

Figs 207-210: Imaginal thorax, ventral view: *Lycostomus praeustus* (Fabricius) (207); *Platerodrilus* sp. (208); *Lyroneces optabilis* (Kleine) (209); *Calopteron reticulatum* (Fabricius) (210).

- As there is no clarity with respect to homology of the postlabial structures (also discussed above in the Larvae section), their primitive condition is considered unknown. Similarly, there seems to be no relevant information to determine the direction of evolution of the labial palps with respect to the number of the palpomeres.

- The divided prementum, in conformity with Snodgrass's opinion (1935), is deemed primitive.
- As the labium is homologized with the second maxillae, its position between them vs. its anterior position, as in *Pyractomena* (Fig. 156), is deemed primitive.

Gula: A pair of gular sutures in Coleoptera normally extends forward from the occipital foramen bounding the gular region and lying posteriad of the posterior tentorial pits (Snodgrass, 1935). Internally, the gular sutures are represented by a pair of flanges, from which the tentorium arises. In the Lycidae the gula is typically absent, as the posterior tentorial pits are usually positioned in the anterior extremities of the postoccipital suture; the ventral closure often being nothing but a narrow process connecting the genal areas (e.g. *Lyroneces*, *Aferos*, Figs 114, 150), sometimes fused with them (e.g. *Helcophorus*, Fig. 106). The gula is, however, present in *Platerodrilus*, as well as in *Cantharis* and *Phengodes*, with the posterior tentorial pits advanced anteriorly (Figs 94, 153, 159), probably as a consequence of the transition of the ventral closure in the opposite direction.

- The absent gula, following Snodgrass (1935), is deemed primitive.

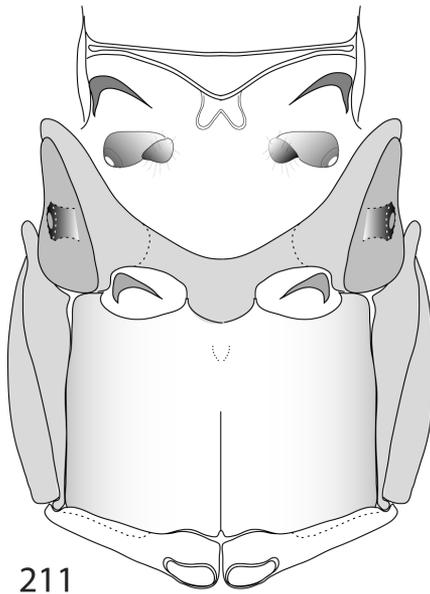
Cervix: The cervical sclerites in the Lycidae are typically represented by a pair of two relatively well sclerotized parts, an elongate tube-like sclerite, which is open from one side, usually ventrally, and a more heavily sclerotized annuliform sclerite (e.g. *Lycinella*, *Macrolycus*, *Taphes*, *Lycostomus*, Figs 87, 100, 124, 135). In a few taxa these sclerites are less sclerotized, the annuliform sclerite becoming inconspicuous or hardly noticeable (e.g. *Ceratoprion*, Fig. 120). The larger sclerite articulated to the head base ventrally is typically pubescent, while the annuliform one, which is not articulated but to the other cervical sclerite, is glabrous. Sometimes there is an evident third sclerite located basad of the other two (e.g. in *Plateros*, *Macrolycus*, Figs 142, 222).

The cervical sclerites are reported to be absent in Archostemata, Adephaga and Myxophaga (Crowson, 1981). Sometimes presence of these sclerites in Polyphaga is referred to as an apomorphy of the taxon developed for «reflexing the head against the thorax» (Crowson, 1981), which makes it hard to explain the development of the same structure in a vast number of other hexapod orders.

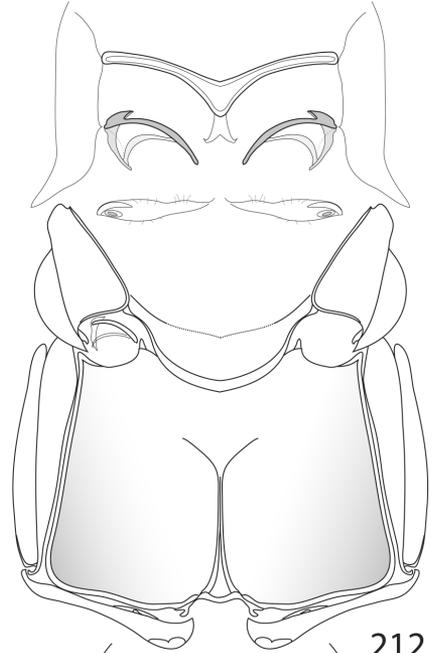
Interestingly, the cervical sclerites in Lycidae are structurally similar to the sclerites related to the thoracic spiracles, in terms of shape, position, sclerotization and pubescence. In fact, in some cases, i.e. in *Lycostomus* or *Plateros* (Figs 87, 142) they differ from the spiracular sclerites of the thorax only in lacking the trachea (Fig. 90). It should be noted that cervical sclerites retain their natural shape with the annuliform sclerite making an annulus, when the head itself is in its natural position, i.e. deflexed against the prosternum; these sclerites are stretched and distorted, along with the ventral membrane of the neck, when the head is fixed in a way that the mandibles are directed forward and/or the mouth parts, as well as the cervical sclerites are made observable from below.

Snodgrass (1935) indicates that there is a direct proof of existence in the primitive insects of the tracheal invaginations in all three thoracic segments; the prothoracic spiracles have also been reported in the embryonic stage of some hexapods (e.g. Cholodkowsky, 1891).

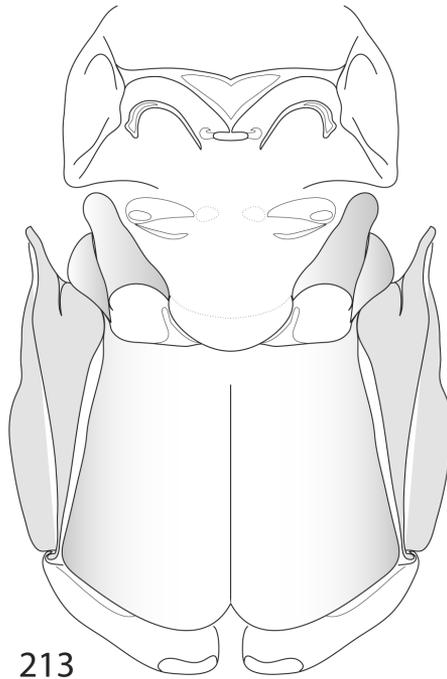
- These peculiarities of the cervical sclerites suggest that they may represent rudiments of the pair of spiracles located between the head and the thorax and



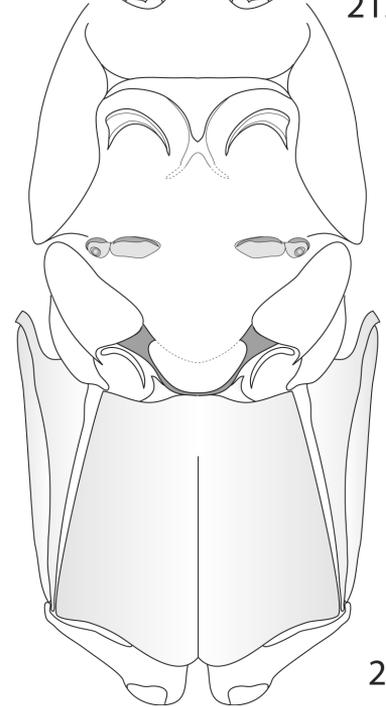
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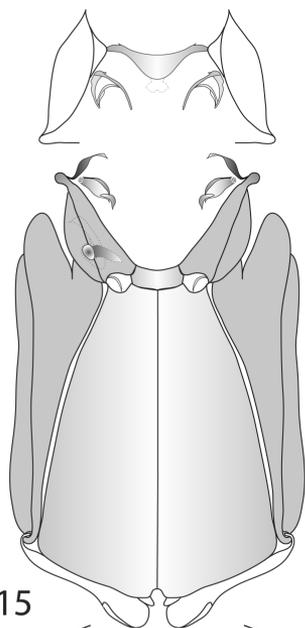


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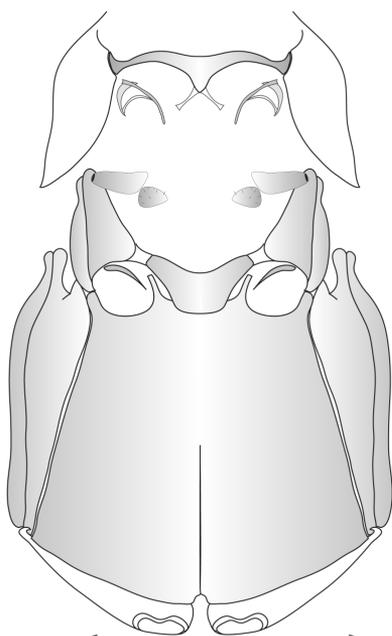


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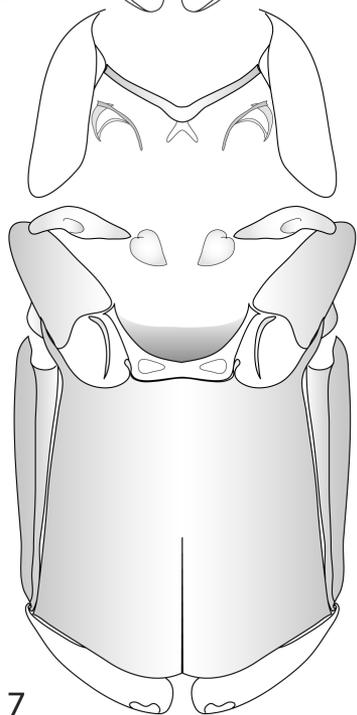
Figs 211-214: Imaginal thorax, ventral view: *Dictyopectera aurora* (Herbst) (211); *Helcophorus miniatus* Fairmaire (212); *Taphes brevicollis* Waterhouse (213); *Aferos* sp. (214).



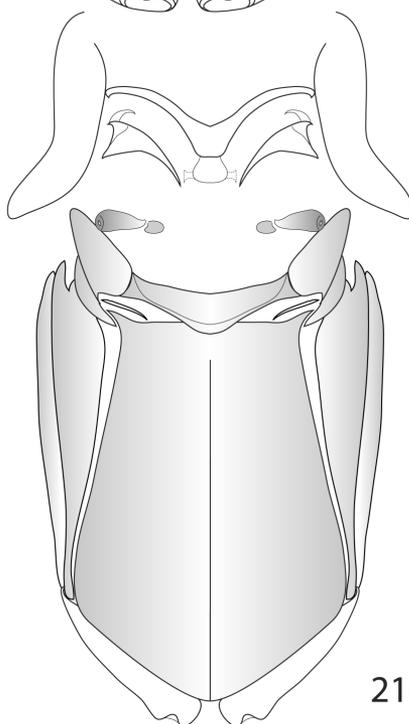
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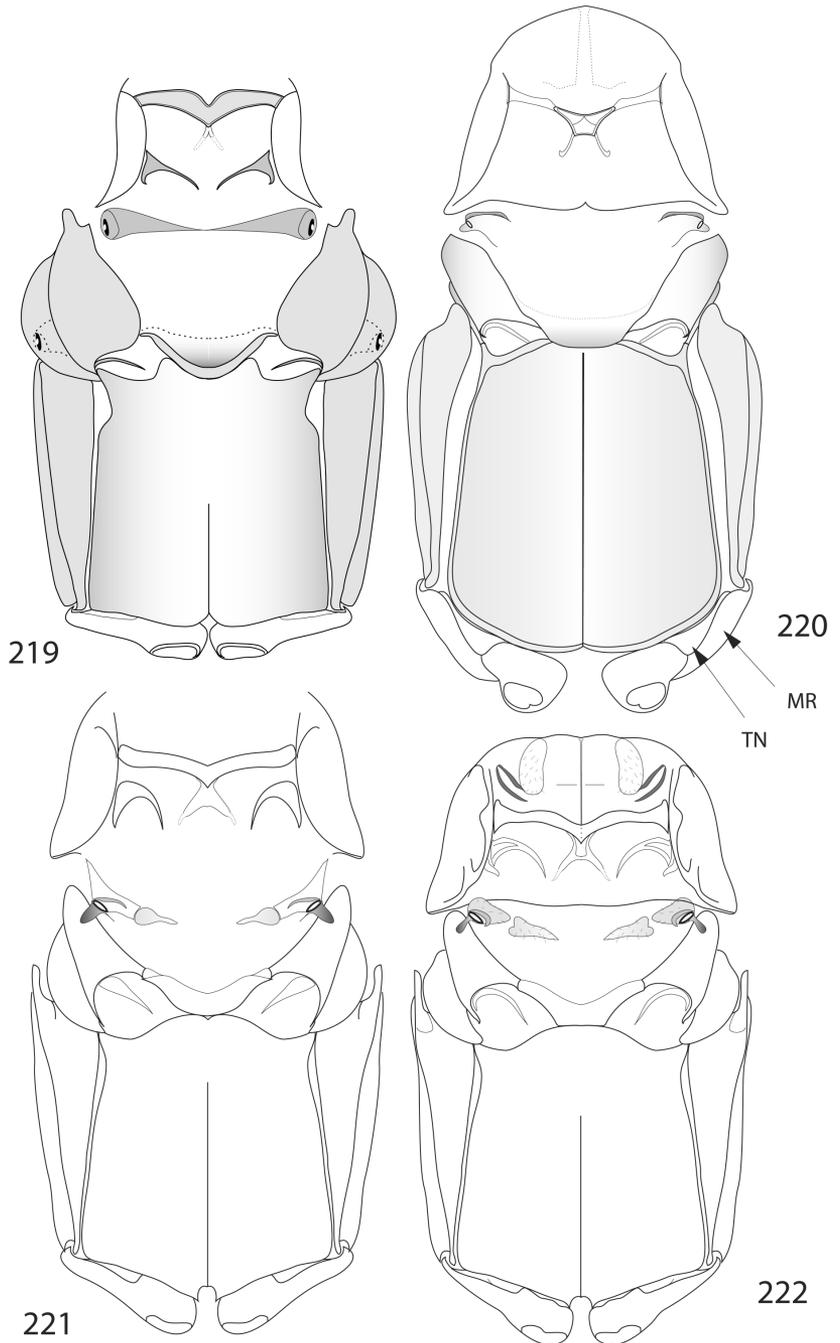


