus*, Fig. 37) or triforous (e.g. mesospiracles of *Lycus*, or *Calopteron*, Figs 36, 48). Biforous spiracles are reported in *Metriorrhynchus* (Bocák & Matsuda, 2003). The spiracles may lie in the bottom of a deep and large cavity occupying considerable portion of the epipleurite (*Platerodrilus*, Fig. 20), with the lip-type greater opening surrounded by smaller seemingly biforous spiracles opened into the same atrium and another biforous spiracle situated posteriorly at the rim of the cavity (Fig. 6a). The separate posterior spiracle does not open into the atrium, presumably connected to the tracheal trunk by a narrow branch attached to the outer surface of the cavity (Fig. 6b). The orifice of a spiracle may be contained in a peritreme (as in the mesospiracles of *Lygisterus* and metaspiracles of *Lycus*, Figs 37, 43). The closing apparatus is absent (e.g. Fig. 6b). The functional spiracles may be similar in the meso- and metathorax (in *Platerodrilus*, Fig. 20) or dissimilar in the thoracic segments (*Lycus*, Figs 34, 36, 37). All of the thoracic spiracles may be similar to the abdominal ones (*Platerodrilus*, Fig. 20) or the metaspiracles may be dissimilar (e.g. *Lycus*, Figs 34, 36-38).

In Lampyridae (*Pyractomena*) the spiracles are located anterior-laterally on a conspicuous epipleurite. The mesospiracle is similar to the abdominal spiracles, being biforous; the non-functional metaspiracle is annuliform (Figs 77-79).

Crowson (1981) suggests that the «normal» closing apparatus between the atrium and the main tracheal trunk is primitive in Coleoptera, but acknowledges a breach of Dollo's Law in a number of advanced and unrelated Elateriformia lineages that have assumedly redeveloped the definite type of the closing apparatus, after the more primitive groups of the series, including the aquatic or living in very damp surroundings in larval stage Ptilodaclidae or Psephenidae, had allegedly lost it.

- Two pairs of functional thoracic spiracles are considered a primitive condition.
- Similarity of the meso- and metaspiracles is considered primitive.
- Similarity of the thoracic and abdominal spiracles is considered primitive.
- Primitive condition of the type (structure) of spiracles is unclear.
- The absence of closing apparatus is deemed primitive.

Leg: The leg consists of coxa, trochanter, femur, tibiotalus and pretarsus. The trochanter is clearly divided into two parts, trochanter 1 and trochanter 2, in *Platerodrilus*, *Lycus*, *Calopteron*, *Lyponia* (Figs 20, 39, 53, 64), *Xylobanus* (Pototskaya, 1981) and *Porrostoma* (Bocák & Matsuda, 2003). Examination of muscles in both parts of the trochanter demonstrates origin of the reductor in trochanter 2 (e.g. *Platerodrilus*, Fig. 9). The undivided trochanter has been found in *Lygistoris* (Fig. 45) and is reported for *Lopheros* (Burakowski, 1990), *Cautires* (Hayashi, 1954) and *Pyropterus* (Bocák & Matsuda, 2003). The joint between the coxopodite and coxa is monocondylic, with the distal end of the trochantin not attached to the coxa; the joint between the coxa and trochanter 1 is dicondylic; trochanter 1, trochanter 2, when present (Figs 20, 39, 53, 64), and femur are attached more or less rigidly; the joint between the femur and tibia is again monocondylic (e.g. *Lycus*, *Platerodrilus*, *Lygistoris*, Figs 20, 39, 45). *Pyroptomena* has the same structure of segmental joints, except that the trochantin is distally attached to the coxa (Fig. 77).

The coxa may be elongate or transverse. In *Platerodrilus*, *Lyponia* and *Lycus* the elongate coxae are part of the limb, being implanted in the membranous pleural wall and articulated to the pleuron (Figs 20, 39, 64). In *Lygistoris*, on the contrary, the mobility of the coxa is considerably lost and it became a movable support for the rest of the limb by assuming the form of a plate of the body of the wall (Fig. 45). Similarly short coxae are reported in *Macrolycus*, *Porrostoma* and some other Lycidae (Bocák & Matsuda, 2003). In most of lycid larvae, however, the coxa is in the intermediate condition (e.g. *Calopteron*, McCabe & Johnson, 1979b; Costa *et al.*, 1988; *Plateros*, Miller, 1997). In *Lyponia* there is a conspicuous coxal suture (Fig. 64), which is also present in *Pyroptomena* (Fig. 77). In the latter taxon the coxa has also a meral suture (Fig. 77).

- Division of the trochanter into two parts, trochanter 1 and trochanter 2, not known in Pterygota other than Odonata (Snodgrass, 1935), is deemed primitive.
- Only pleural articulation of the lycid coxa, as opposed to the pleural and trochantinal articulation of the Lampyridae, is considered primitive.
- As suggested by Snodgrass (1935), the elongate coxa making part of the limb is considered plesiomorphic.
- Plesiomorphic condition of the coxal suture (present vs. absent) is unclear.

Abdomen: The lycid abdomen appears to have eleven segments, segments 10 and 11 positioned on the ventral surface of segment 9 (*Platerodrilus*, *Lycus*, *Lygistoris*, Figs 20, 34, 41). The structure of an abdominal segment of *Lycus* and *Platerodrilus* has been found to be similar to the thoracic one, with the difference

practically limited to presence or absence of the coxopleurite (Figs 20, 34). In *Lygisterus* the discrepancies between a thoracic and abdominal segment include disappearance in the abdomen of the hypopleurite and the fused condition of the sternum (Fig. 41). On the other hand, the sternopleurite, persistent in *Lycus* (Fig. 34) and *Lygisterus* (Fig. 41), is absent in the abdominal segments of *Platerodrilus* (Fig. 20). In *Pyractomena* the structure of a thoracic and abdominal segment appears to be completely different, consisting in the latter of the undivided sternum and one spiracle-bearing pleurite (epipleurite) (Fig. 77). Segment 9, typically without posterior processes, may bear a pair of processes, which when not separated by a suture are considered urogomphi (e.g. *Lygisterus*, Fig. 41; *Lyponia*, Bocák & Matsuda, 2003), sometimes branched (e.g. *Cautires*, Fig. 67). Segment 9 does not have spiracles and its sclerotization is usually only tergal (Figs 20, 34, 41); segment 10, on the contrary, consists only of sclerotized sternite (Figs 20, 34, 41), the pygopodium seeming to represent segment 11 (Figs 20, 41).

The ventral surface of abdominal segment 9 in *Calopteron* sp. from Peru under the almost transparent cuticle has whitish substance, similar to that of luminous areas of the Lampyridae; which allows assuming possible luminosity in this species.

- The abdominal structure, with the abdominal segment not differing from the thoracic one, but in absence of the coxopleurite, is deemed plesiomorphic.

Tergites: The dorsum of abdominal tergites 1-8 may be apparently tripartite, as in *Plateros* (Bugnion, 1907; Hayashi & Takenaka, 1960; Miller, 1997), may have a median suture or line (*Calopteron*, McCabe & Johnson, 1979; Costa *et al.*, 1988; *Xylobanellus*, Burakowski, 1988; as well as *Pyractomena*), or may lack any conspicuous longitudinal sutures or lines (e.g. *Lygisterus*, Fig. 42; *Lopheros*, Burakowski, 1990; *Eros*, *Platycis*, *Pseudosynchonnus*, Bocák & Matsuda, 2003). *Pyropterus*, *Porrostoma* and *Metriorrhynchus* appear to have the dorsum of tergum 9 divided as well (Bocák & Matsuda, 2003). In *Platerodrilus* the tergite has a large lateral process (Figs 20-31), while in *Cautires* (Fig. 66), *Lyponia* and *Porrostoma* (Bocák & Matsuda, 2003) the posterior margin of each of abdominal terga I-VIII may bear four processes. Abdominal terga in *Cautires* may also be equipped with a pair of additional dorsal processes (Fig. 67). In some taxa the bases of the tergal processes are separated by sutures (e.g. *Cautires*, Fig. 67). In *Macrolycus* larva the abdominal terga have longitudinal suture only anteriorly (Bocák & Matsuda, 2003). Tergites 1-8 of *Lycus* (Fig. 35) and *Calopteron* are complimented with a pair of conspicuous posterior postnotal plates, similar to those of the thorax. These sclerites are absent in all other studied taxa.

- Presence of postnotal plates in abdominal segments is deemed primitive.
- The primitive condition of the dorsum of abdominal tergites (tripartite vs. bipartite or simple) is unclear.

Pleurites: There are maximum three and minimum two pleurites in a larval abdominal segment in the Lycidae. One of them, the epipleurite, appears to be structurally a laterotergite, and bears a spiracle; its origin may be related to development of sclerotization around the spiracle. The second pleurite, the hypopleurite, lying posteriad of the epipleurite, and also probably a laterotergite, is evidently homologous with the thoracic hypopleurite (*Lycus*, *Platerodrilus*, Figs 20, 34); the hypopleurite disappears in abdominal segment 8 in *Lycus* (Fig. 34). The third pleurite, presumably the sternopleurite, has been found only in the abdominal segments of *Lycus* (Fig. 34). *Calopteron*, as well as *Lygisterus* (Fig. 41)

and *Plateros* (Bocák & Matsuda, 2003), are characterized by the absence of the hypopleurite in all abdominal segments, due to its possible fusion with the epipleurite. The epipleurite in *Platerodrilus* has a conspicuous lateral process (Fig. 20). *Pyractomena* has only one pleurite, the epipleurite (Fig. 77).

Sternites: The sternite of segments 1-8 is usually an undivided plate (Figs 20, 34, 41), but may be divided into two sclerites in some taxa (e.g. *Plateros*, Bocák & Matsuda, 2003). It may have a pair of conspicuous posterior processes provided with a brush of setae (*Platerodrilus*, Fig. 20).

Sternite 9 may have conspicuous diagonal incisions at posterior angles (*Platerodrilus*, *Lygistropterus*, Figs 20, 41), but typically does not have any (e.g. *Lycus*, Fig. 34).

Abdominal spiracles: The eight pairs of abdominal spiracles in lycid larvae may be located ventrally (e.g. *Platerodrilus*, Figs 20), laterally (*Plateros*, Miller, 1997) or dorsally (*Calopteron*, McCabe & Johnson, 1979; Costa *et al.*, 1988), usually on a conspicuous epipleurite; however, their ventral, lateral or dorsal position in all studied taxa, except *Platerodrilus*, apparently depends on how expanded the abdomen is. The spiracles may be positioned at the posterior margin of the epipleurite (e.g. *Lycus*, Fig. 34). The spiracles may lie in the bottom of deep and large cavities occupying considerable portion of the sclerite (*Platerodrilus*, Fig. 6, 20), they may be lip-type (e.g. *Platerodrilus*, Figs 6, 20) or triforous (e.g. *Lycus*, Figs 34, 38). Their orifice may have a peritreme (e.g. *Lygistropterus*, Fig. 43).

In *Pyractomena* the abdominal spiracles are located anterolaterally on a large epipleurite and are biforous (Figs 77-78).

PUPA

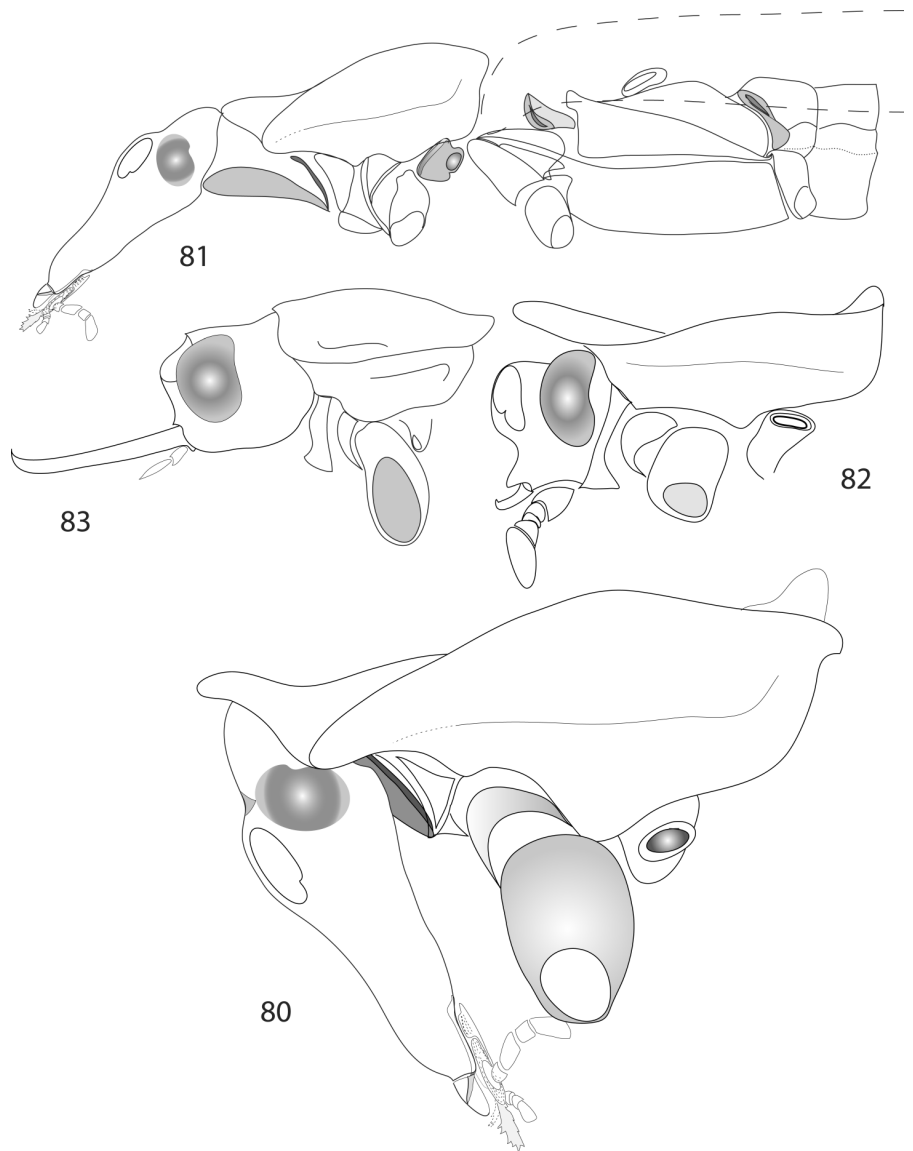
The pupa in the Lycidae is typically free, but pupation may also occur within the last larval exuviae, as in *Calopteron*, *Caenia* and *Lycostomus* (Bocák & Matsuda, 2003). The pupa of Lycidae usually offers little morphological characters to consider for phylogenetic and taxonomic purposes. Among the few characters that seem to differ in the few described lycid pupae are the pronotal marginal tubercles (Bocák & Matsuda, 2003), structure of the mesonotum, which may include a noticeable posterior projection of the scutellum (e.g. *Lyponia*, Hayashi, 1954; *Lopheros*, Burakowski, 1990) or may lack it (*Platycis*, McCabe & Johnson, 1979) and presence of urogomphi in taxa that usually do not have them in larval stage, i.e. in *Calopteron* or *Lycus* (Bocák & Matsuda, 2003).