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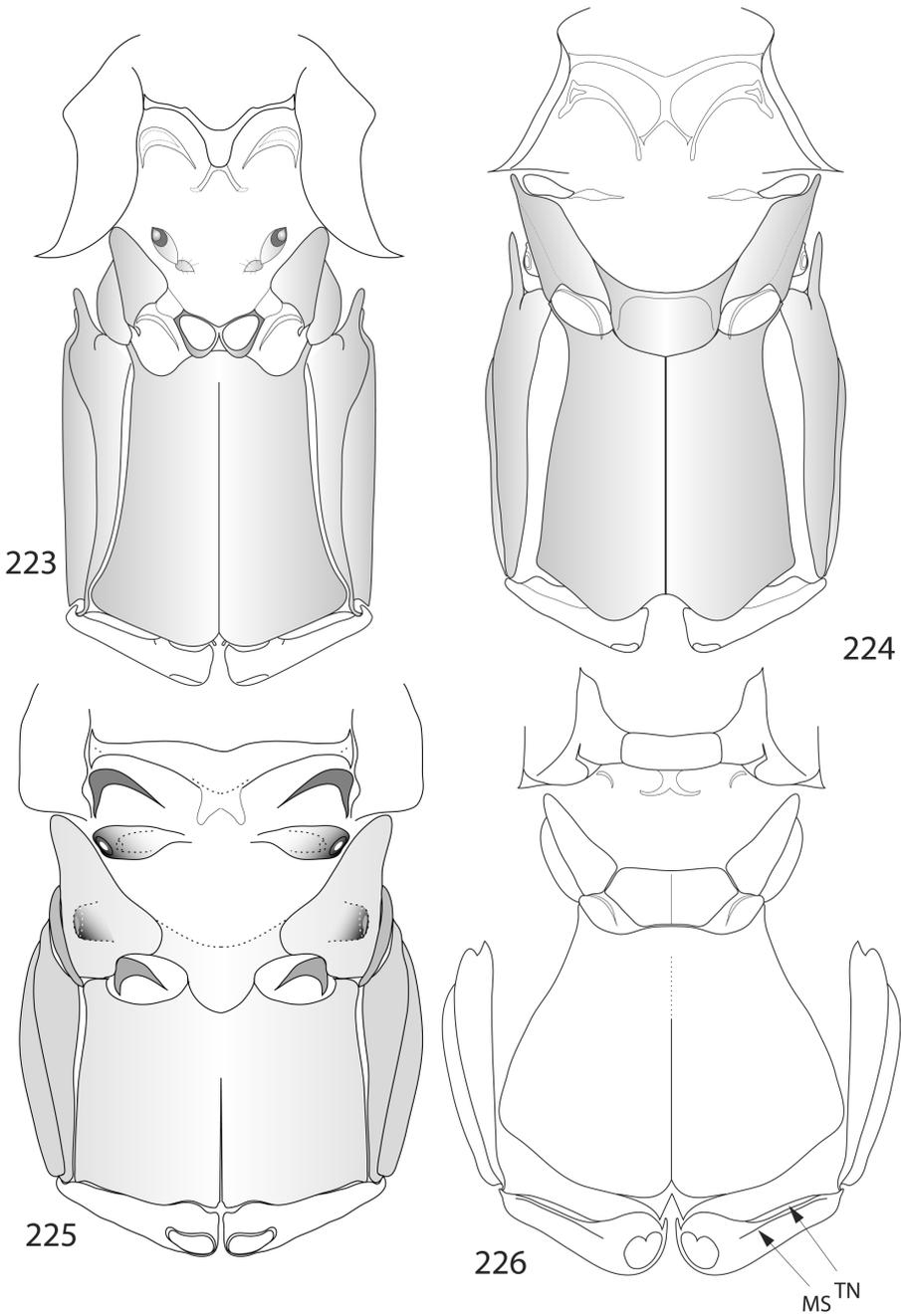


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Figs 215-218: Imaginal thorax, ventral view: *Dexoris tessmani* Bocák & Bocáková (215); *Plateros flavoscutellatus* Blatchley (216); *Metriorrhynchus thoracicus* (Fabricius) (217); *Lycinella parvula* Gorham (218).

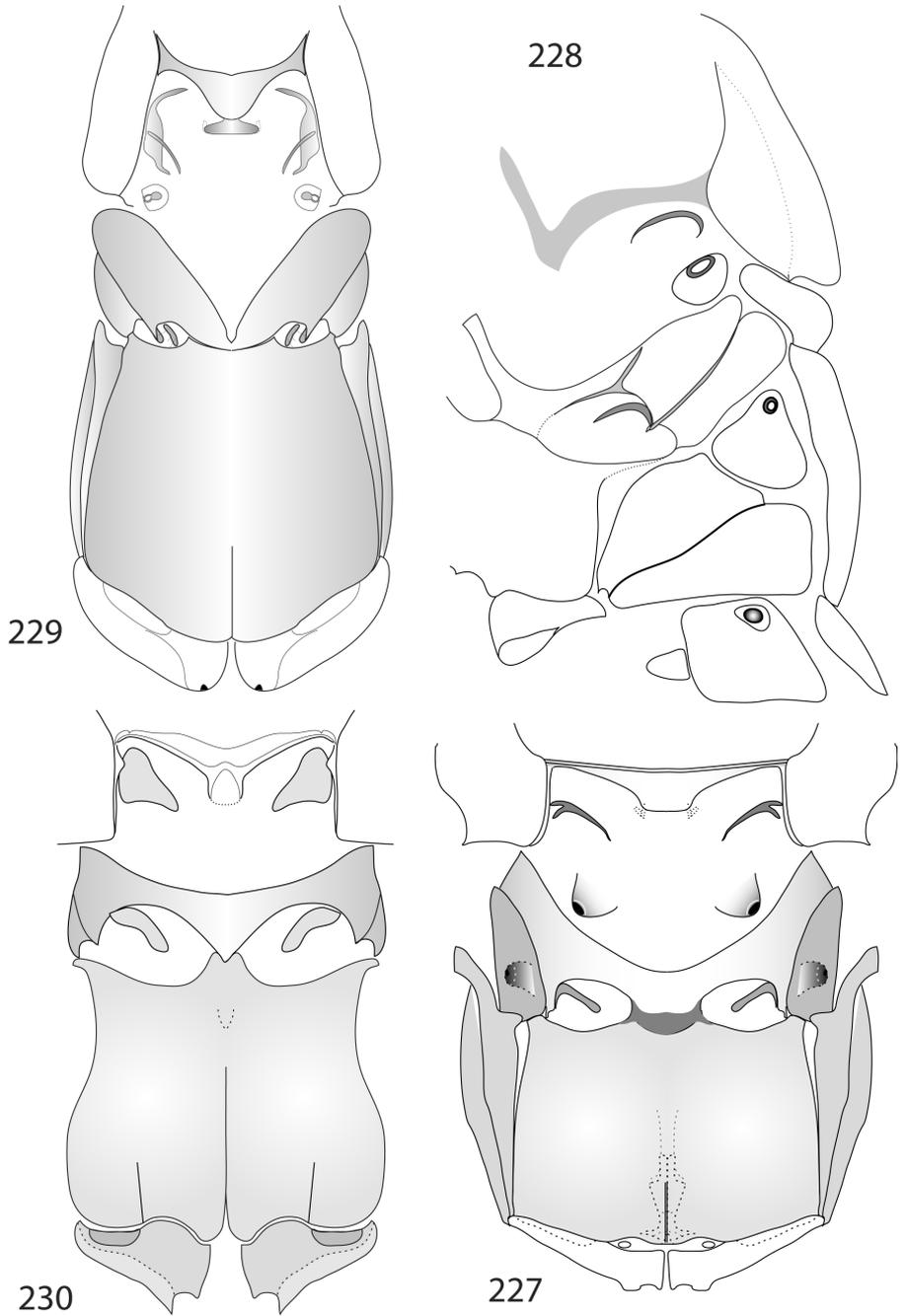


Figs 219-222: Imaginal thorax, ventral view: *Scarelus umbrosus* Kleine (219); *Mesolyclus shelfordi* (Bourgeois) (220); *Conderis signicollis* (Kirsch) (221); *Macrolyclus flabellatus* (Motschulsky) (222). MR - meron; TN - trochantin.

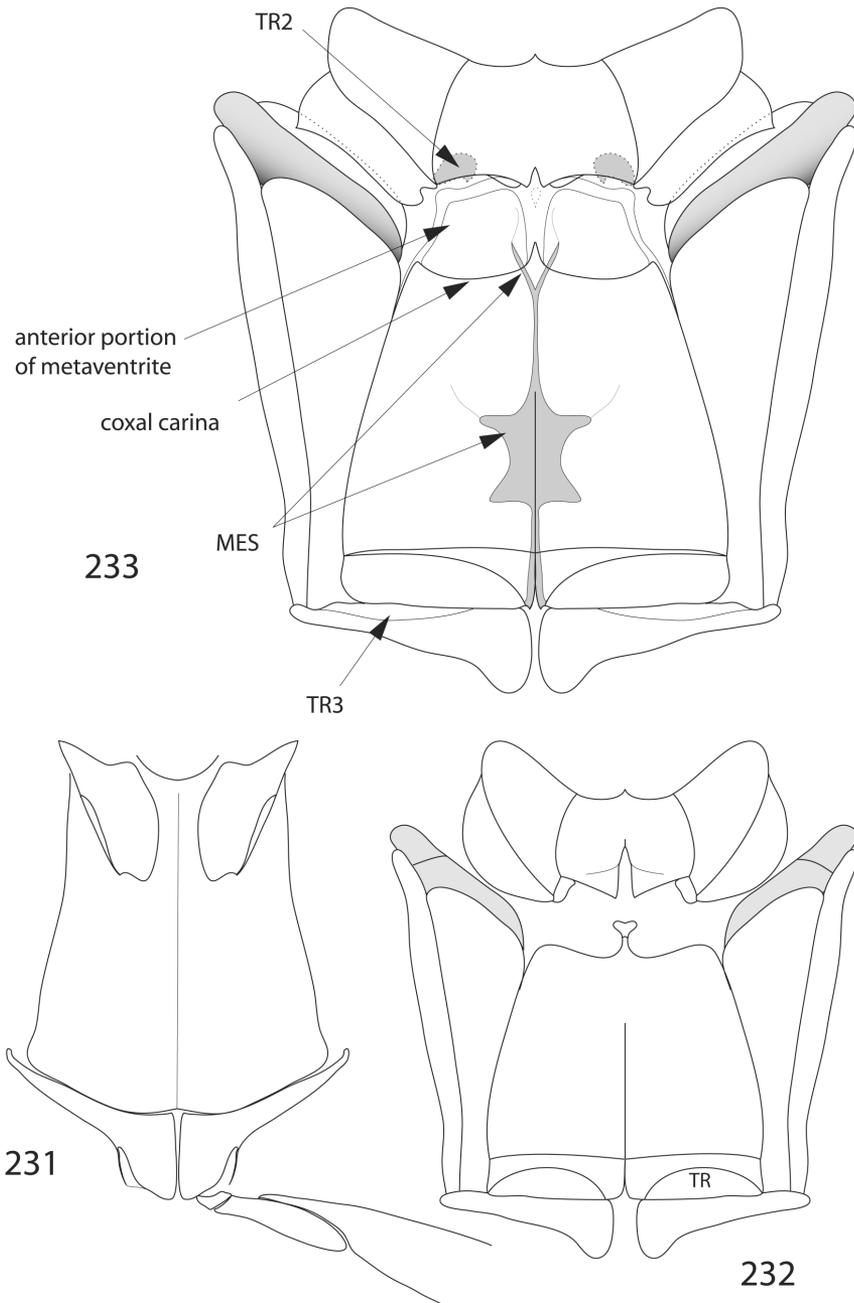


Figs 223-226: Imaginal thorax, ventral view: *Caenia kirschi* Bourgeois (223); *Ceratoprion* sp. (224); *Calochromus glaucopterus* (Guerin-Meneville) (225); *Thilmanus obscurus* (Baudi) (226).

MS - meral suture; TN - trochantin.

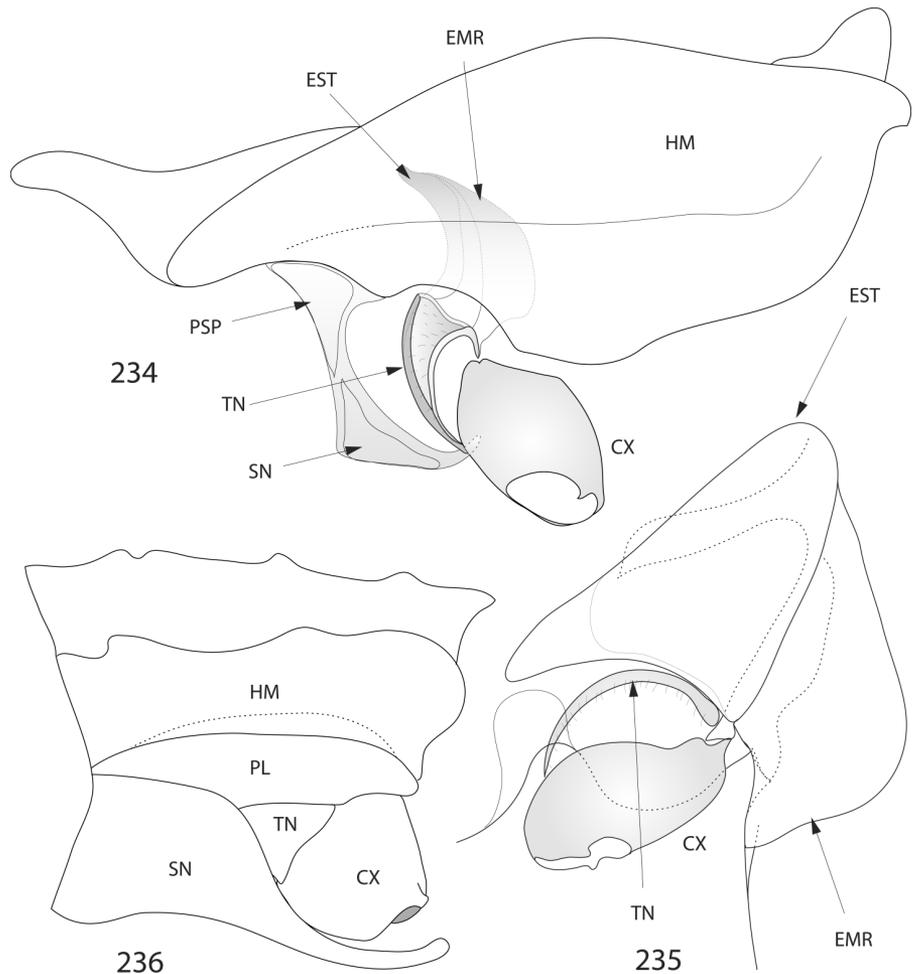


Figs 227-230: Imaginal thorax, ventral view: *Lampyris* sp., male (227); *Lampyris noctiluca* female, after Cicero, 1988 (228); *Phengodes* sp. (229); *Cantharis fusca* Linnaeus (230).



Figs 231-233: Imaginal thoracic structures, ventral view: *Mimolibnetis ruwenzoriensis* Kazantsev, male, metaventricle (231); *Priacma serrata*, meso- and metathorax, after Crowson, 1981 (232); *Tenomerga moultoni* (Gestro), meso- and metathorax (233).

MES - metendosternite; TR - trochanter.



Figs 234-236: Imaginal thoracic structures, lateral view: *Lycostomus praestus* (Fabricius), prothorax (234); same, mesothoracic structures (235); *Priacma serrata*, prothorax, after Hlavac, 1972 (236).

CX - coxa; EMR - epimeron; EST - episternum; HM - hypomeron; PL - pleuron; PSP - prosternal process; SN - sternum; TN - trochantin.

related to the prothorax; and in this respect the developed cervical sclerites resembling spiracular ones may be in plesiomorphic condition.

Prothorax: The prothorax is usually divided into notum, sternum, trochantin and cryptopleuron. The latter two segments do not form the prothoracic wall, being a prolongation of the leg, partly internal (*Lycostomus*, Fig. 234). The ventral surface of the pronotum, the hypomeron, is often not differentiated from the notum other than by a marginal swollen rib. The trochantin is entirely exposed and articulated to the coxa both distally and proximally (Fig. 234). The trochantin and cryptopleuron are rigidly attached to each other and articulated to the coxa, being otherwise free

(Fig. 234). The cryptopleuron in the Lycidae is also partially exposed proximally, being almost completely exposed in the prothorax of *Phengodes* (Fig. 229). Ventrally the prothorax is distant from and not coadapted to the pterothorax (Figs 207-226). No grooves or other cavities to receive antennae or legs are noticeable in the lycid prothorax. Margins of the anterior and posterior openings of the prothorax do not lie in parallel planes and its dorsal length is conspicuously greater than its ventral length (Figs 81-86), even in cases when the head appears prognathous (*Platerodrilus*, Fig. 83).

The cryptopleuron is homologous with the episternum and epimeron of the other two thoracic segments, their homology confidently confirmed both by the larval (e.g. *Lycus*, Fig. 34) and imaginal condition of these structures, with the cryptopleural plate in Lycidae separated by a conspicuous suture into the episternal and epimeral parts (*Lycostomus*, Fig. 234), just as the pleural sclerite of the mesothorax (*Lycostomus*, Fig. 235). At the same time the pleuron of the Archostemata and Adephaga, which is homologous with the cryptopleuron of the Polyphaga, appears to include the fused episternum and epimeron (e.g. *Priacma*, Fig. 236). Thus there are two basic conditions of the cryptopleuron/pleuron in the Coleoptera, a) making part of the lateral wall, attached to all of the hypomeron, sternum and coxa, as well as to the trochantin, being at the same time exposed, (*Priacma*, Fig. 236), and b) free, except being attached to the trochantin, at the same time becoming an internal sclerite (cryptopleuron). The first condition is come across in some Archostemata, Myxophaga and Adephaga, the second is characteristic of all Polyphaga. In the more derived groups of the Archostemata (Micromalthidae) the hypomeron, pleuron, trochantin and sternum are all fused together without even the slightest vestige of sutures (Hlavac, 1975), while in more derived Polyphaga the trochantin is fused with the cryptopleuron and/or the trochantin is little exposed or concealed altogether.

There may be some reasons to believe that an exposed pleuron is primitive as opposed to a concealed one, yet there seems to be a stronger ground to consider a free cryptopleuron, consisting of well-differentiated episternum and epimeron and attached only to the trochantin, to be more primitive, compared to the pleuron with fused episternum and epimeron, which is attached to all adjacent sclerites.

- The absence of grooves or other cavities on the prothorax to receive antennae or legs is considered primitive.
- The free, totally exposed prothoracic trochantin attached to, but not fused with the free and partially exposed cryptopleuron, consisting of differentiated episternum and epimeron, is deemed primitive.

Pronotum: There exists a great range of various modifications of pronotum in the Lycidae, which are willingly used for higher taxonomic purposes. They all may be congested, however, to different modifications of such discal structures, as the median longitudinal carina, transverse carina, and marginal carinae. The anterior area, typically inflated to receive the base of the head, in most cases bears noticeable rugulosity or porosity, sometimes transformed into a more or less defined row of four areolae (as in *Metriorrhynchus* or *Platycis*). The posterior area often has inconspicuous additional pair of swollen curved ribs, at most attaining the sides of the median cell (*Taphomimus* Kazantsev).

The median longitudinal carina may be complete and undivided (*Calopteron*) or divided, forming a median cell, from very narrow (*Scarelus*) or occupying only basal half (*Leptolycus*, *Conderis*, *Metriorrhynchus*) to relatively broad and long, attaining both anterior and posterior margins (*Dexoris*, *Dictyoptera*, etc.). The me-

dian longitudinal carina may also be vestigial, represented by a short carina anteriorly, sometimes accompanied by an incomplete and obscure cell posteriorly (*Lycostomus*, *Plateros*, etc.).

The transverse carina may be complete, emerging from lateral margins slightly anterior of the posterior pronotal angles and reaching the median longitudinal structure (either carina or cell) (*Dexoris*, *Dictyoptera*); it may also be vestigial, conspicuous only near the lateral margins (*Eropterus*) or totally obsolete (*Lycostomus*, *Calopteron*). The pronotal margins may be swollen (*Calochromus*) or explanate along the edge (*Platerodrilus*, *Lycostomus*). In certain lycid taxa all carinae and cells are represented merely as folds and depressions (*Calochromus*, *Lygistropterus*).

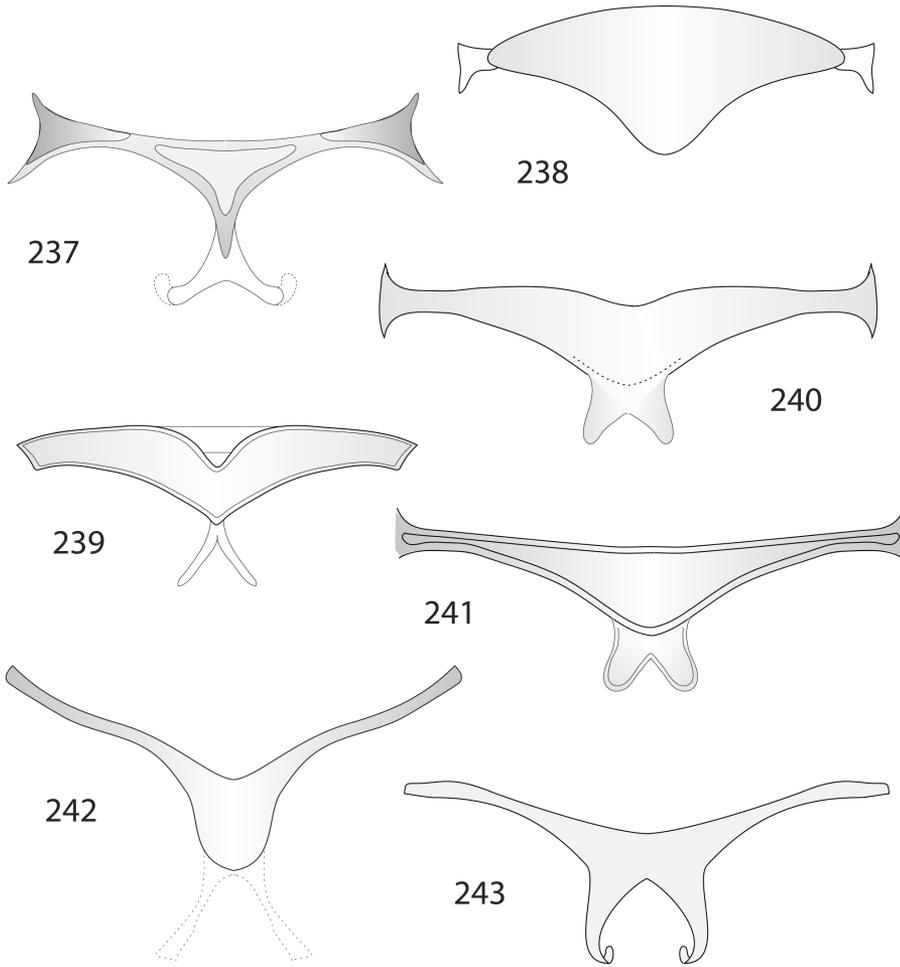
- Plesiomorphic condition of pronotal structures is unknown.

Prosternum: The prosternum is usually medially short and Y-shaped, but may be triangular and relatively long (in *Lyroneces*, Fig. 238 and *Leptolycus*), and may also be in somewhat intermediate condition (*Scarelus*, *Calochromus*, Figs 239, 240). The anterior margin, being typically concave (e.g. Figs. 244-248) may be almost straight, as in *Aferos* (Fig. 249) or convex, as in *Lyroneces* (Fig. 238). The intercoxal process is usually short, bifurcated posteriorly, its furca usually less sclerotized, its apices concealed internally under the membrane (e.g. Figs 243-249). It can sometimes lie completely internally (*Calopteron*, Fig. 242). The intercoxal process may sometimes be absent altogether (*Lyroneces*, Fig. 238). In some taxa, i.e. *Lycostomus*, *Lyroneces*, *Mesolycus* (Figs 237, 238, 254), the prosternum is conspicuously divided into the median part (the prosternum proper) and sternopleural processes connecting it with the hypomeron; in the latter taxon the prosternum proper is also divided by sutures into a median and two lateral sclerites (Fig. 254). The hypomeral process is absent, which makes the coxal cavities open. The intercoxal process, when present, does not have any articulation to the coxae.

- The absence of intercoxal process is deemed plesiomorphic.
- The absent hypomeral process is considered plesiomorphic.
- The absence of articulation between the coxae and the intercoxal process is deemed plesiomorphic.
- The prosternum with differentiated median part is considered primitive, this character not reported before in the Coleoptera (Crowson, 1981: 33).
- Plesiomorphic condition of the prosternum proper, i.e. its division into three sclerites (this character not reported before in the Coleoptera either) vs. undivided condition, is unknown.

Mesothorax: The mesothorax in Lycidae is divided into the mesonotum, mesoventrite, mesotrochantin and mesopleuron; the latter is subdivided into the mesepisternum and mesepimeron. The mesothorax is attached to the metathorax both medially, in the posterior portion of the mesoventrite, and laterally, where the mesepimeron meets the anterolateral projection of the metaventrite (Figs 207-214, 216-226). The only exception is *Dexoris*, where the latter attachment is achieved by means of a separate process (Figs 215, 298). The attachment between the same two sclerites is achieved by a narrow projection of the marginal sulcus of the metaventrite in *Lyroneces*, *Ceratoprion* and *Mesolycus* (Figs 295, 296, 591).