- Primitive condition of pupal character states is unknown.

ADULTS

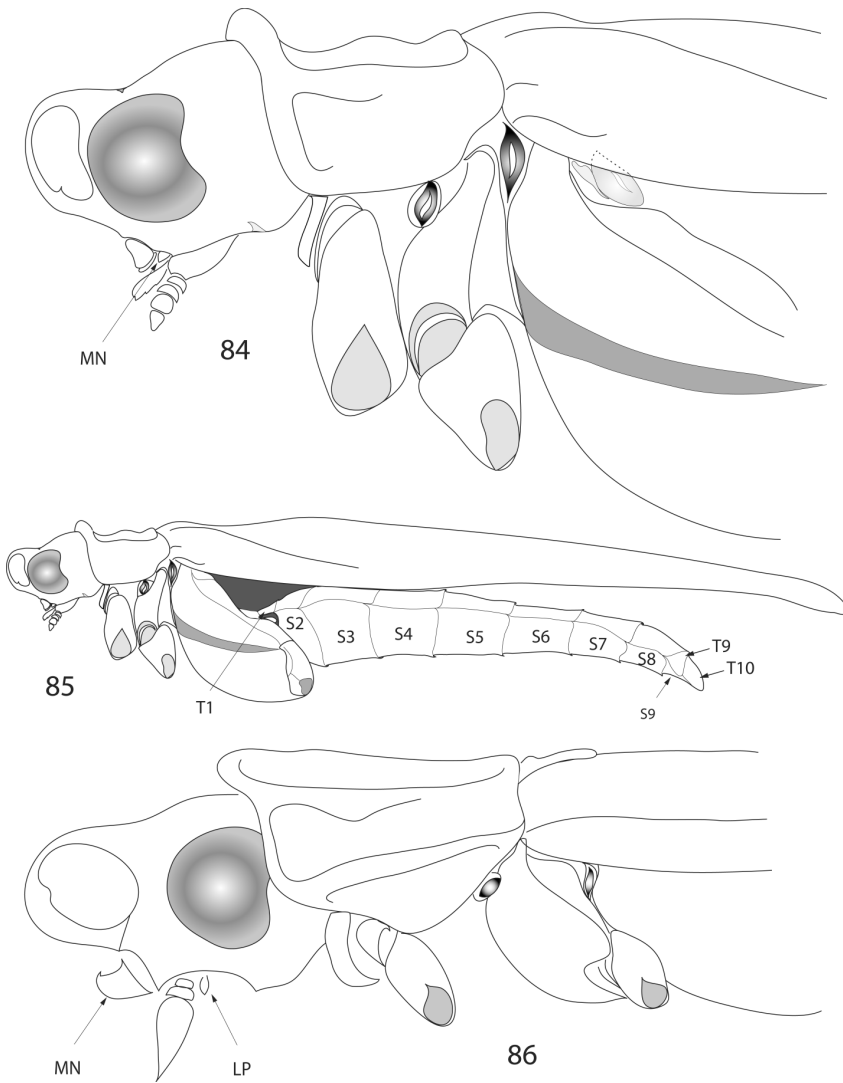
[The larviform females of *Platerodrilus* are excluded from this section, as they either do not have structures mentioned below or have them in condition specified for *Platerodrilus* larva.]

Cuticle: Typically the cuticle of adult Lycidae is finely punctulate and shows no stratification or striation. In *Dexoris*, however, the cuticle of all sclerites, including



Figs 80-83: Imaginal structures: *Lycostomus praestus* (Fabricius), head and prothorax, lateral view (80); same, head, thorax and abdominal segments I and II, lateral view (81); *Calopteron reticulatum* (Fabricius), head and prothorax, lateral view (82); *Platerodrilus* sp., head and prothorax, lateral view (83).

mandibles and legs, but excluding elytra, is alveolate (Fig. 113), the shape of the alveoli uneven, but their size more or less uniform all over the body. The cuticle of *Lyroneces* is also alveolate in most of the body sclerites, except the legs, but the shape of the alveoli is roundish and their size is relatively much smaller than in *Dexoris*; in the prothorax and elytra, however, the cells are similar to those of *Dexoris*.

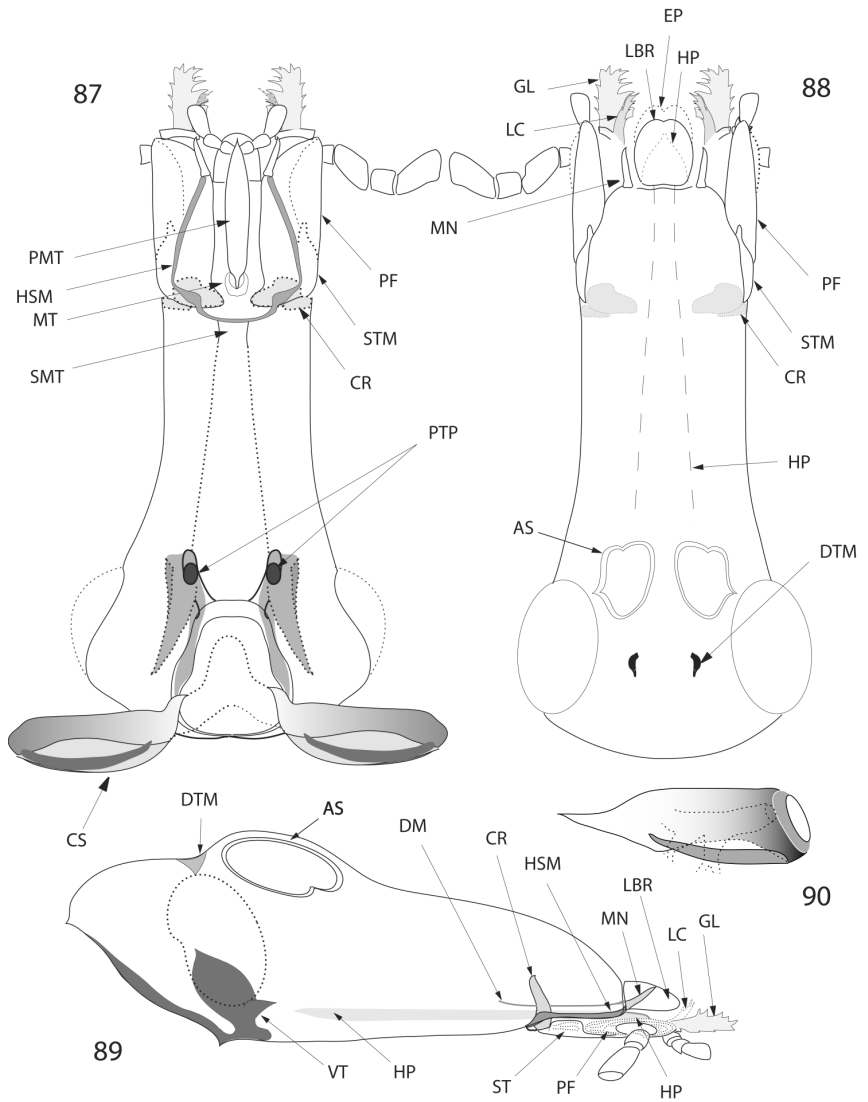


Figs 84-86: Imaginal structures: *Ceratoprion* sp., head, pro- and mesothorax, lateral view (84); same, body, lateral view (85); *Dexoris tessmani* Bocák & Bocáková, head pro- and mesothorax, lateral view (86).

LP -labial palps; MN - mandible; S - sternite; T - tergite.

Similar structure of the cuticle with relatively large roundish cells is often noticeable in pronotal margins of various lycid taxa, being most manifest anteriorly, sometimes occupying one third to one half of the pronotum.

The alveolate cuticle, known in the larvae of some Coleoptera (Kapzov, 1911), has not been reported in the adult beetles, where the exocuticula is usually a simple tissue showing no striation, while the endocuticula consists of horizontal bars

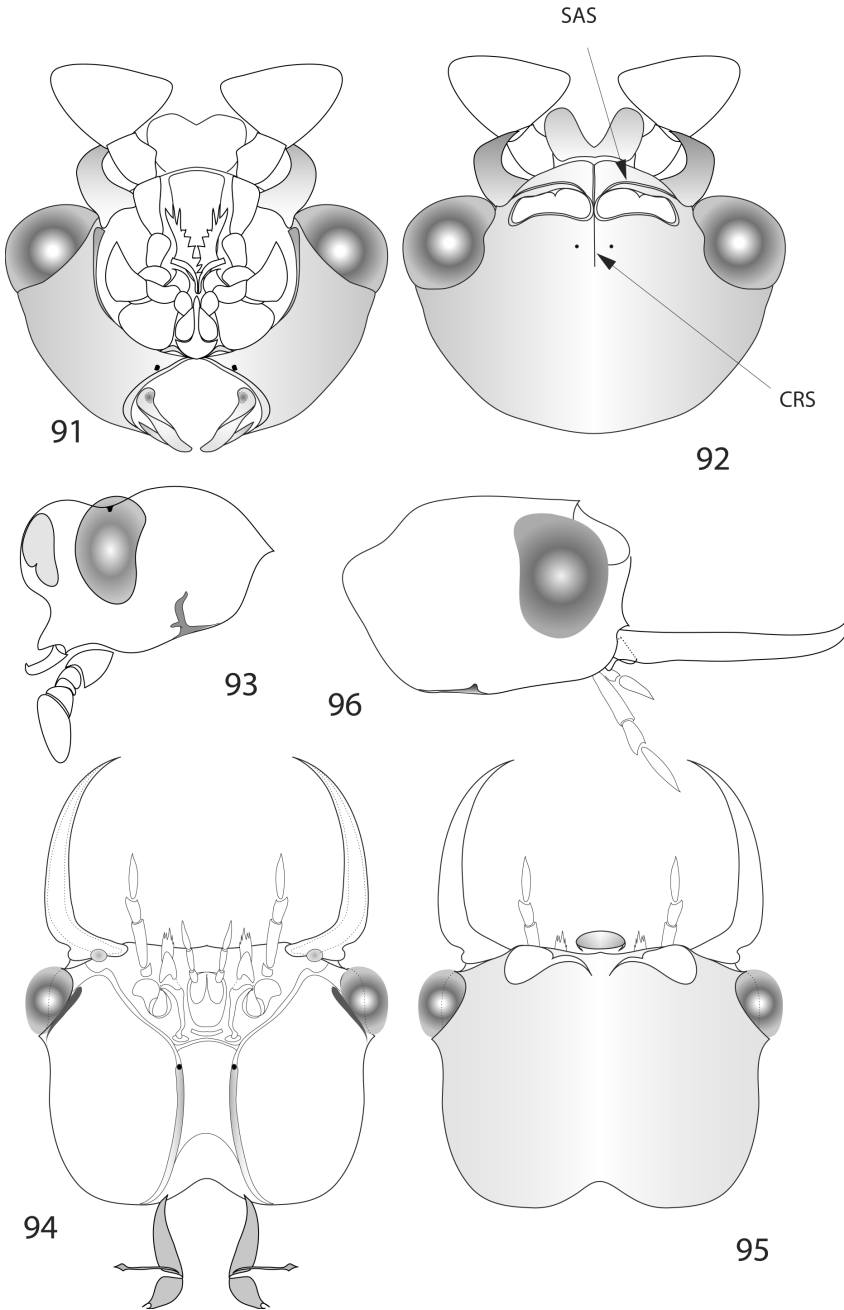


Figs 87-90: Imaginal structures: *Lycostomus praeustus* (Fabricius), head, ventral view (87); same, dorsal view (88); same, lateral view (89); same, sclerites of mesothoracic spiracle (90).

AS - antennal suture; CR - cardo; DT - dorsal arms of tentorium; DTM - dorsal tentorial maculae; EP - epipharynx; GL - galea; HP - hypopharynx; HSM - hypostomal margin; LBR - labrum; LC - lacinia; MN - mandible; PF - palpifer; PTP - posterior tentorial pits; STM - stipes of maxilla; VT - ventral arms of tentorium.

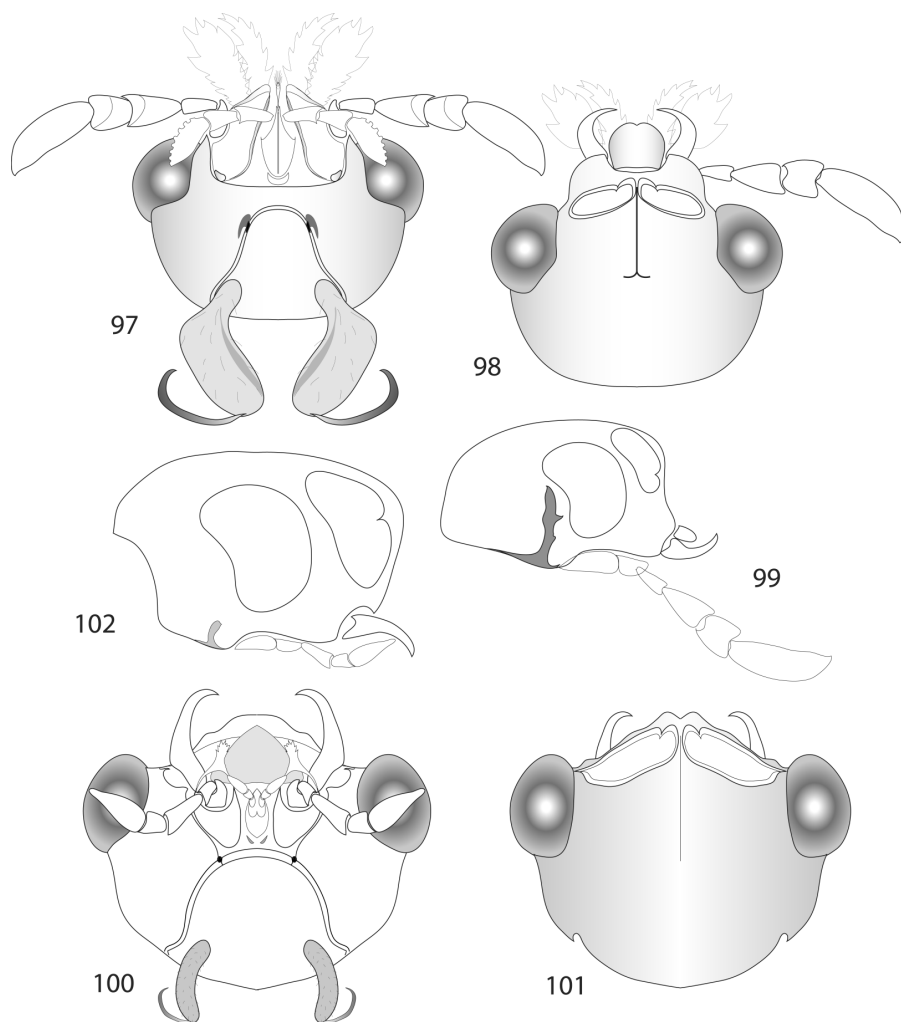
arranged in well-formed strata (Kapzov, 1911; Casper, 1913). Such structure of the adult beetles is considered much more complicated (Snodgrass, 1935).

- The alveolate cuticle structure, similar to that of the larvae, manifest in all body sclerites, except elytra, is deemed primitive.



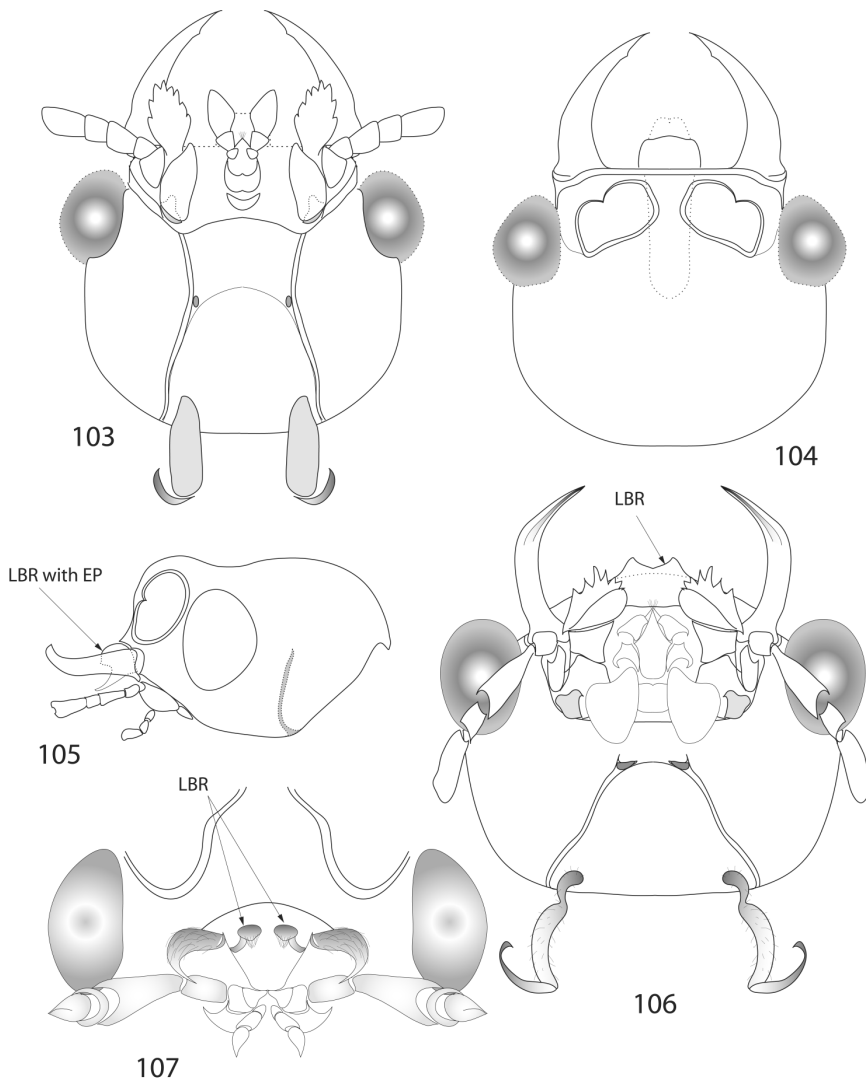
Figs 91-96: Imaginal head structures: *Calopteron reticulatum* (Fabricius), head, ventral view (91); same, dorsal view (92); same, lateral view (93); *Platerodrilus* sp., head, ventral view (94); same, dorsal view (95); same, lateral view (96);

CRS - coronal suture; SAS - subantennal suture.



Figs 97-102: Imaginal head structures: *Caenia kirschi* Bourgeois, head, ventral view (97); same, dorsal view (98); same, lateral view (99); *Taphes brevicollis* Waterhouse, head, ventral view (100); same, dorsal view (101); same, lateral view (102).

Setation: The typical outgrowths of the body wall in Lycidae are hair-like. In some taxa the antennae are also provided with scale-like structures, which are characteristic of all Leptolycinae, Miniduliticolinae and a number of taxa belonging in other subfamilies. In some, e.g. *Dilophotes*, the scaliform setae are present on antennomeres 3 to 11, while in others they may be present on all antennomeres (e.g. *Microeron* Kazantsev) or on antennomeres 4 to 11 (e.g. *Autaphes* Kazantsev). At the same time, all parts of the exoskeleton of *Lyroneces*, except the elytra, in addition to «normal» hairs may bear scale-like setae. The elytral vestiture of certain *Dexoris* deserves special mention, being represented by elongate cylindrical setae

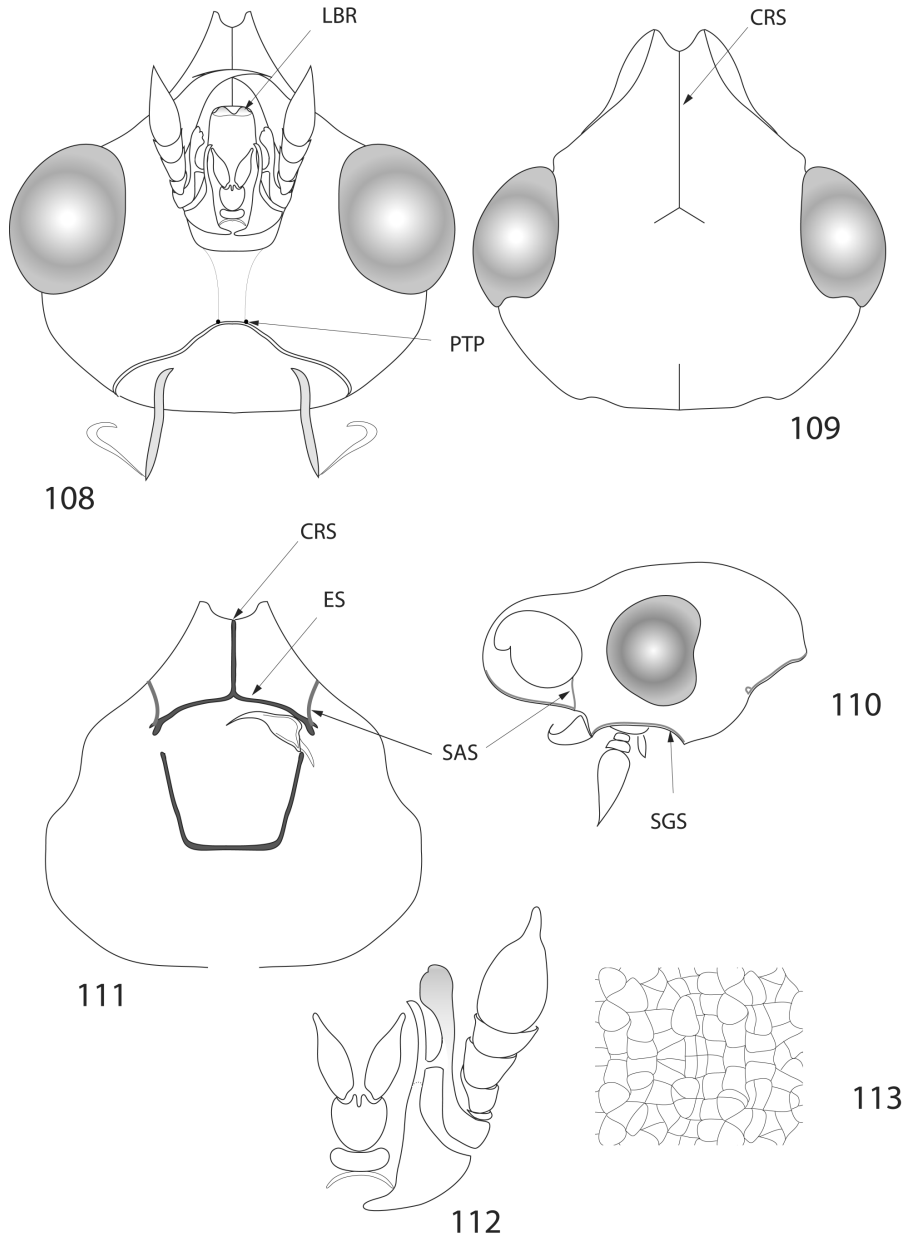


Figs 103-107: Imaginal head structures: *Dictyopectera aurora* (Herbst), head, ventral view (103); same, dorsal view (104); same, lateral view (105); *Helcophorus miniatus* Fairmaire, male, head, ventral view (106); *Proteros sempiternus* Kazantsev, head, anterior view (107).

EP - epipharynx; LBR - labrum.

(Fig. 329), hypothetically a transitional form between scales and hairs, or a derivation of the former.

Head: There exist both prognathous (*Platerodrilus*) and opisthognathous (*Lycostomus*) types of head orientation in Lycidae (Figs 80, 83), while in most of the lycid taxa (i.e. *Calopteron*, *Ceratoprion*, *Dexoris*, etc., Figs 82, 84, 86) the head is more or less hypognathous, though in contrast to most known varieties of a hypognathous



Figs 108-113: Imaginal structures of *Dexoris tessmani* Bocák & Bocáková: head, ventral view (108); same, dorsal view (109); same, lateral view (110); same, head, ventral view, maxillae and labium removed (111); same, left maxilla and labium, ventral view (112); same, cuticular structure (113).

CRS - coronal suture; ES - epistomal sulcus; LBR - labrum; PTP - posterior tentorial pits; SAS - subantennal suture; SGS - subgenal suture.

head, the lycid head is typically elongate in lateral view, i.e. its length noticeably exceeds its height. The mandibles and the rest of the mouthparts may be distant from each other and oriented differently, with the labial palps sometimes directed perpendicular and the mandibles at ca. 45 degrees to the eye-antenna plane (e.g. *Dexoris*, Fig. 86). The posterior edge of the cranium may be incised both in dorsal and lateral views (*Scarelus*, *Thilmanus*, *Phengodes*, Figs 118, 119, 154, 155, 162, 164).

The prolongation of the head before the eyes to form a rostrum (e.g. *Lycostomus*, Fig. 80) is characteristic of floricolous Lycini, Lygisterini and Metriorrhynchini and probably developed independently in each of these lineages to facilitate feeding on deep-seated nectaria.

The ventral closure in Lycidae varies from broad (*Scarelus*, *Platerodrilus*, Figs 94, 117) to very narrow, reduced to narrow process between the cranial sclerites (e.g. *Lyroneces*, *Aferos*, *Calopteron*, Figs 91, 114, 150). The latter condition is referred to by Snodgrass (1935) as the absent gula. In forms with rostrum the ventral closure is typically the broadest (*Lycostomus*, *Metriorrhynchus*, Figs 87, 146), with what might seem gular sutures in *Lycostomus* obviously absent in *Metriorrhynchus*.