The mesotrochantin is free, except being attached proximally to the pleuron and distally to the coxa, and typically similar to the prothoracic trochantin (e.g. *Dictyoptera*, Fig. 211), though in a number of lycid taxa, i.e. *Dexoris*, *Lycinella*, *Scarelus*, *Ceratoprion*, etc. as well as in *Cantharis* and *Phengodes*, it is conspicuously

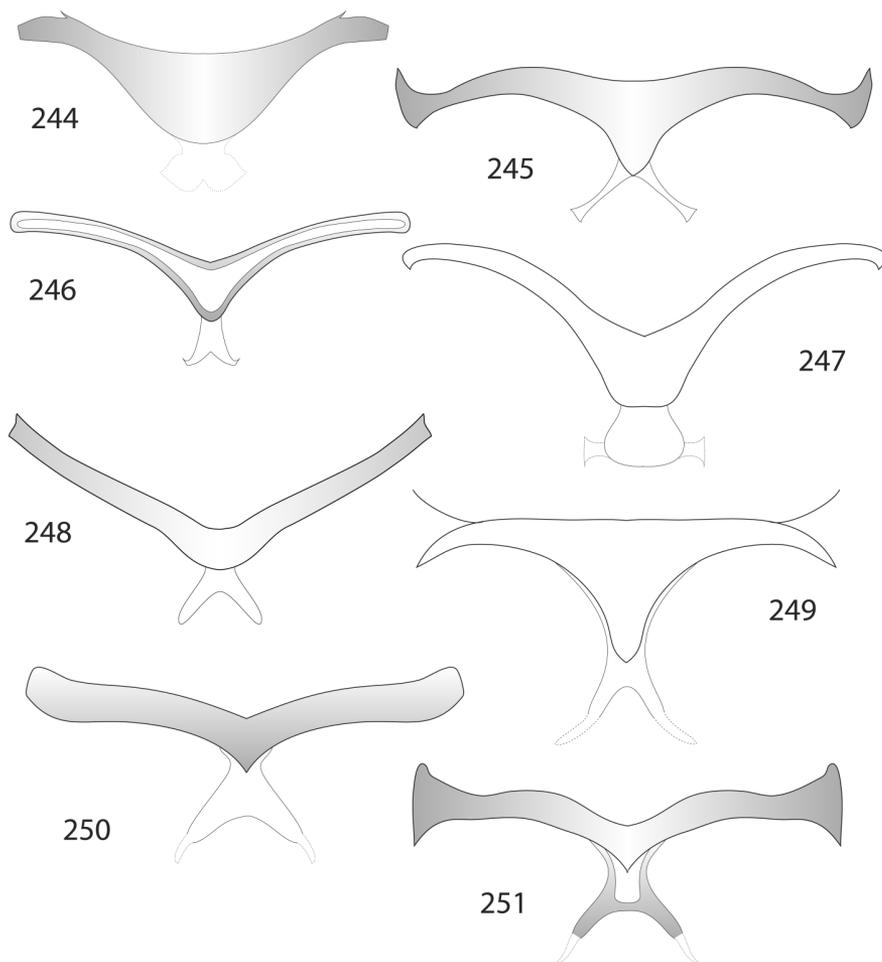


Figs 237-243: Imaginal prosternum, ventral view: *Lycostomus praeustus* (Fabricius) (237); *Lyronectes optabilis* (Kleine) (238); *Scarelus umbrosus* Kleine (239); *Calochromus glaucopterus* (Guerin-Meneville) (240); *Dictyoptera aurora* (Herbst) (241); *Calopteron reticulatum* (Fabricius) (242); *Platerodrilus* sp. (243).

smaller (Figs 215, 218, 219, 224, 230), while in *Thilmanus* conspicuously larger than the prothoracic trochantin (Fig. 226).

- The presence of a separate process connecting the mesepimeron and the metaventrite is hypothesized to be a primitive condition.

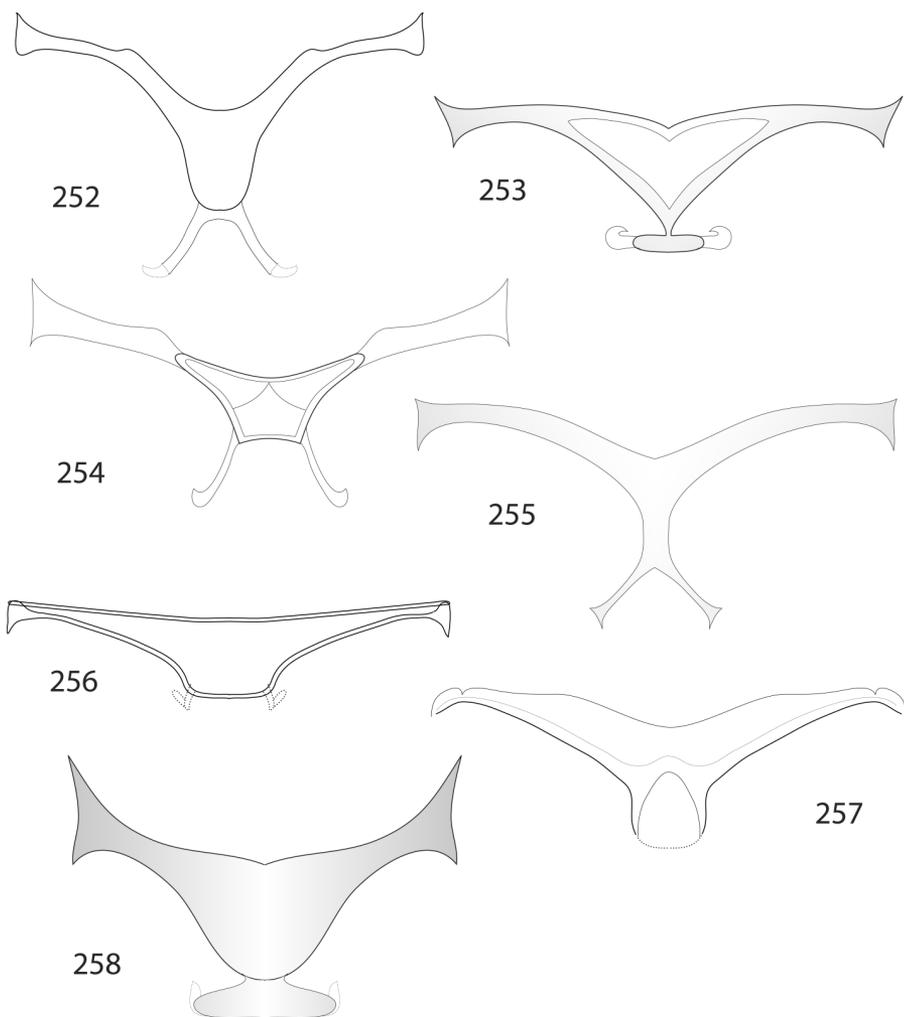
- Indication that in the Archostemata the mesothorax does not meet the metathorax (Crowson, 1981; Kukulova-Peck & Lawrence, 2004; Fig. 232) has not been confirmed, as these two structures were found to be rigidly attached to each other medially dorsad of (under) the mesocoxae, with the coxal cavity mechanically closed, being bordered posteriorly by the metasternal carina that also penetrates between the mesocoxae as the posterior intercoxal process (*Tenomerga*, Fig. 233). Indication of occurrence of a similar condition in Scirtidae, Derodontidae and some



Figs 244-251: Imaginal prosternum, ventral view: *Dexoris tessmani* Bocák & Bocáková (244); *Plateros flavoscutellatus* Blatchley (245); *Helcophorus miniatus* Fairmaire (246); *Lycinella parvula* Gorham (247); *Metriorrhynchus thoracicus* (Fabricius) (248); *Aferos* sp. (249); *Conderis signicollis* (Kirsch) (250); *Macrolycus flabellatus* (Motschulsky) (251).

other Polyphaga (Lawrence, 1999; Kukalova-Peck & Lawrence, 2004) therefore needs reexamination.

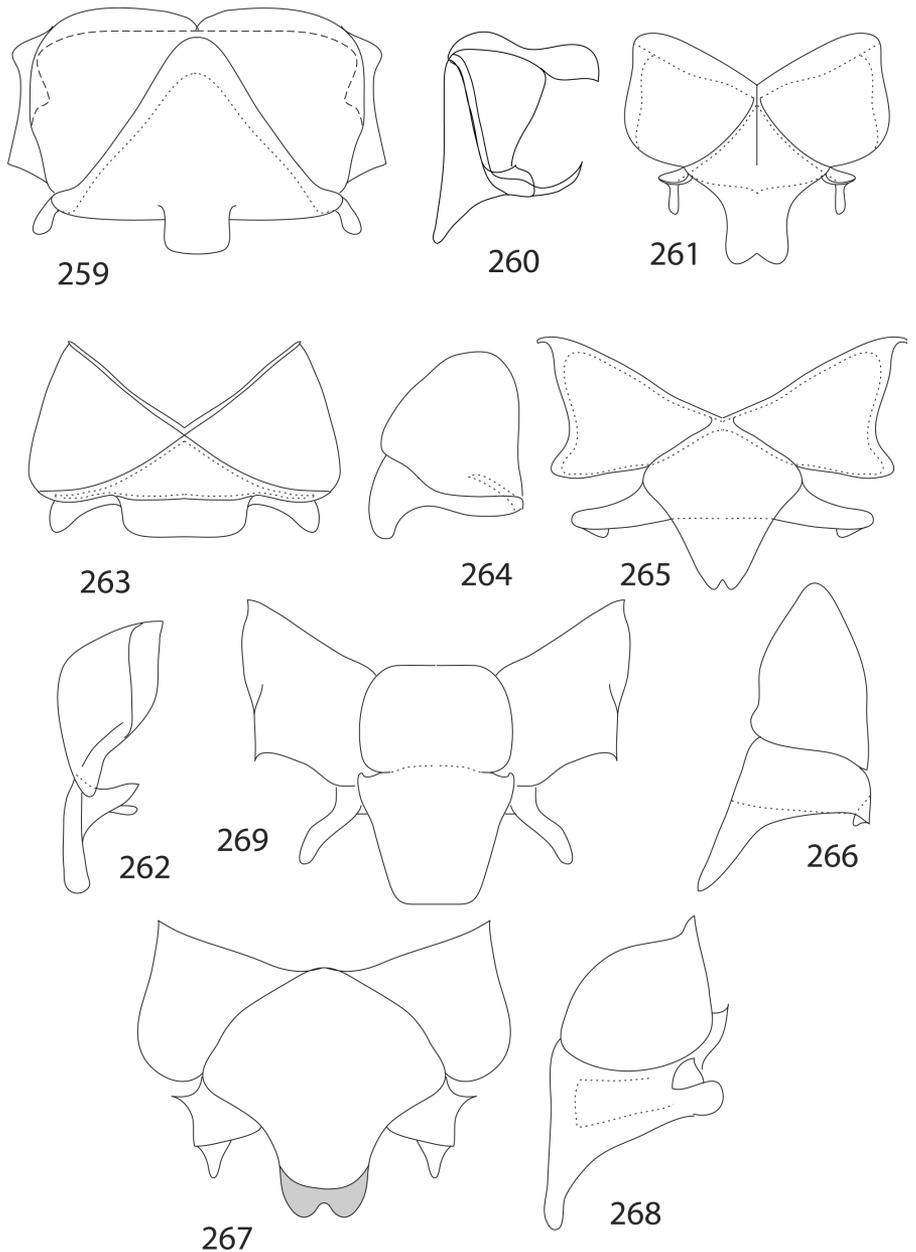
Mesonotum: In the majority of Lycidae the mesoscutum is divided by the scutellum into two separate halves (e.g. *Dexoris*, *Lycinella*, *Macrolycus*, *Mesolycus*, etc., also *Cantharis*, Figs 272, 275, 276, 285, 590), with the scutellum making a significant portion of the anterior margin of scutum in *Lyroneces* and *Platerodrillus* (Figs 265, 269). On the other hand, in some taxa the scutellum does not reach the anterior margin and the scutum is divided anteriorly into two contiguous parts by a median suture (*Calopteron*, *Caenia*, *Plateros*, Figs 270, 274, 280). Each half of the mesoscutum is divided into two sclerites by a transverse intrascutal suture in *Dexoris*,



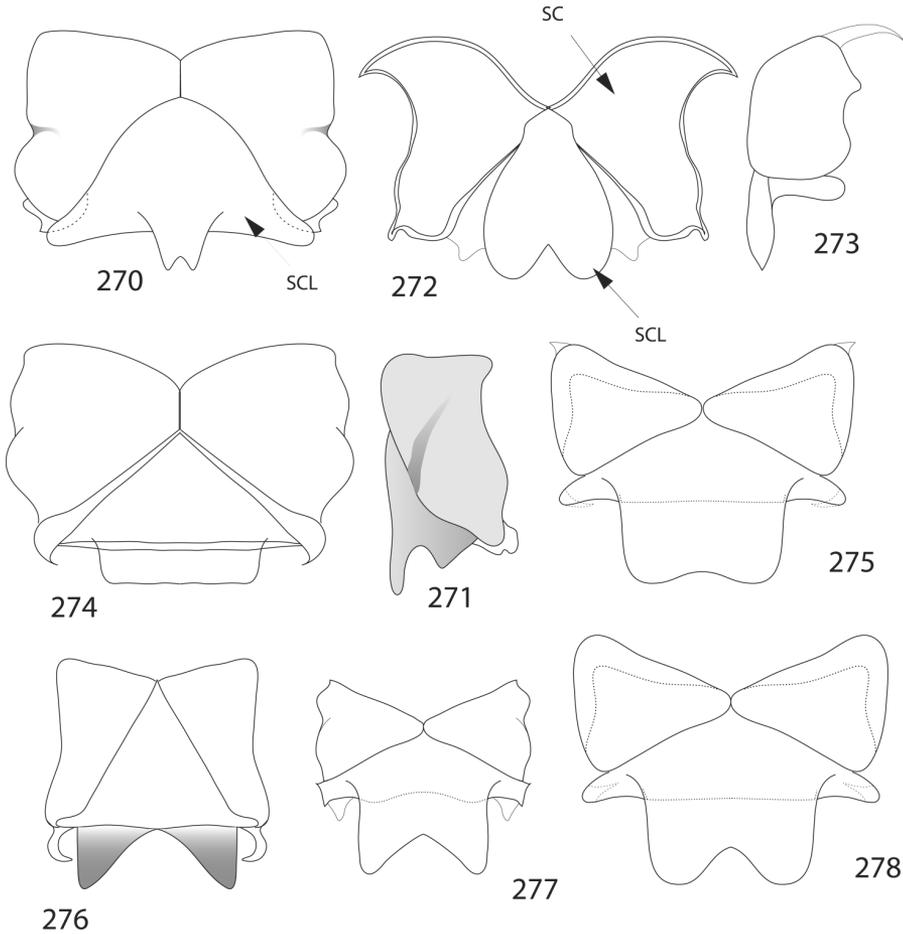
Figs 252-258: Imaginal prosternum, ventral view: *Caenia kirschi* Bourgeois (252); *Taphes brevicollis* Waterhouse (253); *Mesolytus shelfordi* (Bourgeois) (254); *Ceratoprion* sp. (255); *Lampyris* sp. (256); *Cantharis fusca* Linnaeus (257); *Phengodes* sp. (258).

Ceratoprion, *Thilmanus* and *Lampyris* (Figs 272, 279, 281, 283). The mesoscutum and the mesoscutellum appear fused in *Phengodes* (Fig. 282), with only sutures demarcating bases of the latter sclerite. It is also noteworthy that in some taxa the anterior margin of the mesonotum is almost straight (e.g. *Lycostomus*, *Calopteron*, Figs 259, 270), whereas in most of the Lycidae it is conspicuously incised.

In addition to serving as a lid in the notch at the base of elytra, the posterior process of the scutellum functions as a latch to assist holding the elytra in place. In some taxa, however, this function is obviously very primitive or absent (*Caenia*, *Calopteron*, *Lyroneces*, *Ceratoprion*, Figs 270, 280, 338, 342, 344), with the process vestigial. In certain lycids, on the other hand, the scutellum almost perfectly fits in



Figs 259-269: Imaginal mesoscuta: *Lycostomus praeustus* (Fabricius), dorsal view (259); same, lateral view (260); *Dictyopectera aurora* (Herbst), dorsal view (261); same, lateral view (262); *Calochromus glaucopterus* (Guerin-Meneville), dorsal view (263); same, lateral view (264); *Lyroneces optabilis* (Kleine), dorsal view (265); same, lateral view (266); *Scarelus umbrosus* Kleine, dorsal view (267); same, lateral view (268); *Platerodrilus* sp., dorsal view (269).



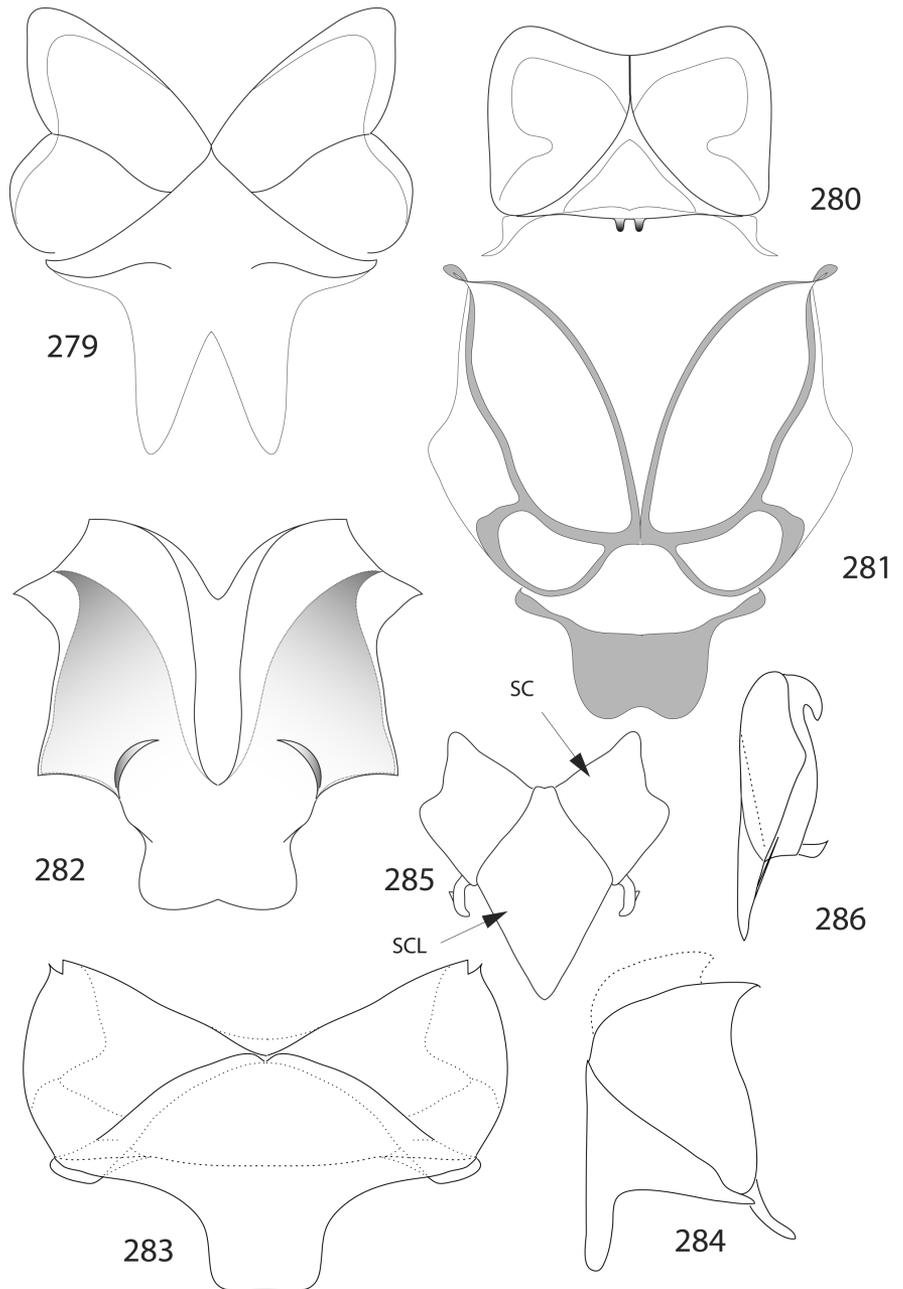
Figs 270-278: Imaginal mesoscuta: *Calopteron reticulatum* (Fabricius), dorsal view (270); same, lateral view (271); *Dexoris tessmani* Bocák & Bocáková, dorsal view (272); same, lateral view (273); *Plateros flavoscutellatus* Blatchley, dorsal view (274); *Macrolycus flabellatus* (Motschulsky), dorsal view (275); *Lycinella parvula* Gorham, ventral view (276); *Metriorrhynchus thoracicus* (Fabricius), dorsal view (277); *Conderis signicollis* (Kirsch), dorsal view (278).

SC - scutum; SCL - scutellum.

or at least almost completely covers the elytral notch (e.g. *Calochromus*, Fig. 263, 337). In *Lampyris* the elytral notch is closed completely (Fig. 345).

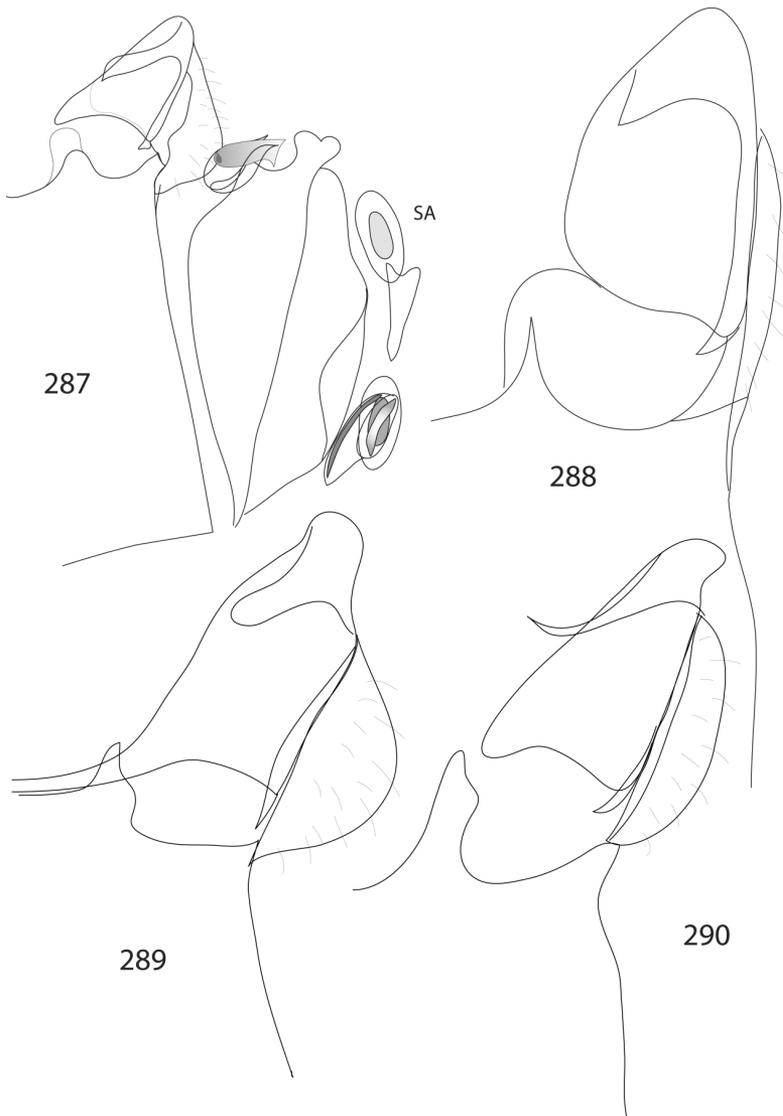
Branham and Wenzel (2003) signal membranous scutellum in cantharoid taxa belonging in the family Telegeusidae (*Telegeusis* and *Pseudotelegeusis*); however, the examination of a *Telegeusis* sp. from Costa Rica has not shown any derivation of its scutellum from a normally sclerotized condition.

- The well-defined mesoscutellum and the absence or vestigial condition of its posterior process is considered a primitive condition.
- Considerable elytro-scutellar dehiscence is considered plesiomorphic.



Figs 279-286: Imaginal mesoscuta: *Ceratoprion* sp., dorsal view (279); *Caenia kirschi* Bourgeois ventral view (280); *Thilmanus obscurus* (Baudi), dorsal view (281); *Phengodes* sp., dorsal view (282); *Lampyrus* sp., ventral view (283); same lateral view (284); *Cantharis fusca* Linnaeus, dorsal view (285); same, lateral view (286).

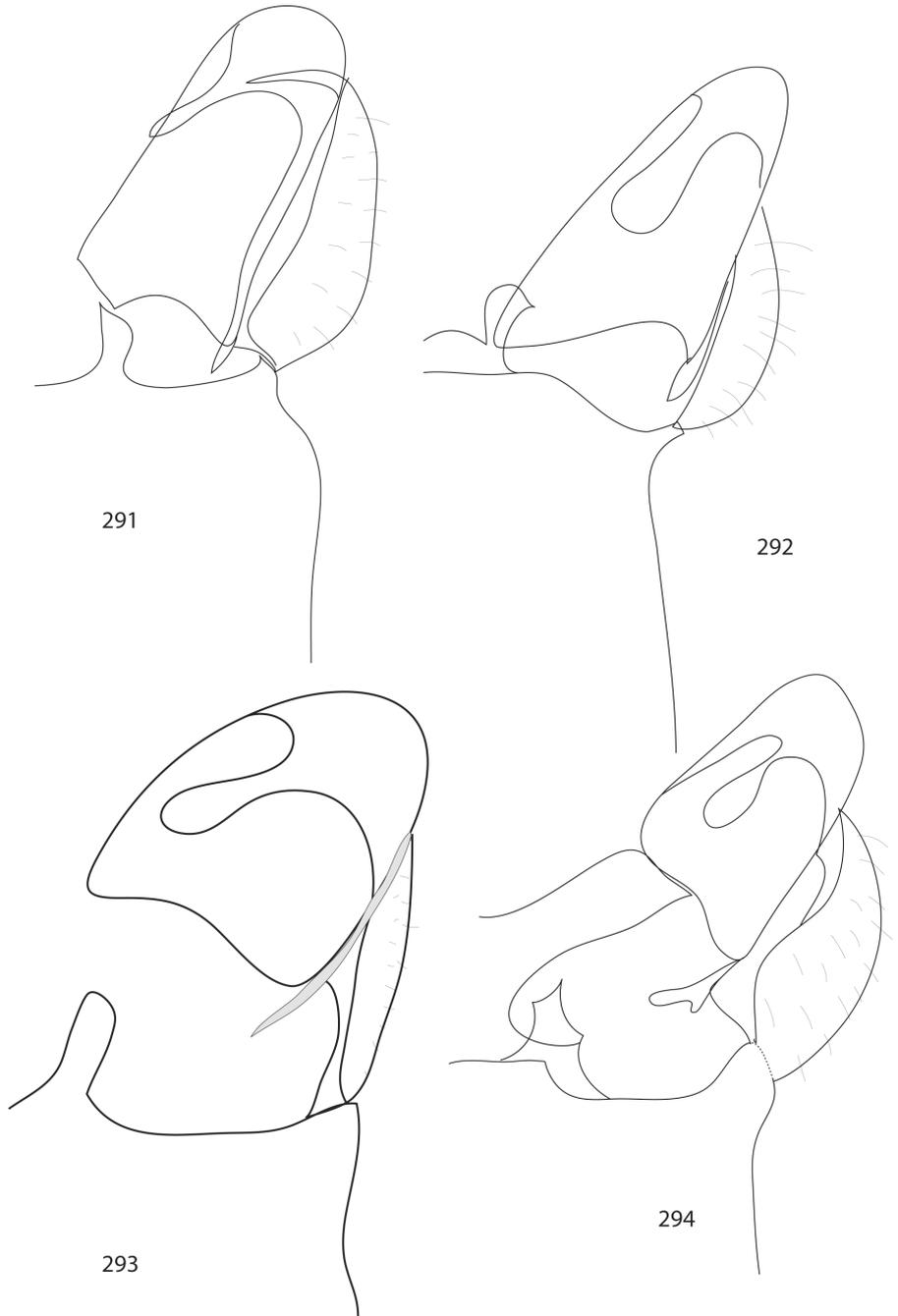
SC - scutum; SCL - scutellum.