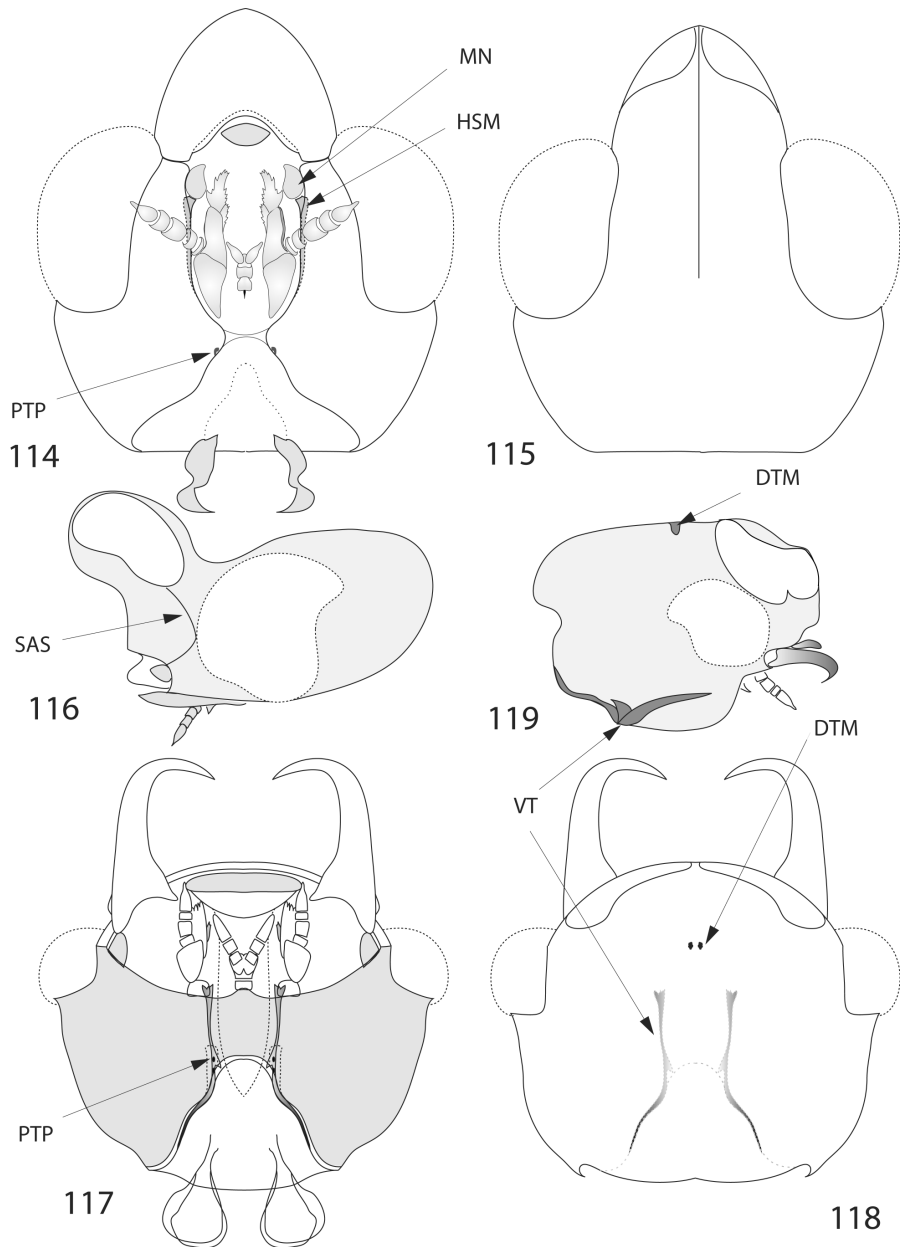
The epicranial/coronal suture reaching the posterior edge of the cranium is present in few taxa, such as *Macrolycus* and *Dilophotes* (Figs 136, 138). Partial development of the coronal suture posteriorly of the antennal sockets is more widespread, characteristic of *Lyroneces*, *Dexoris*, *Calopteron*, *Ceratoprion*, *Caenia*, *Taphes*, *Plateros*, *Metriorrhynchus* and *Mesolycus* (Figs 92, 98, 101, 109, 115, 121, 140, 143, 147), in which it may be forked posteriorly (*Dexoris*, *Caenia*), sometimes to end in the dorsal tentorial maculae (*Ceratoprion*, *Plateros*, *Metriorrhynchus*). In rare cases (*Dexoris*, *Calopteron*) the coronal suture is prolonged anteriorly of the antennal sockets to the epistoma (Figs 92, 111). In *Metriorrhynchus* the coronal suture is divided in two (Fig. 147). Condition of the frontal sutures is unclear, as the antennal sockets are typically approximate. Similarly, due to close proximity of the antennal and ocular sclerites to the epistomal sulcus it is often impossible to define condition of the subantennal sutures (e.g. *Scarelus*, Figs 118, 119). In *Lampyrus* the short frontal sutures emerge from the ventral margin of the antennal suture and go under the eyes (Fig. 156).

The postoccipital suture is typically well developed (e.g. *Mesolycus*, Fig. 139). Subgenal sutures are always more or less developed, but inconspicuous (e.g. *Dexoris*, *Mesolycus*, Figs 110, 140).

The epistomal sulcus is usually similar to other cranial sulci and sutures (e.g. *Dilophotes*, *Aferos*, *Thilmanus*, Fig. 138, 151, 163), but sometimes may be broad and conspicuous, developed medially into a clypeus-like projection (*Calochromus*, Fig. 128). It may also be demarcating the clypeus, as in *Phengodes* (Fig. 154).

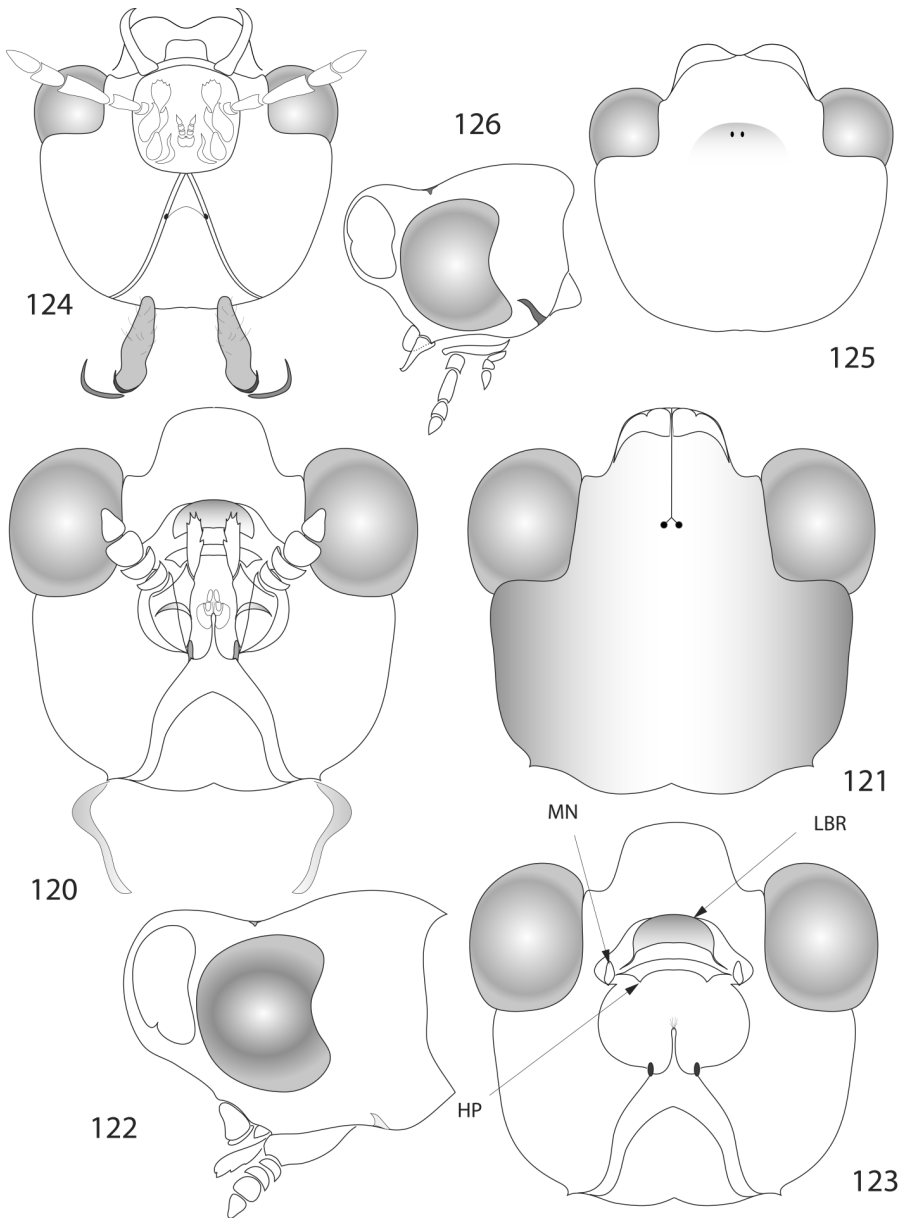
The anterior tentorial pits are absent in Lycidae, but posterior ones are typically present, even when ventral, or posterior arms of tentorium are vestigial or absent (e.g. *Lyroneces*, *Dexoris*, *Calochromus*, Figs 108, 114, 127). The posterior pits are usually positioned in the anterior extremities of the postoccipital suture, however, in *Platerodrilus*, *Cantharis* and *Phengodes* they are advanced anteriorly (Figs 94, 153, 159), which may be a consequence of the transition of the ventral closure in the opposite direction and occurrence of a true gula in these taxa. The dorsal tentorial maculae are often present as well (e.g. *Lycostomus*, *Calopteron*, *Ceratoprion*, *Lycinella*, Figs 88, 92, 121, 125).

The ventral aspect of the head in some Lycidae, especially in *Lyroneces* (Figs 114) resembles the embryo condition (Figs 1-2).



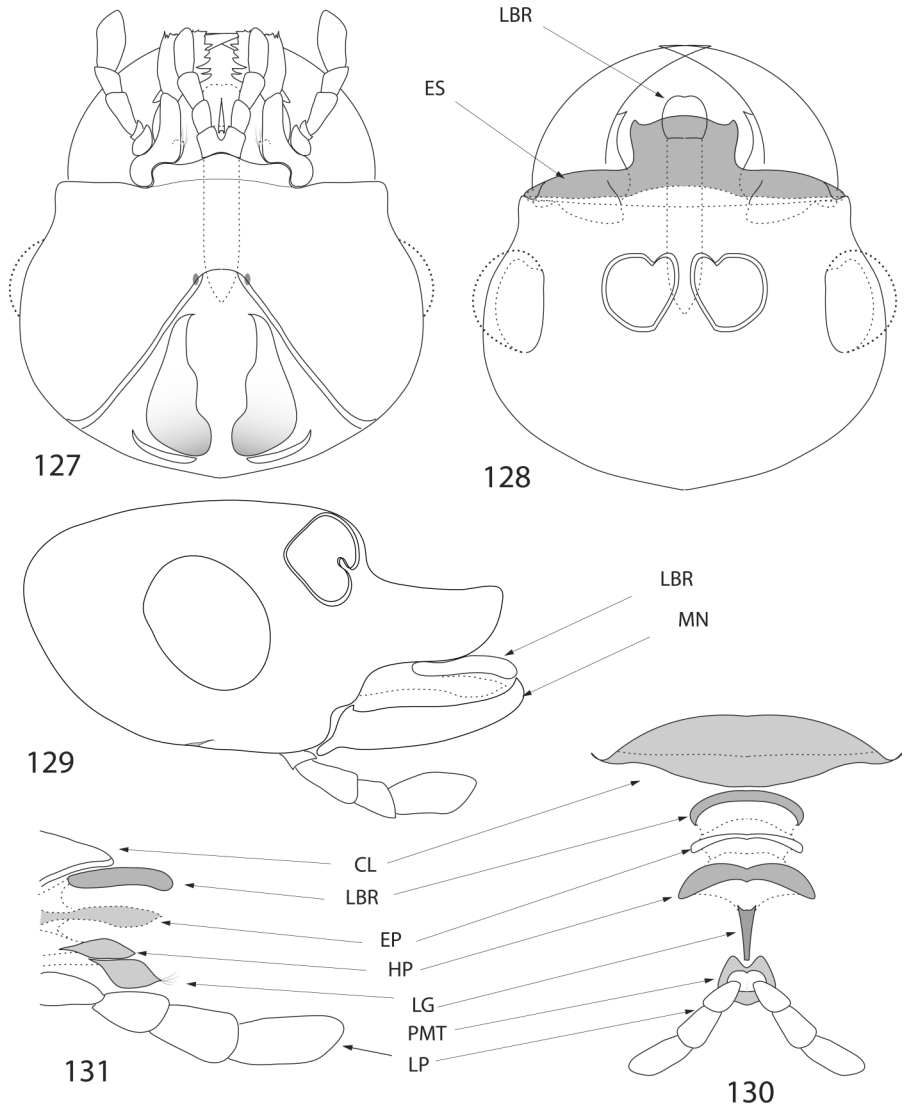
Figs 114-119: Imaginal head structures: *Lyroneces optabilis* (Kleine), head, ventral view (114); same, dorsal view (115); same, lateral view (116); *Scarelus umbrosus* Kleine, head, ventral view (117); same, dorsal view (118); same, lateral view (119).

DTM - dorsal tentorial maculae; HSM - hypostomal margin; MN - mandible; PTP - posterior tentorial pits; SAS - subantennal suture; VT - ventral arms of tentorium.



Figs 120-126: Imaginal head structures: *Ceratoprion* sp., head, ventral view (120); same, dorsal view (121); same, lateral view (122); same, without maxillae and labium, ventral view (123); *Lycinella parvula* Gorham, head, ventral view (124); same, dorsal view (125); same, lateral view (126).

HP - hypopharynx; LBR - labrum; MN - mandible.



Figs 127-131: Imaginal head structures: *Calochromus glaucopterus* (Guerin-Meneville), head, ventral view (127); same, dorsal view (128); same, lateral view (129); same, labrum, hypopharyngeal and labial structures, anterior view (130); same, lateral view (131).

CL - clypeus; EP - epipharynx; ES - epistomal sulcus; HP - hypopharynx; LBR - labrum; LG - ligula; LP - labial palps; MN - mandible; PMT - prementum.

- According to Crowson (1981), the most distinctive feature of the coleopteran head is its broad ventral closure behind the mouthparts. Beutel (1995) also considers unsclerotized and short gula region a groundplan character state of Coleoptera. In this respect, the narrow ventral closure, i.e. absent gula, is deemed primitive.

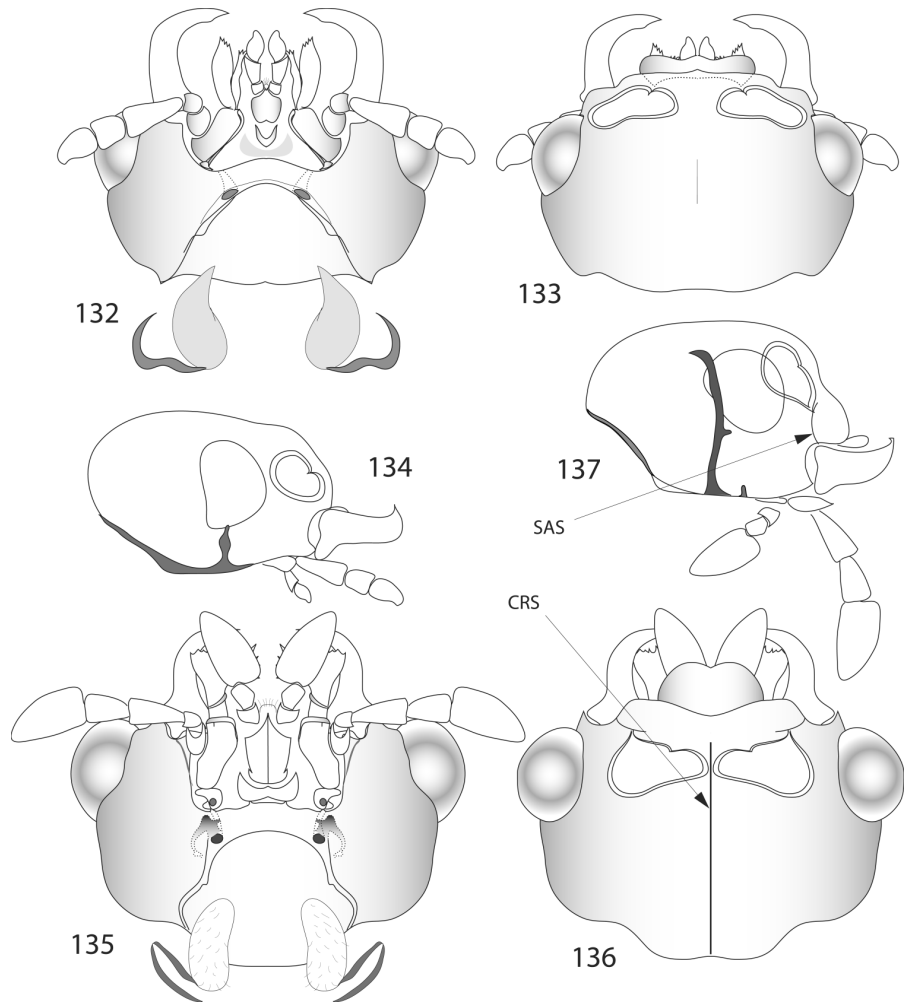
- Given that the hypognathous condition of the head preserves the ventrolateral position of the head appendages typical of ambulatory limbs, the hypognathous head is considered primitive.
- Plesiomorphic condition of the coronal and other cranial sutures appears unclear.

Tentorium: Though Crowson (1981) indicates that Lycidae have membranous tentorium, the tentorium, as the endoskeletal structure bracing the lower edges of the epicranial walls, was found to be absent in Lycidae. In most cases there are only certain sclerotic elements of tentorium, while sometimes it is absent completely. The dorsally projecting processes, the ventral arms, arising from the posterior tentorial pits are manifest in a number of Lycidae (Figs 89, 93, 99, etc.), often in combination with inconspicuous dorsal tentorial maculae (e.g. Figs 88-89, 92-93, 118-119). The location of the dorsal maculae that do not have any connection with the (other) tentorial structures suggests they may be related to ocelli. In some taxa the ventral arms are vestigial or practically absent (*Dexoris*, *Lyroneces*, Figs 110, 116); in others they vary from short (e.g. *Ceratoprion*, *Taphes*, *Platerodrilus*, *Calochromus*, Figs 96, 102, 122, 129), to long, attaining maximum length in *Macrolycus*, *Aferos* and *Plateros* (Figs 137, 144, 152). Not very long, but having additional anteriorly prolonged processes are the ventral arms of such taxa as *Lycostomus*, *Calopteron*, *Scarelus*, *Metriorrhynchus* (Figs 89, 93, 119, 148), probably related to relatively long antennae and/or long rostrum; such anterior processes may be analogous with the front arms of the tentorium. The dorsal maculae are absent in majority of lycids (e.g. *Dictyoptera*, *Aferos*, *Platerodrilus*, *Dilophotes*, *Mesolycus*, etc., Figs 96, 105, 138, 140-141, 152). The anterior arms and anterior tentorial pits alike are absent in all of the Lycidae. The corpotentorium, i.e. the transverse bar connecting ventral arms, is absent in all Lycidae studied, but, though reported lost in all Cantharoidea (Crowson, 1981), was found to occur in *Lampyris* and *Phengodes* (Figs 153, 157-158). In the Cantharidae the well developed and attaining dorsal surface ventral arms may be separate, as in *Cantharis* (Figs 159-160), or fused posteriorly, as in *Podabrus* or *Chauliognathus* (Brancucci, 1980).

Thilmanus, which had been transferred to Drilidae (Medvedev & Kazantsev, 1992) due to the allegedly well-developed and sclerotized tentorium (following Crowson, 1972) and presence of the elytral epipleuron (opposing Crowson, 1972), was found not to differ considerably from Lycidae in the structure of the tentorium, with only non-connected ventral arms present (Fig. 164).

- The absent tentorium, a condition similar to that of the larvae and the hypothesized predecessor of Amyocerata, is considered plesiomorphic. Similarly, the absent or weakly developed tentorial structures, such as the dorsal and ventral arms, are deemed to be plesiomorphic.

Subantennal suture: The subantennal suture is complete and conspicuous in *Calopteron*, *Macrolycus*, *Metriorrhynchus*, *Dilophotes* and *Dexoris* (Figs 92, 110-111, 136-137, 138, 147), absent or vestigial in the rest of the studied taxa. In *Mesolycus* the subantennal suture is reduced (Figs 140-141), in *Lyroneces* curved and touching the ocular suture (Fig. 116). In *Calopteron*, unlike in other taxa, the subantennal suture connects the inner edges of the antennal suture and the dorsal mandibular condyles (Fig. 92). The latter taxon is also unique in having both the frontal part of the coronal suture and the subantennal sutures (Fig. 92). However, due to close proximity of the antennal and ocular sclerites to the epistomal sulcus

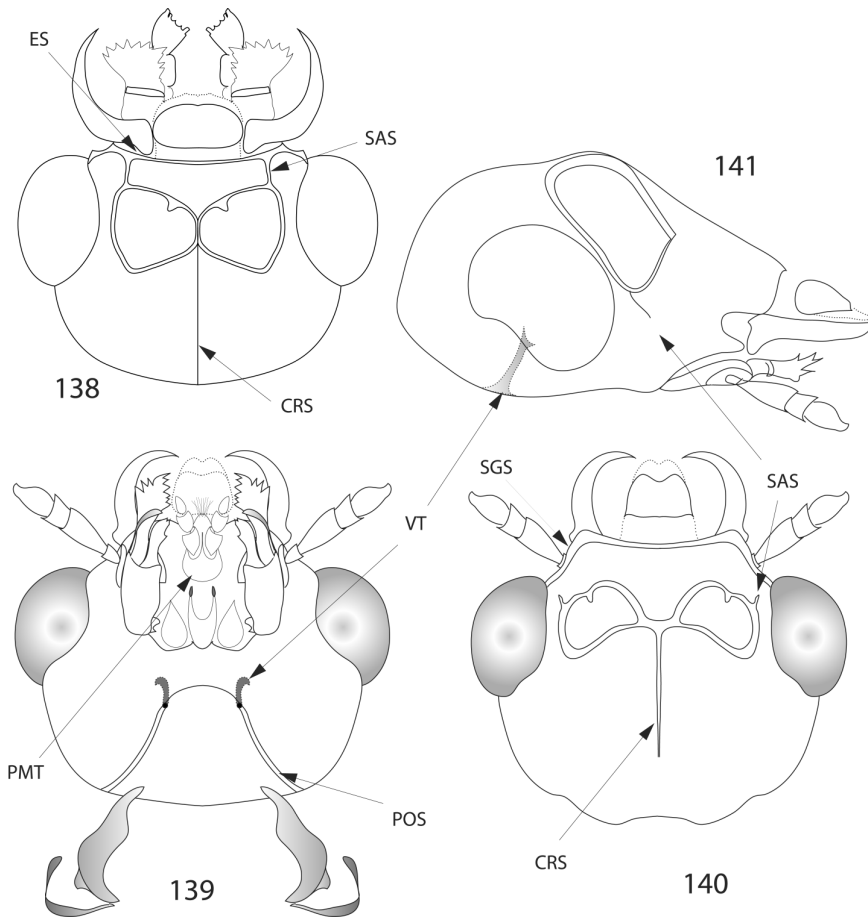


Figs 132-137: Imaginal head structures: *Conderis signicollis* (Kirsch), head, ventral view (132); same, dorsal view (133); same, lateral view (134); *Macrolycus flabellatus* (Motschulsky), head, ventral view (135); same, dorsal view (136); same, lateral view (137).

CRS - coronal suture; SAS - subantennal suture.

in a number of lycid taxa, it is often impossible to define the actual condition of their subantennal sutures (e.g. *Scarelus*, Figs 118, 119).

Antennal prominence: The antennal prominence varies in the adult Lycidae from relatively inconspicuous (e.g. *Calochromus*, Fig. 129) to prominent, occupying considerable part of the head (e.g. *Dexoris*, *Lyroneces*, Figs 109-110, 115-116, 122). There seems to be a correlation between the size of the antennal prominence and the degree of reduction of mandibles: cf. *Lyroneces*, with greatest antennal

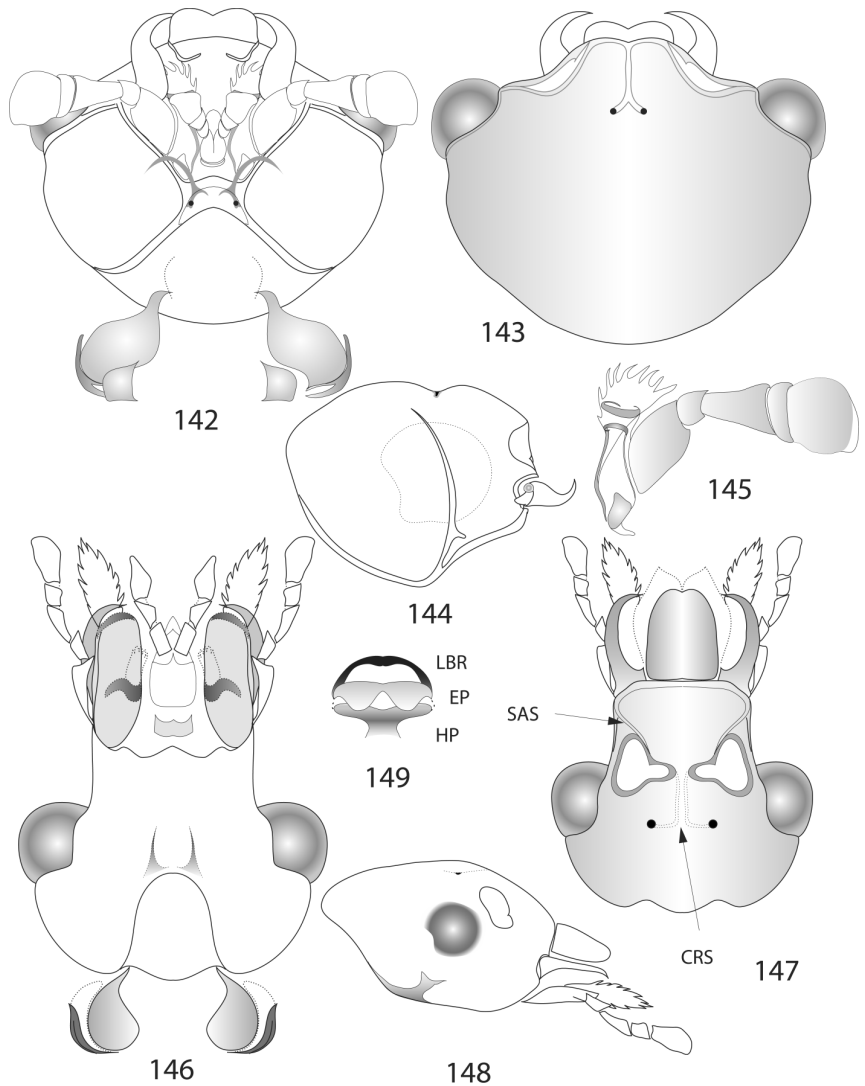


Figs 138-141: Imaginal head structures: *Dilophotes depressicornis* Pic, head, dorsal view (138); *Mesolycus shelfordi* (Bourgeois), head, ventral view (139); same, dorsal view (140); same, lateral view (141).

CRS - coronal suture; ES - epistomal sulcus; PMT - prementum; POS - postoccipital suture; SAS - subantennal suture; SGS - subgenal suture; VT - ventral arms of tentorium.

prominence and vestigial mandibles (Figs 114, 116) vs. *Dexoris* with smaller antennal prominence and minute mandibles (Figs 110-111) or vs. *Calochromus* with almost obsolete antennal prominence and large powerful mandibles (Fig 128-129).