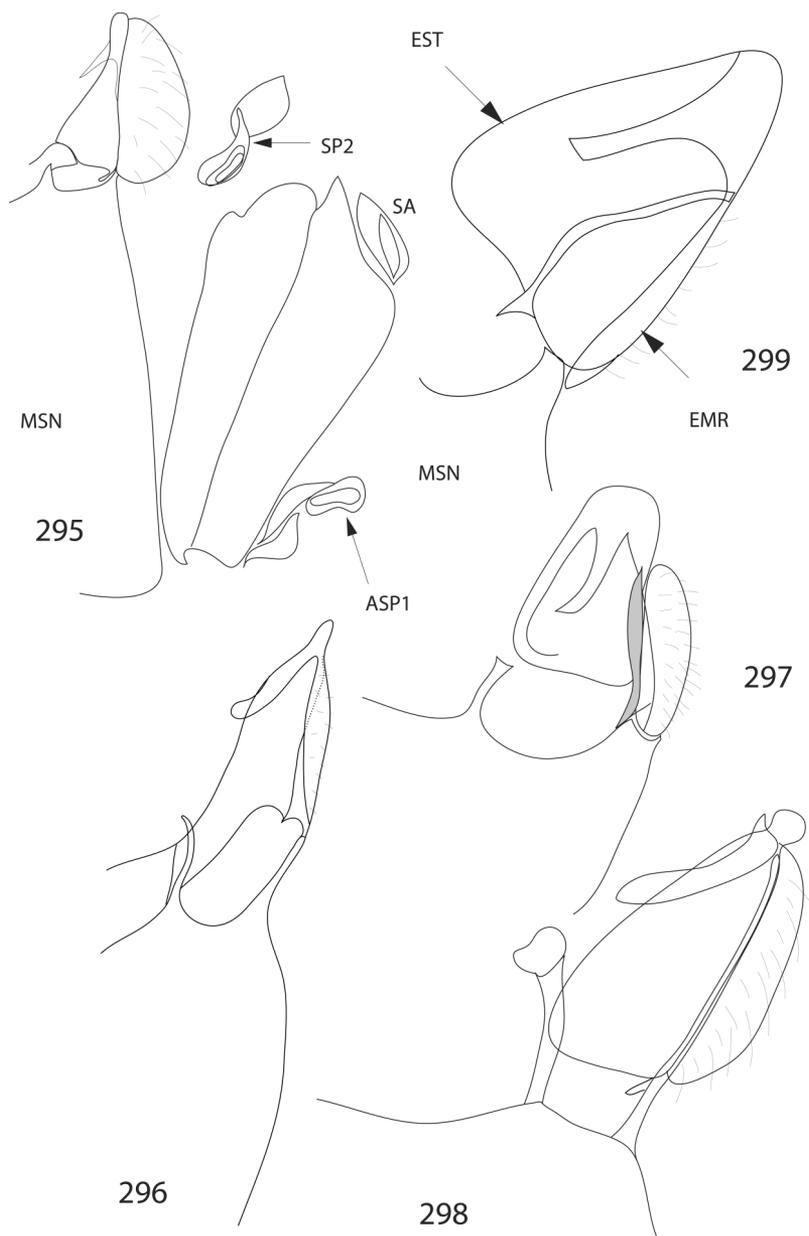
Figs 287-290: Imaginal thoracic structures, interior view: *Lycostomus praeustus* (Fabricius), mesepisternum, mesepimeron and metathoracic sclerites (287); *Calochromus glaucopterus* (Guerin-Meneville), mesepisternum, mesepimeron and fragment of metasternum (288); *Platerodrilus* sp., mesepisternum, mesepimeron and fragment of metasternum (289); *Scarelus umbrosus* Kleine, mesepisternum, mesepimeron and fragment of metasternum (290).

SA - subalare.

Mesopleuron: The mesepisternum is elongate and rigidly connected to the mesepimeron and mesoventrite. The mesepimeron is reflexed in all Lycidae and *Lampyris*, being attached only to the mesepisternum anteroventrally and to the metasternal projection posteriorly (e.g. Figs 287- 301). It may be as long as the mesepisternum and not extending beyond the base of the latter sclerite (*Lyroneces*,

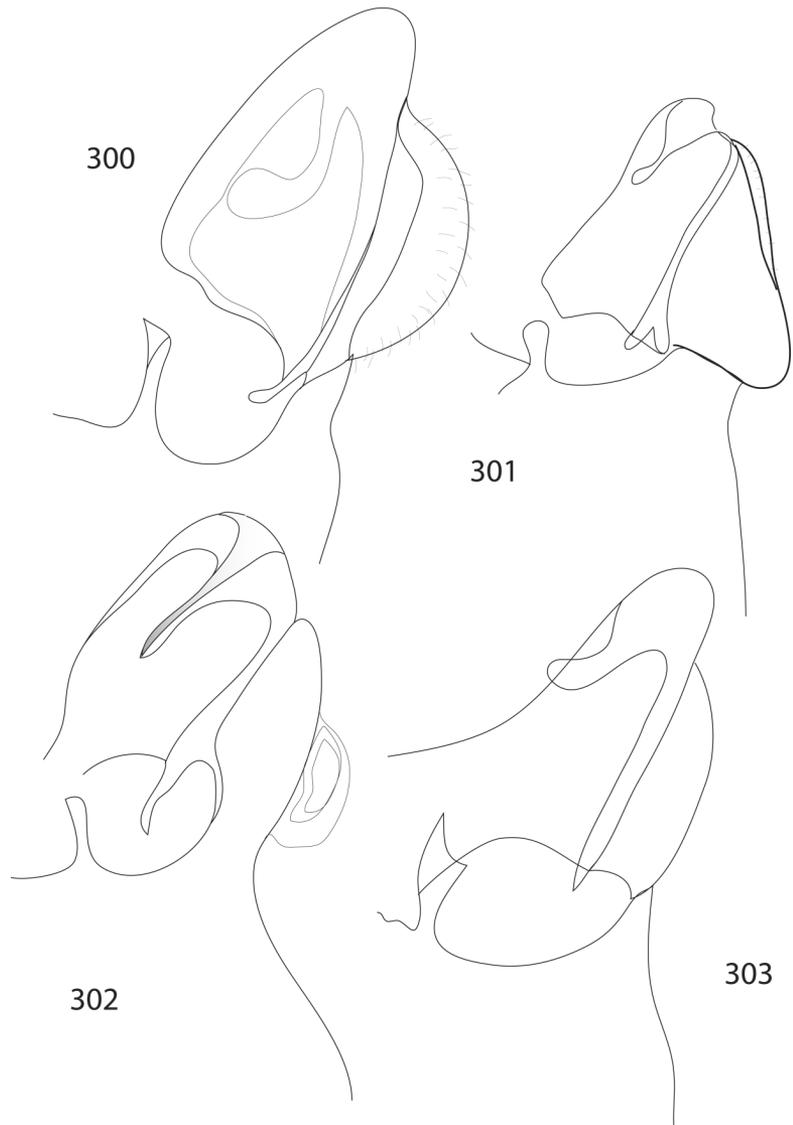


Figs 291-294: Imaginal mesepisternum, mesepimeron and fragment of metasternum, interior view: *Dictyopectera aurora* (Herbst) (291); *Lycinella parvula* Gorham (292); *Metriorrhynchus thoracicus* (Fabricius) (293); *Macrolycus flabellatus* (Motschulsky) (294).



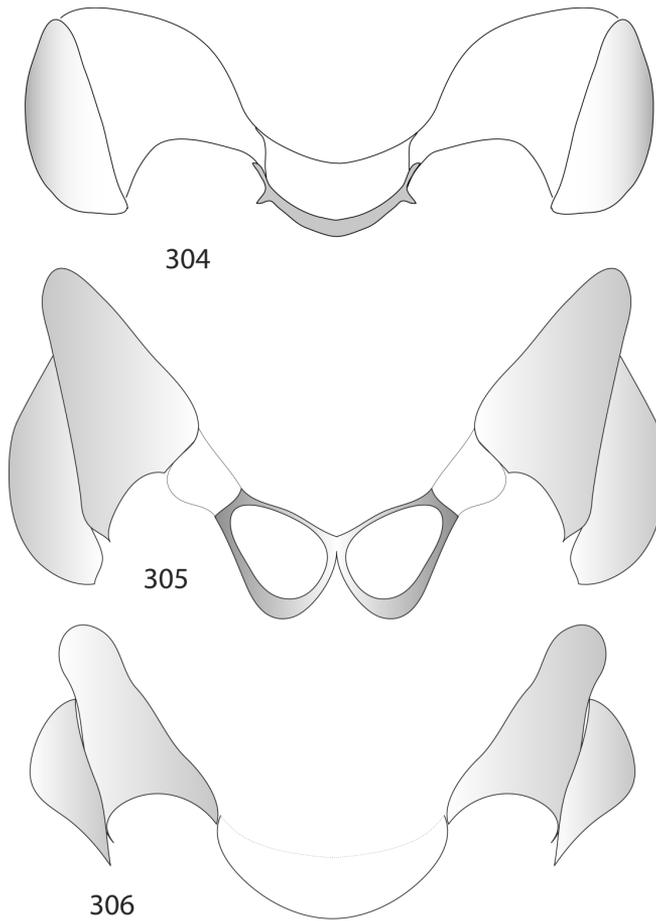
Figs 295-299: Imaginal thoracic structures, interior view: *Lyroneces optabilis* (Kleine), mesepisternum, mesepimeron and metathoracic sclerites (295); *Ceratoprion* sp., mesepisternum, mesepimeron and fragment of metasternum (296); *Calopteron reticulatum* (Fabricius), mesepisternum, mesepimeron and fragment of metasternum (297); *Dexoris tessmani* Bocák & Bocáková, mesepisternum, mesepimeron and fragment of metasternum (298); *Plateros flavoscutellatus* Blatchley, mesepisternum, mesepimeron and fragment of metasternum (299).

ASP - abdominal spiracle; EMR - epimeron; EST - episternum; MSN - metasternum; SA - subalare; SP- thoracic spiracle.



Figs 300-303: Imaginal mesepisternum, mesepimeron and fragment of metasternum, interior view: *Caenia kirschi* Bourgeois (300); *Lampyris* sp. (301); *Phengodes* sp. (302); *Cantharis fusca* Linnaeus (303).

Ceratoprion, *Dexoris*, Figs 295, 296, 298), or shorter than the mesepisternum, but extending beyond the base of the latter sclerite (as in most of lycid taxa, e.g. *Calopteron*, *Metriorrhynchus*, Figs 293, 297). The lycid mesepimeron is typically broadly folded and pubescent on the dorsal side of the fold (Figs 287-300, 591), being very narrowly folded in *Lampyris* (Fig. 301). The fold may occupy the entire width of the sclerite (*Lyroneces*, *Dexoris*, Figs 295, 298) or be considerably less than its half (*Plateros*, Fig. 299), this character obviously correlated with the relative



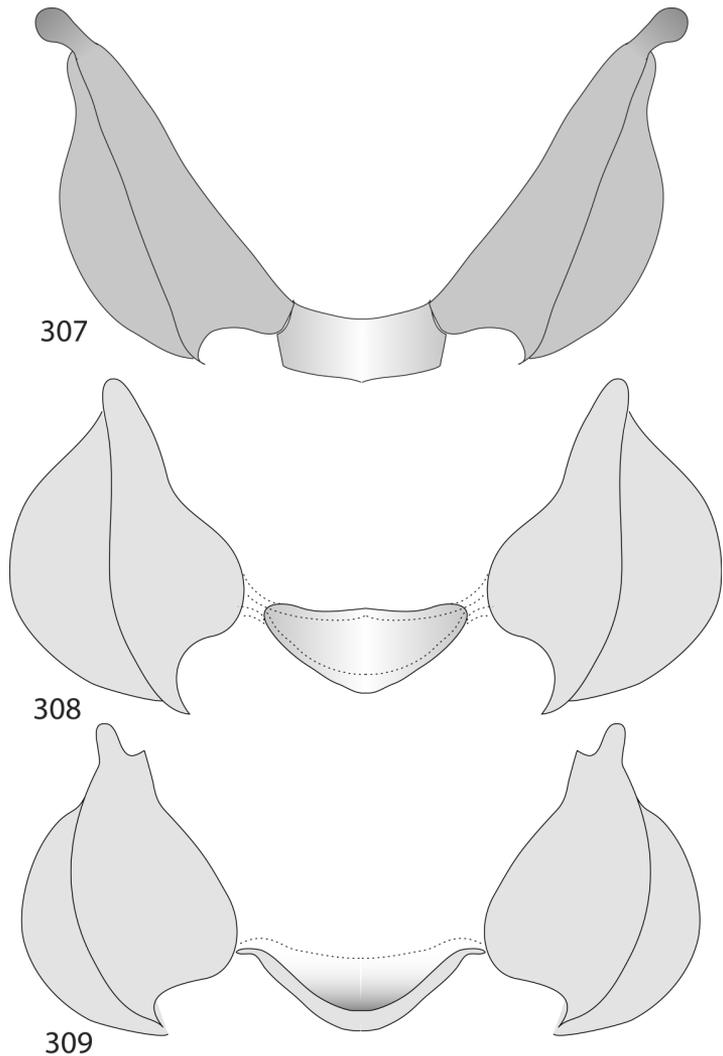
Figs 304-306: Imaginal mesothorax, ventral view: *Lycostomus praeustus* (Fabricius) (304); *Caenia kirschi* Bourgeois (305); *Taphes brevicollis* Waterhouse (306).

mesepimeral length and its position with respect to the mesepisternum. The subalare is separate and noticeable, the basalare apparently fused to the mesepisternum.