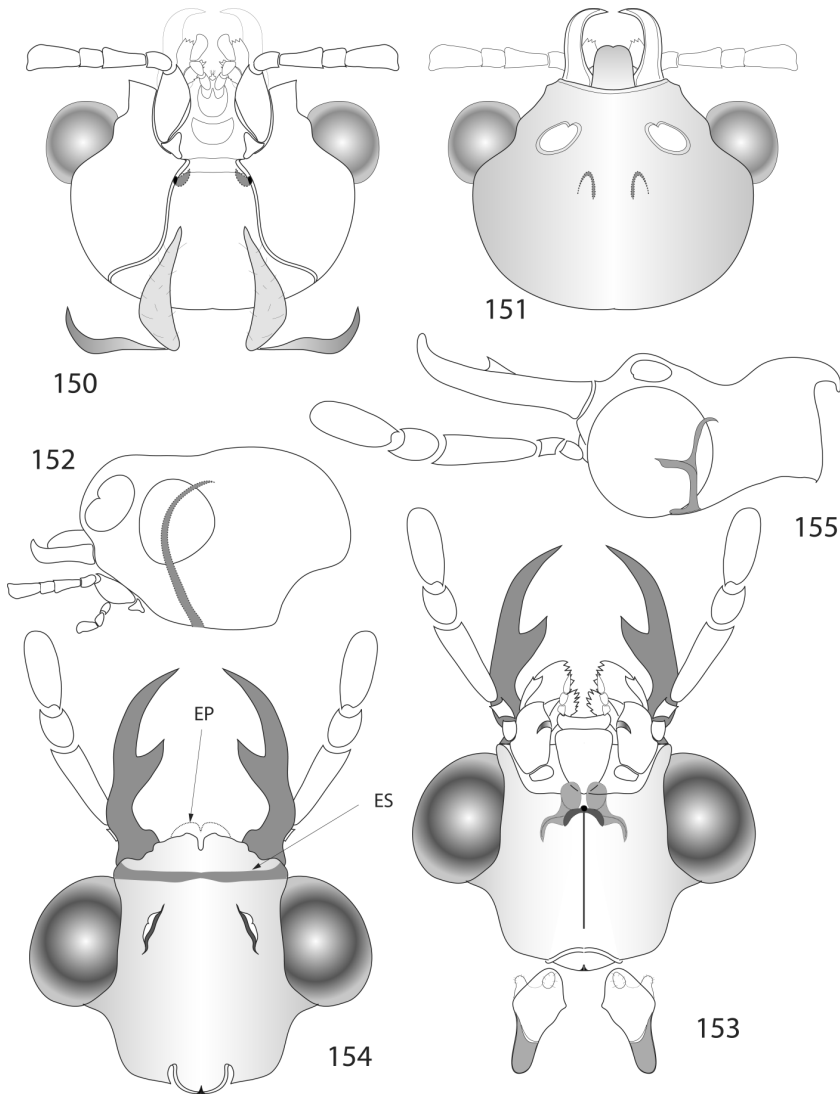
Antennae: Typically the lycid antennae are positioned anteriorly, the antennal sockets often occupying the entire anterior or anterodorsal part of the cranium (e.g. *Dexoris*, *Lyroneces*, *Calopteron*, Figs 82, 92-93, 110, 115-116). In *Lycostomus* the antennal sockets are positioned lower, obviously due the development of a rostrum, but still remain anterior of the other head appendages, when the head is in its normal deflexed position (Fig. 80). The antennae may be 11-segmented (most of the Lycidae) or 10-segmented (Lyropaeini, *Dexoris*).



Figs 142-149: Imaginal structures: *Plateros flavoscutellatus* Blatchley, head, ventral view (142); same, dorsal view (143); same, lateral view (144); same, left maxilla, ventral view (145); *Metriorrhynchus thoracicus* (Fabricius), head, ventral view (146); same, dorsal view (147); same, lateral view (148), same, labor-hypopharyngeal organ, anterior view (149).

CRS - coronal suture; EP - epipharynx; HP - hypopharynx; LBR - labrum; SAS - subantennal suture.

The antennal muscles in some Lycidae, due to the absence of the tentorium, are attached on the cranium, condition observed also in chilopods and considered primitive, as opposed to their attachment on the tentorium (Snodgrass, 1935), while those of *Cantharis* and *Lampyris* are attached on the tentorial arms.

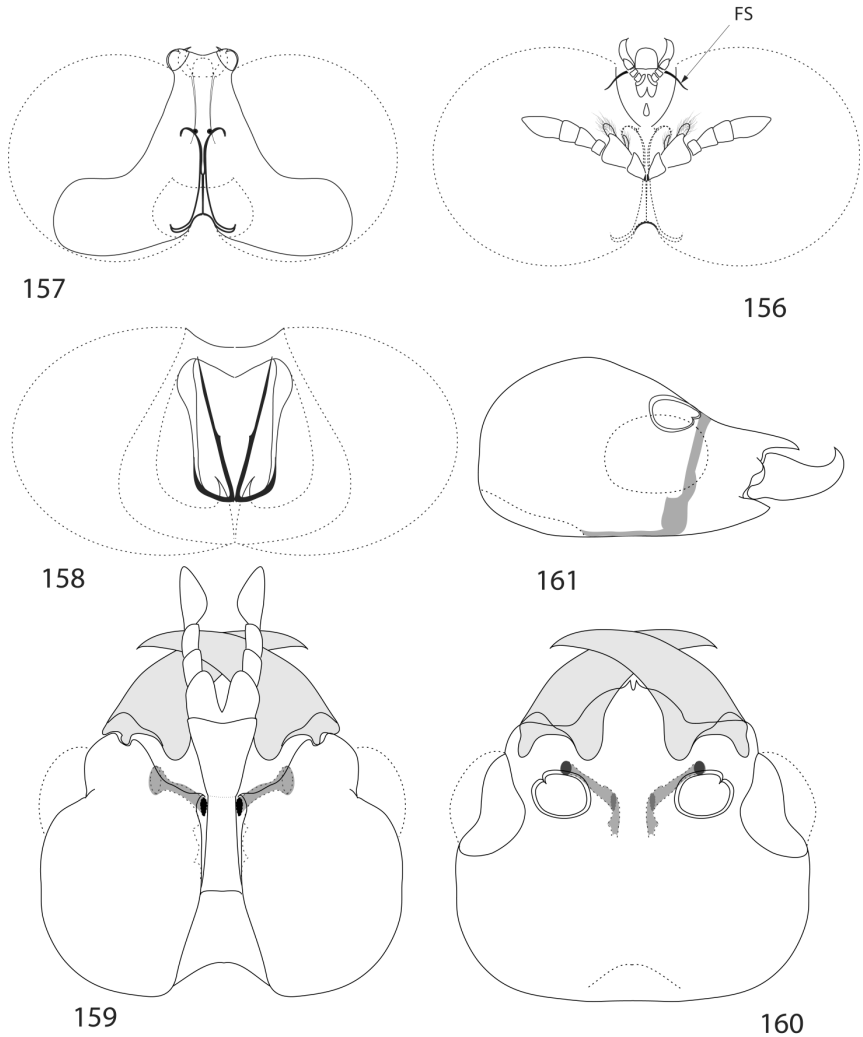


Figs 150-155: Imaginal head structures: *Aferos* sp., head, ventral view (150); same, dorsal view (151); same, lateral view (152); *Phengodes* sp., head, ventral view (153); same, dorsal view (154); same, lateral view (155).

EP - epipharynx; ES - epistomal sulcus.

- The morphologically preoral position of the nerve centers of antennae (Snodgrass, 1935) suggests that the antennae belong in the preoral part of head and their primitive location is on a segment anterior to mandibles. Therefore, the anterodorsal position of the antennal insertions is considered plesiomorphic.

- Cranial attachment of antennal muscles is deemed primitive.
- Plesiomorphic condition of the number of antennomeres appears unclear.

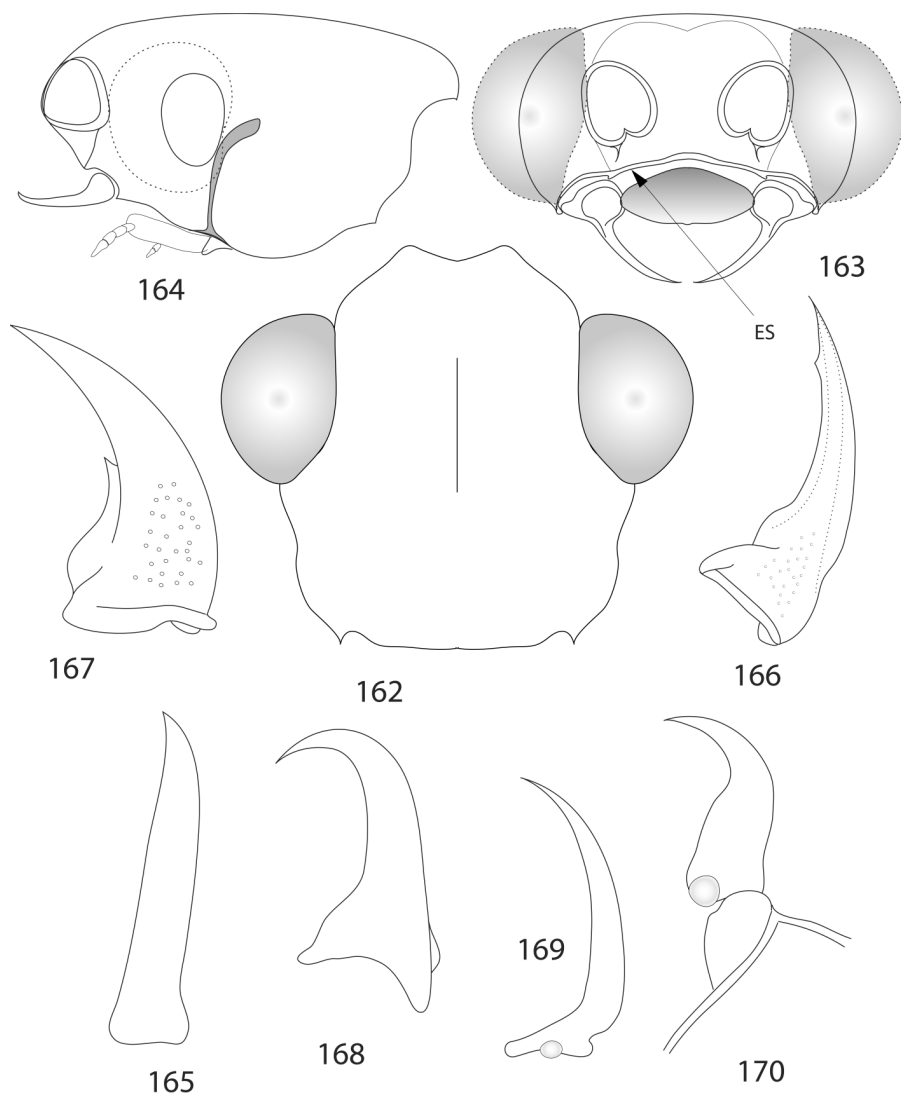


Figs 156-161: Imaginal head structures: *Lampyris* sp. (Greece), head, ventral view (156); same, dorsal view (157); same, posterior view (158); *Cantharis fusca* Linnaeus, head without maxillae, ventral view (159); same, dorsal view (160); same, lateral view (161).

FS - frontal suture.

Antennifer: The orientation of the antennifer may be external, when it is positioned on the anterior-lateral margin of the antennal sclerite, as in *Dictyoptera* (Fig. 104) or internal, when it is oriented towards the intersection of the median line and the frontoclypeal sulcus, as in *Platerodrilus*, *Mimolibnetis*, *Lampyrolycus*, *Dexoris*, *Metriorrhynchus*, *Plateros*, etc. (Figs 95, 110, 143, 147). The antennifer is in the intermediate state in *Lycostomus*, *Calochromus* and *Calopteron*, directed more or less straight forward (Figs 88, 92, 128).

- Plesiomorphic condition of the antennifer orientation is unknown.

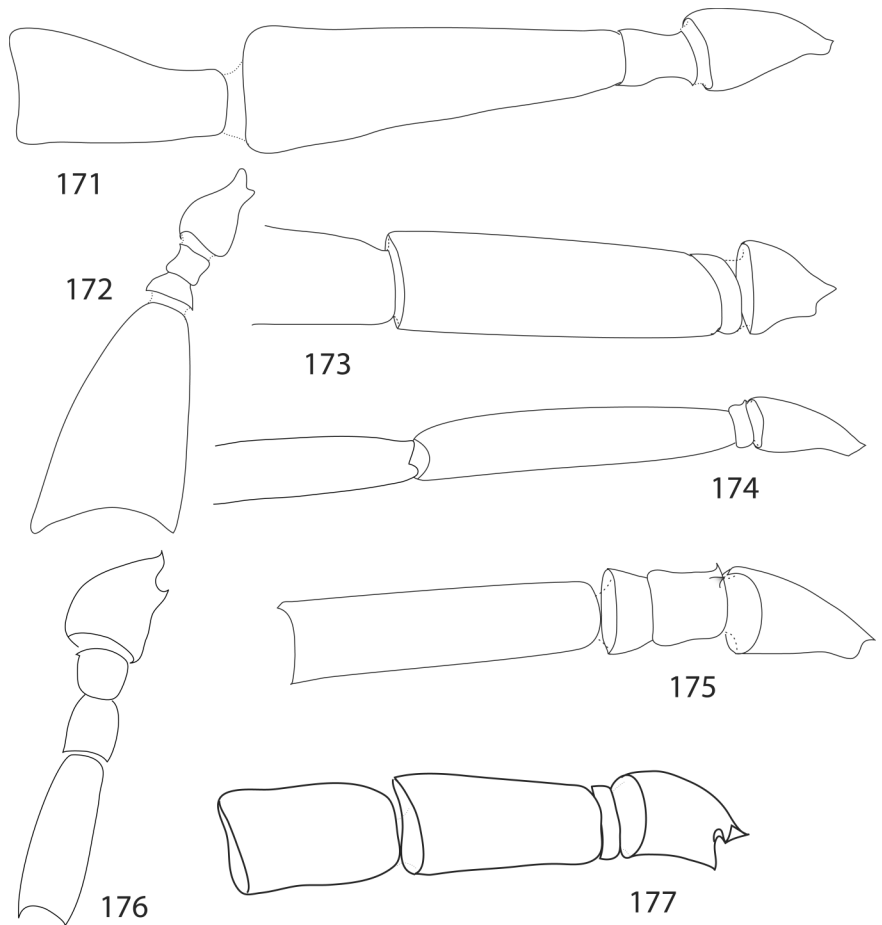


Figs 162-170: Imaginal structures: *Thilmanus obscurus* (Baudi), head, dorsal view (162); same, anterior view (163); same, lateral view (164); mandible, dorsal view: *Lycostomus praeustus* (Fabricius) (165); *Dictyoptera aurora* (Herbst) (166); *Calochromus glaucopterus* (Guerin-Meneville) (167); *Scarelus umbrosus* Kleine (168); *Platerodrilus* sp. (169); *Plateros flavoscutellatus* Blatchley (170).