In *Lampyrus*, *Phengodes* and *Cantharis* the weakly (*Lampyrus*) or not folded mesepimeron is the only part of the mesopleuron separated by a suture from the mesoventrite (Figs 301-303).

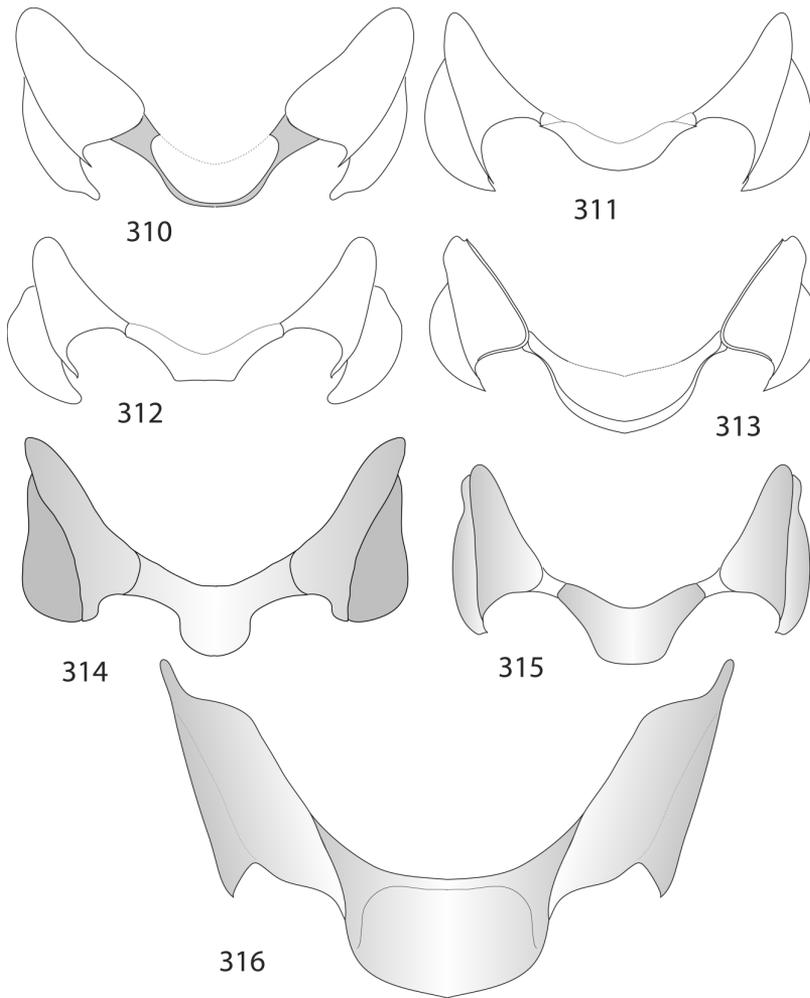
- Broadly folded mesepimeron, not succumbing to the mesepisternum in length and not extending beyond the base of the latter sclerite, with the fold occupying its entire width, is deemed primitive, as the extension of the mesepimeron, which is correlated with the rest of the above characters, seems to represent a step towards a more derived connection between the mesothorax and the metathorax, which in its turn is considered a derived condition.

Mesoventrite: The mesoventrite (the true mesosternum being totally invaginated, forming the endosternites - Campau, 1940; Ferris, 1940, Beutel & Hass, 2000,



Figs 307-309: Imaginal mesothorax, ventral view: *Dexoris tessmani* Bocák & Bocáková (307); *Lyroneces optabilis* (Kleine) (308); *Scarelus umbrosus* Kleine (309).

Lawrence, 1999) in Lycidae is coadapted with and directly attached to the metaventricle (with the exception of *Calopteron*, in which it is attached thereto by means of an intermediate process, Figs 210, 319) and is separated from the mesopleuron by a suture. In general, the mesoventrite shows greater variability than the prosternum and the metaventricle. In some cases (*Lyroneces*, *Caenia*, *Plateros*, Figs 305, 308, 315) the mesoventrite and the mesopleuron are separated by a sternopleural process. In some taxa (e.g. *Metriorrhynchus*, *Caenia*, Figs 305, 318) the mesoventrite appears subdivided into two sclerites; while in *Thilmanus* (Fig. 321) it is divided into two parts by a median suture. Sometimes the mesoventrite is

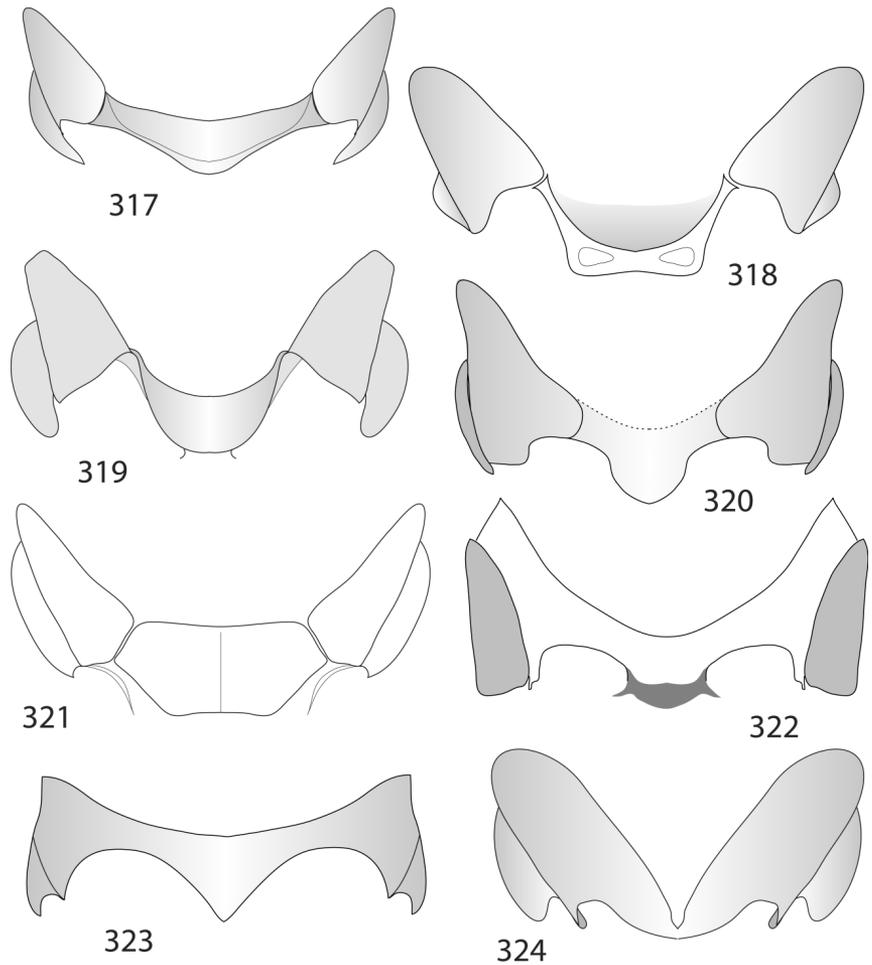


Figs 310-316: Imaginal mesothorax, ventral view: *Aferos* sp. (310); *Conderis signicollis* (Kirsch) (311); *Macrolycus flabellatus* (Motschulsky) (312); *Helcophorus miniatus* Fairmaire (313); *Dictyoptera aurora* (Herbst) (314); *Plateros flavoscutellatus* Blatchley (315); *Ceratoprion* sp. (316).

confined to a narrow process, with the anterior area gradually losing sclerotization (*Scarelus*, *Helcophorus*, *Taphes*, *Metriorrhynchus*, Figs 306, 309, 313, 318). The relative size of the mesoventrite in *Dexoris* and *Lyroneces* (Figs 307, 308) is considerably smaller than that in other lycids. No grooves or other cavities to receive the posterior prosternal process are noticeable in lycid mesoventrite .

In *Lampyris*, *Phengodes* and *Cantharis* the mesoventrite includes the mesepisternum that is fused to it without any noticeable suture (Figs 322, 323, 324).

- The small non-coadapted mesoventrite is deemed primitive;
- Presence of a sternopleural process connecting the mesoventrite and the mesopleuron is considered a plesiomorphy.

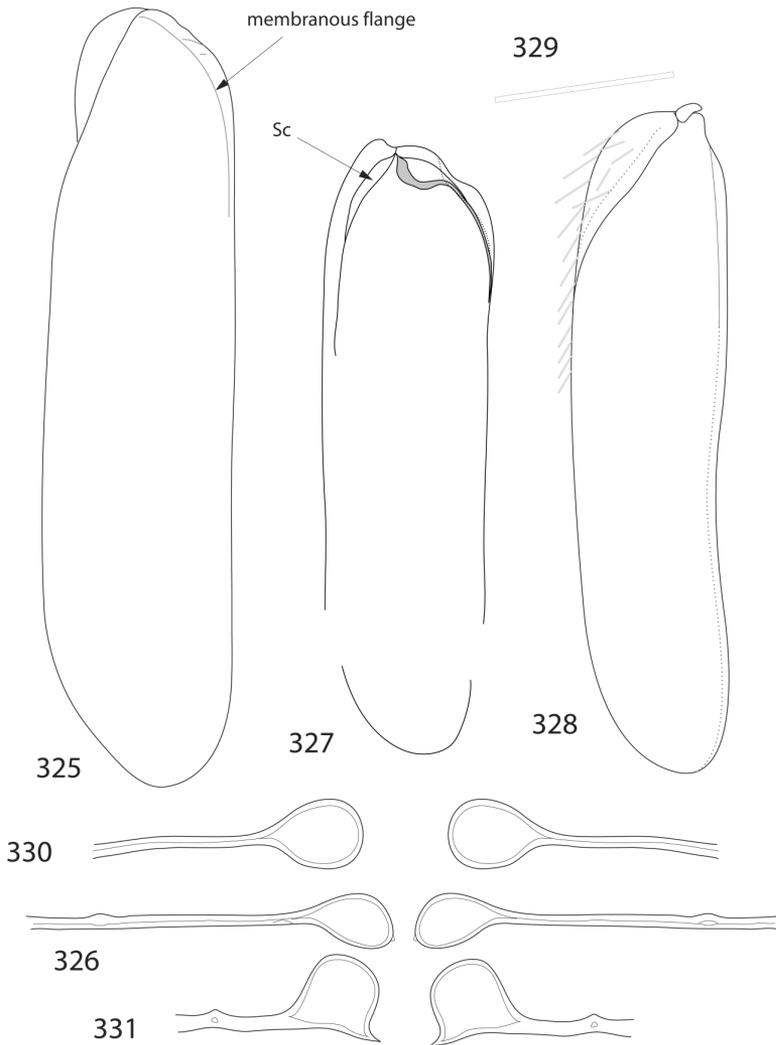


Figs 317-324: Imaginal mesothorax, ventral view: *Lycinella parvula* Gorham (317); *Metriorrhynchus thoracicus* (Fabricius) (318); *Calopteron reticulatum* (Fabricius) (319); *Calochromus glaucopterus* (Guerin-Meneville) (320); *Thilmanus obscurus* (Baudi) (321); *Lampyris* sp. (322); *Cantharis fusca* Linnaeus (323); *Phengodes* sp. (324).

- Another possible plesiomorphy is the division of the mesoventrite by a medial suture.

Elytron: Apart from being sometimes absent in females that are almost completely larviform, the elytra in the Lycidae, especially in males, are very rarely noticeably reduced. The only known example is *Alyculus* from Borneo, in which the elytra of a male are only slightly extending beyond the thoracic segments; the unfolded hind wings in this genus considerably extend from under the elytra and lie on the abdomen, significantly surpassing its length.

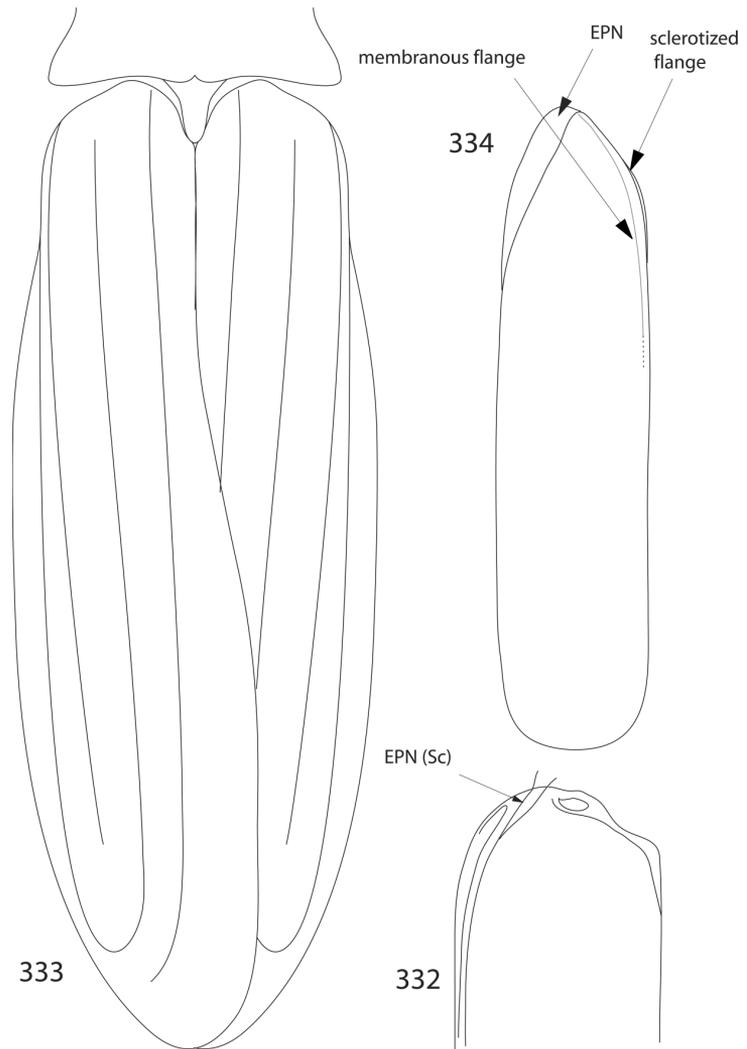
Co-adaptation: in Lycidae the elytra are not coadapted with the thoracic and abdominal structures. The ventral surface of the lycid elytron is never modified to



Figs 325-331: Elytral structures: *Lycostomus praeustus* (Fabricius), right elytron, ventral view (325); same, suture area at middle, transverse section (326); *Metriorrhynchus thoracicus* (Fabricius), right elytron, ventral view (327); *Dexoris tessmani* Bocák & Bocáková, right elytron, ventral view (328); same, elytral seta (329); same, suture area at middle, transverse section (330); *Dictyoptera aurora* (Herbst), suture area at middle, transverse section (331).