ES - epistomal sulcus.

Scape: The scape is usually considerably longer and more robust than pedicel (Figs 171-172, 174-184), but in *Lyroneces* it is small and even slightly wider than long (Fig. 173), while in *Thilmanus* not considerably differing in width from the pedicel (Fig. 185).

- Plesiomorphic condition of the scape is unknown.

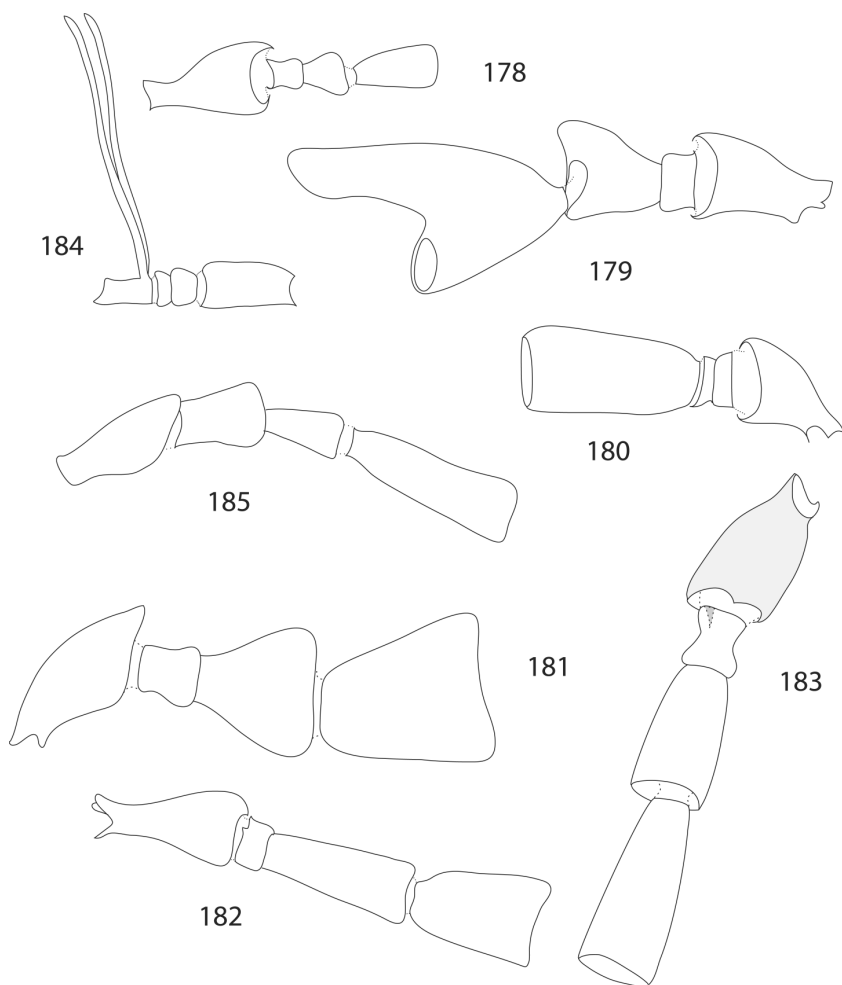


Figs 171-170: Imaginal antennomeres 1-4: *Lycostomus praeustus* (Fabricius) (171); *Ceratoprion* sp. (172); *Lyroneces optabilis* (Kleine) (173); *Scarelus umbrosus* Kleine (174); *Platerodrilus* sp. (175); *Lycinella parvula* Gorham (176); *Dexoris tessmani* Bocák & Bocáková (177).

Pedicel: The pedicel is rigidly attached to antennomere 3 in all lycid taxa (Figs 171-183), even when the third segment is flabellate or serrate (e.g. *Caenia*, Fig. 179), or the antennae are 10-segmented (e.g. *Dexoris*, *Lyroneces*, Figs 173, 177). The same condition was found in *Thilmanus*, *Phengodes*, *Cantharis*, *Lampyris* (e.g. Figs 184-185), as well as in *Tenomerga* (Cupedidae) and *Xanthochroa* (Oedemeridae), and is apparently characteristic of all Coleoptera.

Antennomeres: The antennomeres of flagellum vary from filiform to compressed and flabellate (Figs 171-185). The relative size of antennomere 3 (its ratio to antennomeres 2 and 4) and its shape is sometimes used for genus-group taxonomy, but is probably of little importance for phylogenetic considerations or suprageneric classification.

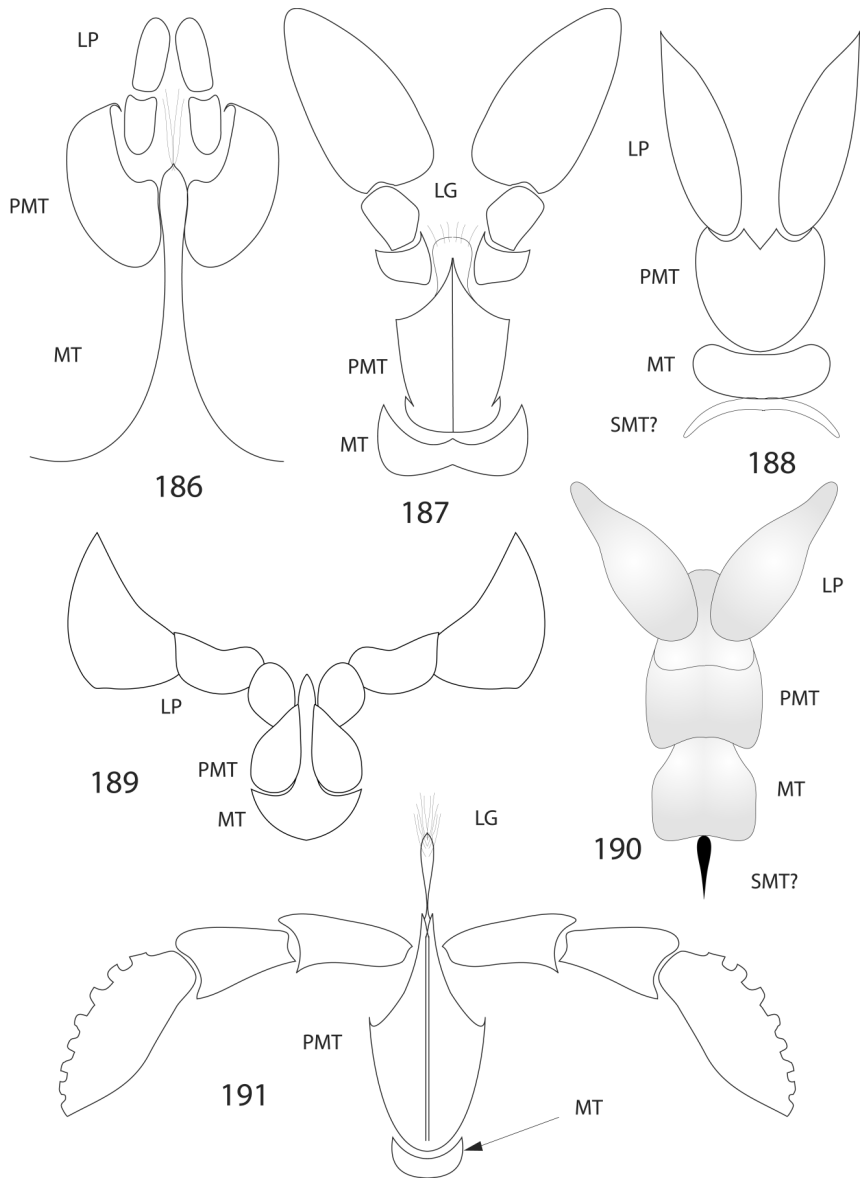
- Plesiomorphic condition of the antennomeres is not obvious.



Figs 178-185: Imaginal antennomeres 1-4: *Aferos* sp. (178); *Caenia kirschi* Bourgeois (179); *Taphes brevicollis* Waterhouse (180); *Plateros flavoscutellatus* Blatchley (181); *Metriorrhynchus thoracicus* (Fabricius) (182); *Calochromus glaucopterus* (Guerin-Meneville) (183); *Phengodes* sp. (184); *Thilmanus obscurus* (Baudi) (185).

Vertex: Apart from often having a median groove anteriorly due to the presence of antennal prominence, the vertex may be impressed medially where the dorsal tentorial maculae are located (e.g. *Lycinella*, Fig. 125) and bear an additional median impression, especially when the coronal suture is prominent (e.g. Figs 136, 140).

The fastigium, or the angle between the vertex and the face/frons, may vary from acute (e.g. *Dilophotes*, *Lyroneces*, Figs 116, 138) to blunt (*Mesolycus*, *Calochromus*, Figs 129, 141) and in some cases, at least in related taxa, such as *Dilophotes* and *Mesolycus*, seems to be correlated with reduction of coronal and sub-antennal sutures in one of them. In general the fastigium is undoubtedly



Figs 186-191: Imaginal labium: *Ceratoprion* sp. (186); *Macrolycus flabellatus* (Motschulsky) (187); *Dexoris tessmani* Bocák & Bocáková (188); *Calopteron reticulatum* (Fabricius) (189); *Lyroneces optabilis* (Kleine) (190); *Caenia kirschi* Bourgeois (191).

LG - ligula; LP - labial palps; MT - mentum; PMT - prementum; SMT - submentum.

correlated with the degree of development of the antennal prominence. In *Dexoris* the fastigium is only slightly more than 30 degrees (Fig. 110).

- Plesiomorphic condition of the vertex is unclear.

Clypeus: The clypeus is the sclerotized area lying anterior of the epistomal sulcus, whether the latter is expressed or not (Chapman, 1998). The Lycidae often have very short anterior part of frons that is limited to a narrow epistomal margin, i.e. in most cases the clypeus is absent, and the labrum muscles are attached to the frons posterior of the epistoma. The clypeus may be traced only in few lycid taxa where the epistomal margin is wide and the epistomal sulcus not demarcated (*Calochromus*, Fig. 128). Therefore, indication of the «free» clypeus for members of Calochrominae (Green, 1950) or Duliticolinae (Kazantsev, 2002) should be referred to the labrum. At the same time the clypeus is quite conspicuous in *Phengodes* and *Cantharis*, being in both taxa fused to the epistoma (Figs 154, 160).

- Plesiomorphic condition of the clypeus is unclear.

Labrum: The labrum is usually free, but may be rigidly attached to the epistoma (e.g. *Lygisteropterus*, *Lycostomus*, Fig. 88) or fused thereto (*Lucaina* Duges). When free, it is usually proximally located inside the oral cavity (e.g. *Taphes*, *Helcophorus*, *Calochromus*, Figs 100, 106, 128-129), being to certain extent retractable, with its distal portion partially exposed, but may lie completely anterior of the epistomal margin (e.g. *Platerodrilus*, *Metriorrhynchus*, Figs 95, 147). It may be sclerotized only distally (e.g. *Dexoris*) or uniformly (e.g. *Lycostomus*, *Metriorrhynchus*, *Calochromus*, etc.). The shape may be bilobed (e.g. *Calopteron*, Fig. 92), slightly emarginate distally (e.g. *Helcophorus*, *Macrolycus*, Figs 106, 136) or semicircular anteriorly (e.g. *Lyroneces*, *Platerodrilus*, *Ceratoprion*, Figs 95, 114, 123). The bipartite, divided into two independent lobes labrum was found in *Proteros* (Fig. 107). The epipharynx is typically well developed (e.g. *Dictyoptera*, *Calochromus*, *Metriorrhynchus*, Figs 105, 130-131, 147, 149). In *Phengodes* and *Cantharis* the labrum appears to be fused to the clypeus, with the membranous epipharynx underlying it (Figs 154, 160).

- To determine the direction of evolution of the labrum it appears necessary to define if it evolved from paired somites of the head or a preoral cranial lobe. Despite the fact that the shutter of the larval mandibular structure, which is articulated to the cranium, is tentatively homologized with the labrum, there seem to be no grounds to assume that the imaginal labrum, a structure often lying completely within the oral cavity (e.g. *Dexoris*, *Proteros*, Figs 107, 108), originated as a cranial lobe. Given its presumed function as part of the larval mandibular structure, as well as the presence of paired labral lobes in prekatatrepsis embryo (Cicero, 1994), the bipartite/bilobed free labral structure retracted, at least partially, inside the oral cavity is deemed primitive.

Mandibles: A developed lycid mandible has the usual dorsal acutabular fossa (receiving a condyle at the corner of the frons) and ventral condyle (received in fossa in the genal region). The imaginal mandible may be vestigial and non-opposable, evidently not functional from the feeding standpoint, either roundish and hardly acute distally (*Lyroneces*, Fig. 114), resembling those of adult Lepidoptera, or narrow, straight and acute distally (*Lycostomus*, Figs 88, 165). The functional mandibles may be slightly rounded (e.g. *Dictyoptera*, Fig. 166), evenly rounded (e.g. *Proteros*, Fig. 107), or strongly hooked (e.g. *Scarelus*, Fig. 168). The mandible may be almost uniformly narrow, as in *Platerodrilus* (Fig. 169), or conspicuously widened proximally, as in *Plateros* or *Scarelus* (Figs 168, 170); the incisor edge of mandible may be provided with a tooth, either apically, as in *Dictyoptera* (Fig. 166), or medially, as in *Calochromus* (Fig. 167). The degree of sclerotization also seems to vary, obviously being inconsiderable in the vestigial

mandibles of *Lyroneces* or *Lycostomus*. A functional lycid mandible is typically provided with a internal channel allowing the sucking of liquid food (Fig. 166).

- Plesiomorphic condition of the imaginal mandibles is not clear, as vestigial mandibles that appear apomorphic are typically correlated with absent tentorium and other hypothetically primitive features (e.g. in *Lyroneces*).

Hypopharynx: Unlike in the larval condition, where the hypopharynx includes a pair of heavily sclerotized suspensoria and hypopharyngeal apodemes, the adult hypopharynx in Lycidae is typically weakly sclerotized, though sometimes it may bear more heavily sclerotized lingua (e.g. *Calochromus*, Figs 130-131). The length and shape of the lycid hypopharynx is variable (e.g. Figs 88, 123, 127-130).

Maxilla: The lycid maxilla rather uniformly consists of cardo, stipes, palpifer and the palps (*Caenia*, Fig. 97). The exception is *Calochromus* (Fig. 127), where the cardo appears to be non-differentiated from stipes or reduced. The galea and lacinia are typically distinct (*Dexoris*, *Lyroneces*, *Lycostomus*, *Calochromus*, etc., Figs 88, 112, 114, 127), but these two structures may also appear non-differentiated (i.e. *Platerodrilus*, Fig. 94).

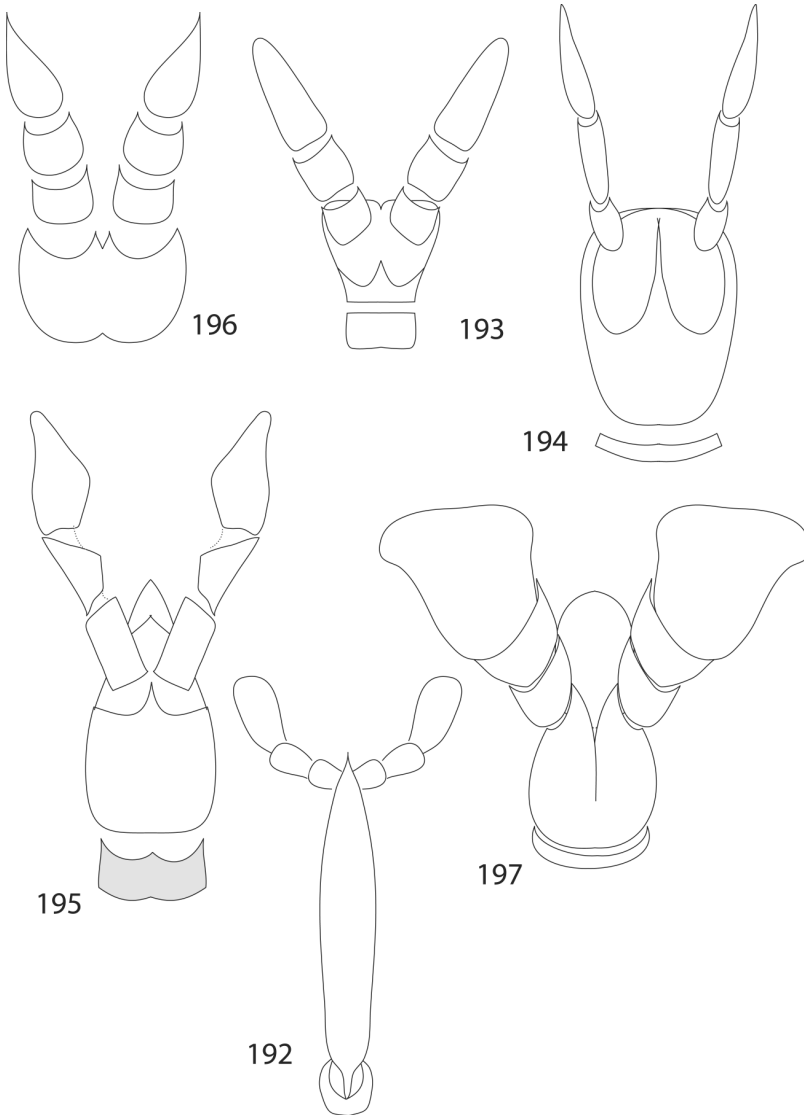
The maxillary palpi are always 4-segmented. The ultimate palpomere has two basic conditions: apically pointed/acuminate (as in *Dexoris*, *Ceratoprion*, *Lyroneces*, *Platerodrilus*, etc., Figs 94, 112, 114, 120) and apically flattened and more or less dilated (e.g. *Calopteron*, *Macrolycus*, etc., Figs 91, 135).

The stipes is divided into a posterior (and outer) basistipes and anterior (and inner) dististipes. The galea is typically one-segmented and may attach to the outer apex of the dististipes or to both the dististipes and the palpifer, while the lacinia, when present, is a non-articulated outgrowth on the inner apex of the stipes and may be attached both to the basistipes and the dististipes (*Plateros*, *Metriorrhynchus*, *Dexoris*, Figs 112, 145, 146)

- All maxillary sclerites developed and ultimate palpomere acuminate are deemed primitive states.

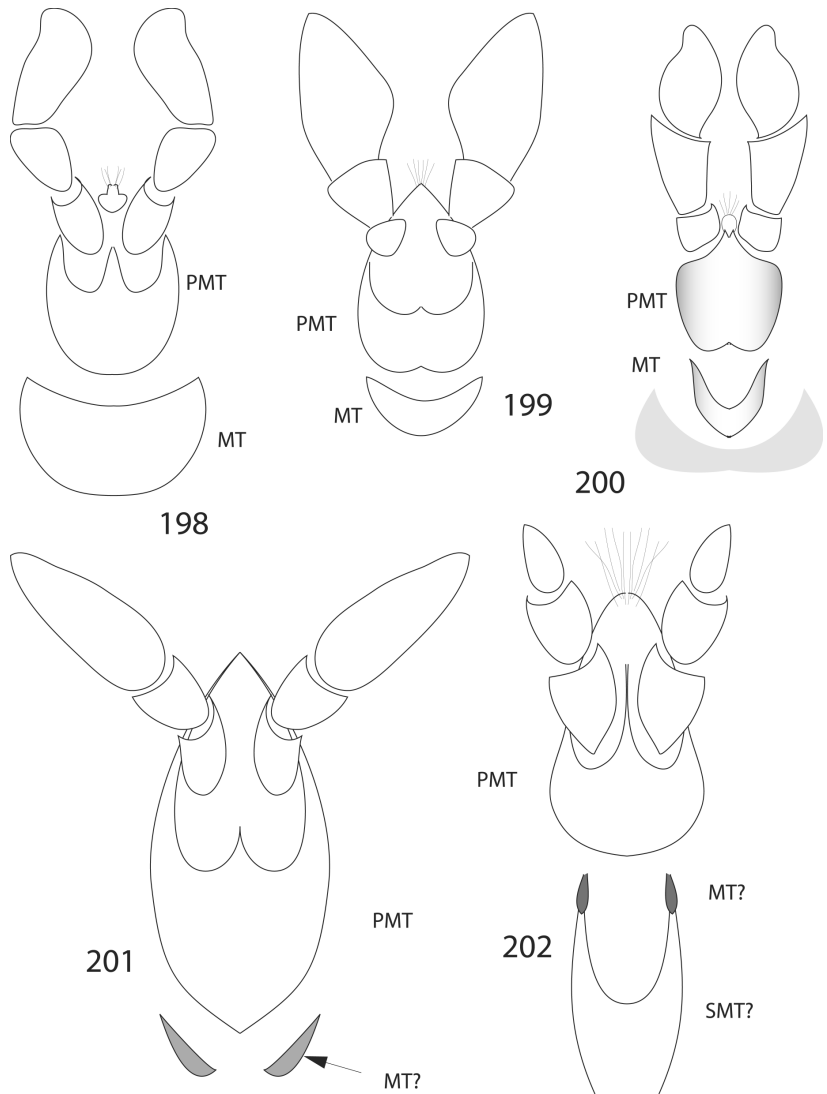
Labium: The labium in Lycidae is a far more variable structure than the maxilla. It usually has a differentiated prementum and mentum. The palpomeres are typically 3-segmented (e.g. *Lycostomus*, *Plateros*, *Metriorrhynchus*, etc., Figs 88, 142, 146, 192-197). The exceptions are *Lyroneces*, *Leptolycus* and *Dexoris* (Figs 188, 190), with 1-segmented palps, and *Ceratoprion* (Fig. 186) and *Flabellocaenia* Pic (Bocák and Bocáková, 1990) with 2-segmented palpi. Bocák and Bocáková (1990) also signaled two labial palpomeres in *Scarelus*, but this taxon appeared to have 3-segmented labial palps (Fig. 193). The distal palpomere may be either pointed (e.g. *Taphes*, *Mesolycus*, *Proteros*, Figs 107, 201, 202) or flattened distally (e.g. *Caenia*, *Dictyoptera*, *Aferos*, Figs 179, 198, 199), in the latter condition sometimes conspicuously widened apically (e.g. *Calopteron*, *Plateros*, *Helcophorus*, Figs 106, 189, 197). In *Phengodes* and *Lampyris* the distal palpomere is pointed (Figs 204, 205), while in *Cantharis* it is flattened and widened (Fig. 206).

The ligula is either absent (e.g. *Lyroneces*, *Scarelus*, *Platerodrilus*, Figs 190, 193, 194) or more or less developed, but undifferentiated into glossae and paraglossae (e.g. *Caenia*, *Calochromus*, *Helcophorus*, *Aferos*, *Conderis*, Figs 106, 179, 183, 198, 200). The labium in the Lycidae is typically positioned between the maxillae (e.g. *Lycostomus*, *Platerodrilus*, *Dexoris*, Figs 87, 94, 108), while in the Lampyridae (e.g. *Lampyris*) it lies considerably anterior of maxillae (Fig. 156).



Figs 192-197: Imaginal labium: *Lycostomus praeustus* (Fabricius) (192); *Scarelus umbrosus* Kleine (193); *Platerodrilus* sp. (194); *Metriorrhynchus thoracicus* (Fabricius) (195); *Lycinella parvula* Gorham (196); *Plateros flavoscutellatus* Blatchley (197).

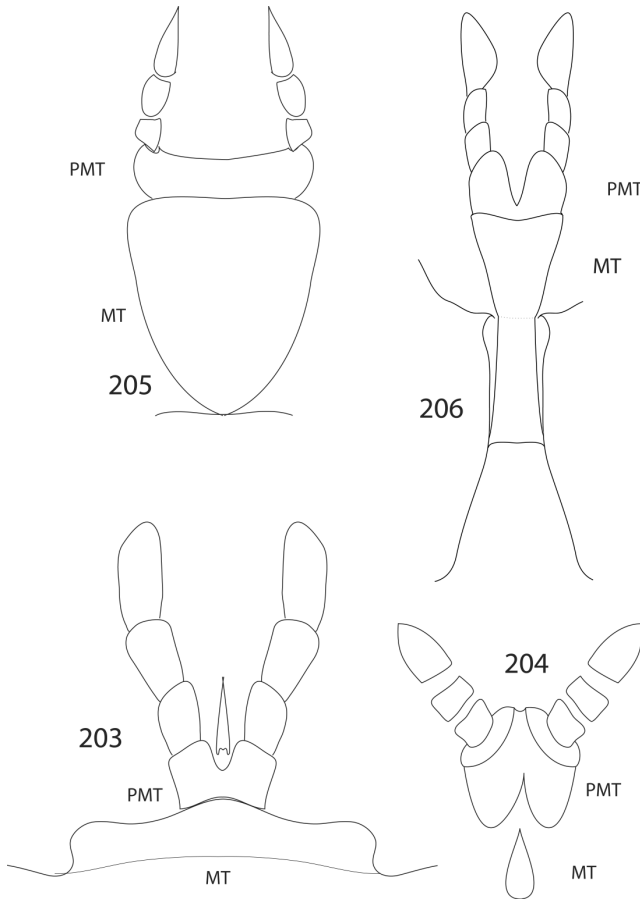
The prementum in the Lycidae may be both divided and undivided. A completely divided prementum is found in *Calopteron* and *Ceratoprion* (Figs 186, 189), with the anterior process of the mentum penetrating between the two stipites. Interestingly, *Calopteron* is characterized by divided prementum also in the larval stage (Fig. 47), whereas the larva of *Ceratoprion* remains unknown. The prementum has a median suture completely or almost completely dividing it in *Macrolycus* and *Caenia* (Figs 187, 191).



Figs 198-202: Imaginal labium: *Aferos* sp. (198); *Dictyoptera aurora* (Herbst) (199); *Conderis signicollis* (Kirsch) (200); *Taphes brevicollis* Waterhouse (201); *Mesolyucus shelfordi* (Bourgeois) (202).

MT - mentum; PMT - prementum; SMT - submentum.

The mentum is typically more or less free in lycids, with the exception of *Ceratoprion* and *Calochromus*, in which it appears to be fused posteriorly to the genal or postoccipital sclerites (Figs 120, 127, 186, 203). The only taxa where the mentum seems to be represented by a pair of free sclerites are *Taphes* and *Mesolyucus* (Figs 201, 202). If these sclerites are to be homologized with cardines, as suggested by Snodgrass (1935: 150), *Taphes* and *Mesolyucus* will possibly be the first hexapods, where such condition is found. However, as discussed in the Larvae section, these



Figs 203-206: Imaginal labium: *Calochromus glaucopterus* (Guerin-Meneville) (203); *Lampyris* sp. (204); *Phengodes* sp. (205); *Cantharis fusca* Linnaeus (206).

MT - mentum; PMT - prementum.

postlabial structures are more likely secondary sclerotizations. The submentum appears to be noticeable only in *Dexoris* and *Lyroneces* (Figs 188, 190), also represented by a vaguely delineated and weakly sclerotized area in *Conderis* (Fig. 200), and possibly in *Mesolycus* (Fig. 202). In *Cantharis* the mentum and submentum are fused, with the submental part of the sclerite forming the gula (Fig. 206).

On the other hand, in the Neuroptera and some Coleoptera, e.g. in Silphidae or Scarabaeidae, the usually transverse plate lying posteriad of the prementum is a part of prementum as well, because the labial median muscles are inserted on it (Snodgrass, 1935). Hence, the pair of small sclerites lying posteriad of the prementum in *Taphes* and *Mesolycus* (Figs 201, 202) may prove to be intermediate sclerites, probably giving insertion to the ventral adductors, as is the case with the larva of *Silpha*. However, an additional study of the labial musculature in Lycidae is needed to properly homologize the sclerite referred to above as the mentum.