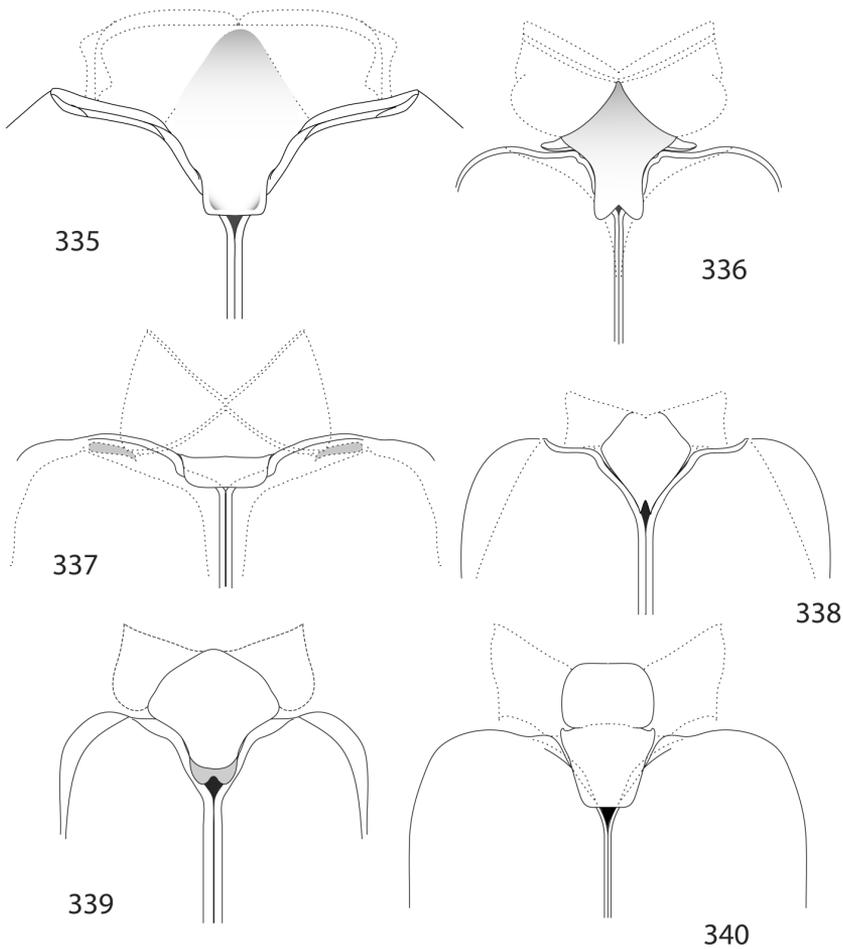
Sc - vein Sc.

ensure locking of the elytra on dorsal surface of the abdomen. Typically there is a basal membranous flange in the scutellar area (Figs 325, 327, 328), whereas the similar structure in *Cantharis* is equipped with heavily sclerotized flange coadapted to the scutellum (Fig. 334). Similarly, the suture margin is not (*Dexoris*, Fig. 330) or is little modified to ensure locking of the elytra together; in case there is a flange it is always membranous, and never dove-tailed (*Lycostomus*, *Dictyoptera*, Figs



Figs 332-334: Elytral structures: *Aferos* sp., elytral base, ventral view (332); *Lygisteropterus* sp. (Bolivia), elytra, dorsal view (333); *Cantharis fusca* Linnaeus, right elytron, ventral view (334). EPN - epipleuron; Sc - vein Sc.

326, 331) and it seldom attains to the apices of the elytra, typically hardly extending beyond the scutellar area. The taxa where this flange may be more developed include *Lycostomus*, *Dictyoptera*, *Platycis*, etc.; the ones where the flange is absent or limited to the scutellar area are *Dexoris*, *Lyroneces*, *Platerodrilus*, *Scarelus*, some *Lycostomus*, *Macrolycus*, etc. It is noteworthy that development of this flange is sometimes variable within a single genus, for example, in *Lycostomus praeustus* this flange attains almost to the elytral apex, while in *L. porphyrophorus* (Solsky) it does not go far beyond the scutellar area. In *Cantharis* this flange, attaining to the elytral apex, is heavily sclerotized and dove-tailed, ensuring secure attachment

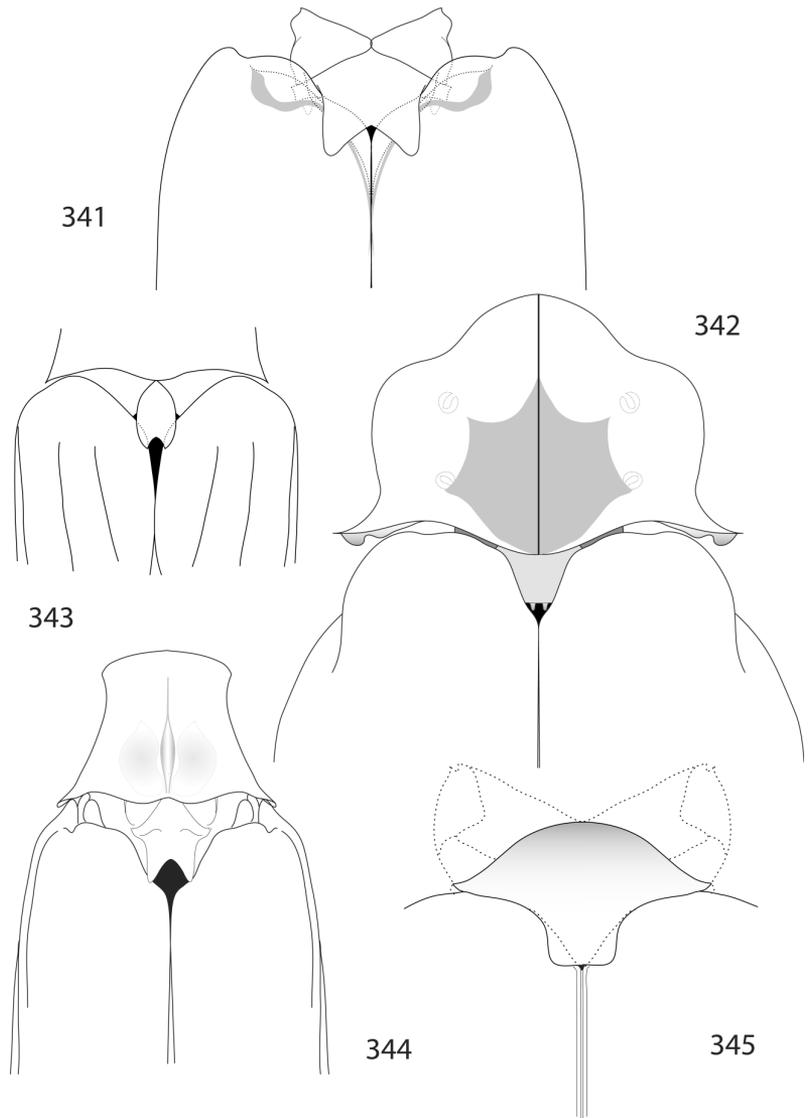


Figs 335-340: Elytra-scutellar area, dorsal view: *Lycostomus praeustus* (Fabricius) (335); *Dictyoptera aurora* (Herbst) (336); *Calochromus glaucopterus* (Guerin-Meneville) (337); *Lyronectes optabilis* (Kleine) (338); *Scarelus umbrosus* Kleine *Dictyoptera aurora* (Herbst) (339); *Platerodrilus* sp. (340).

to the other elytron. Similarly, the outer elytral margin in the Lycidae is never equipped with any ventral flanges that in other Coleoptera may be well developed (Crowson, 1981).

The elytra may be, rarely, overlapping in some lycid taxa (e.g. *Lygisteropus* Fig. 333), but are often dehiscent (e.g. *Dexoris*, Fig. 328). Their apices are sometimes acute and truncate in modified forms of *Lycus*, but typically they are independently rounded (Figs 325, 327, 328, 333). The elytral apices in rare occasions may also be thickened (e.g. in *Minidulitcola*, *Alyculus*).

The surface of the elytron may be smooth, or irregularly to regularly reticulate. The probably basic structure of reticulated elytra would be that with four primary costae numbered from the suture outwards, corresponding to tracheal trunks 1A, Cu, M and R, the 2A trachea corresponding to the sutural and the C tracheal trunk



Figs 341-345: Elytro-scutellar area, dorsal view: *Metriorrhynchus thoracicus* (Fabricius) (341); *Caenia kirschi* Bourgeois (342); *Microeron* (343); *Ceratoprion* sp. (344); *Lampyris* sp. (345).

- to the outer margin (Crowson, 1981). The vein M (primary costa 3) that is considered to be a «weak» one in Pterygota, and tends to disappear in beetle wings (Crowson, 1981), is typically (one of) the weakest in the Lycidae, but is remarkably the strongest one in the *Helcophorus* elytron, as well as in *Omma* (Cupedidae, Archostemata). The two types of a smooth elytron in the Lycidae include the tuberculate elytron of *Dexoris* and finely punctulate elytron of *Miniduliticola*; both types completely lacking any trace of longitudinal costae or striae. The transverse

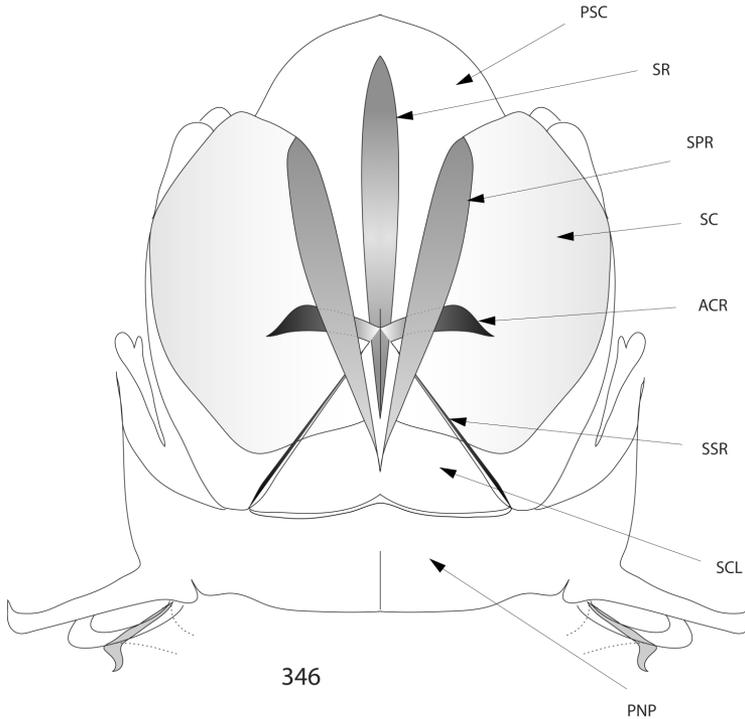


Fig. 346: *Lycostomus praeustus* (Fabricius), imaginal metanotum, dorsal view.

ACR - allocrista; PNP - postnotal plate; PSC - prescutum; SC - scutum; SCL - scutellum; SPR - scutoprescutal ridge; SR - scutellar ridge; SSR - scutoscuteellar ridge.

elytral reticulation is typically associated with the presence of suture flanges; however, there are exceptions: *Scarelus* has the absent suture flange and relatively regular transverse reticulation, whereas *Calochromus* is characterized by the opposite conditions, i.e. developed flange and absent transverse reticulation.

The epipleuron is absent in all studied taxa with the exception of *Aferos*, where it takes the form of a short basal feebly sclerotized sulcus (Fig. 332), being developed in all non-lycid taxa, including *Thilmanus*. In *Thilmanus* it is narrow and limited to the humeral area.

The epipleuron should be absent in the hypothesized primitive beetles, as it is obviously a secondary development for coadaptation of the elytra with the body. Thus the Sc trachea that is considered to be running in the epipleuron (Crowson, 1981) initially would be somewhere on the dorsal surface of the elytron, parallel to or fused to the C trachea. In the Lycidae the Sc trachea is typically fused to C, sometimes noticeable at the base of the elytra as a membranous flange (e.g. in *Metriorrhynchus*, Fig. 327).

- The non-coadapted elytron without epipleuron and with unmodified ventral surface is deemed primitive.
- The suture margin not modified to ensure the locking of elytra together is deemed plesiomorphic.
- Dehiscent elytra are considered to be in plesiomorphic condition.