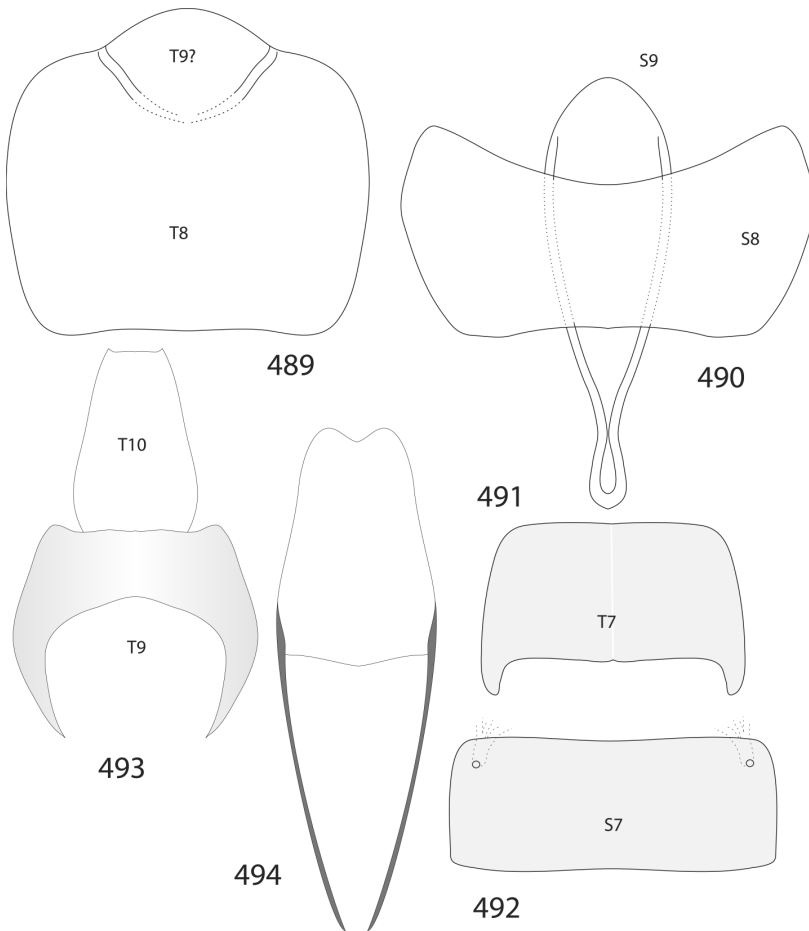Figs 480-488: Imaginal terminal male abdominal segments: *Lyroneces optabilis* (Kleine), tergites, dorsal view (480); same, ventrite, ventral view (481); *Calochromus glaucopterus* (Guerin-Meneville), tergites, dorsal view (482); same, ventrite, ventral view (483); *Calopteron reticulatum* (Fabricius), tergites, dorsal view (484), same, ventrite, ventral view (485); *Ceratoprion* sp., tergites, dorsal view (486), same, ventrite, ventral view (487), same, tergite 6, interior view (488).

Figs 489-494: Imaginal terminal male abdominal segments: *Lampyris* sp., tergite 8 (+9?), dorsal view (490); same, ventrites, ventral view (491); same, tergite 7, dorsal view (482); same, ventrite 7, ventral view (492); *Phengodes* sp., tergites, dorsal view (493), same, ventrite, ventral view (494).

S - sternite; T - tergite.

typically located between Cu$_2$ and 1A (e.g. *Eros*, *Lampyrolycus*, Figs 401, 416). In some cases it moves basally to the Cu fork, making the Cu vein appear trifurcate, as in *Autaphes*, *Eropterus* and *Lycinella* (Figs 408, 412, 414), or even further basally to connect between Cu and 1A (*Dilophotes*, *Proteros*, Figs 402, 413). *Miniduliticola* is the only known taxon where the cu-a connection is positioned at the Cu base (Fig. 409), while in *Dexoris* and *Mimolibnetis* the cu-a brace appears to have merged with the 1A vein (Figs 398, 399). All the major cubital and anal veins are almost parallel in *Eropterus* (Fig. 414).

The anal lobe is present only in *Thilmanus* (Fig. 420). Posterior and anterior edges of the hind wing are typically without fringes of long hairs, the opposite condition found in *Miniduliticola* (Fig. 409), while *Phengodes* has bristling hairs on both dorsal and ventral surfaces of the costal margin.
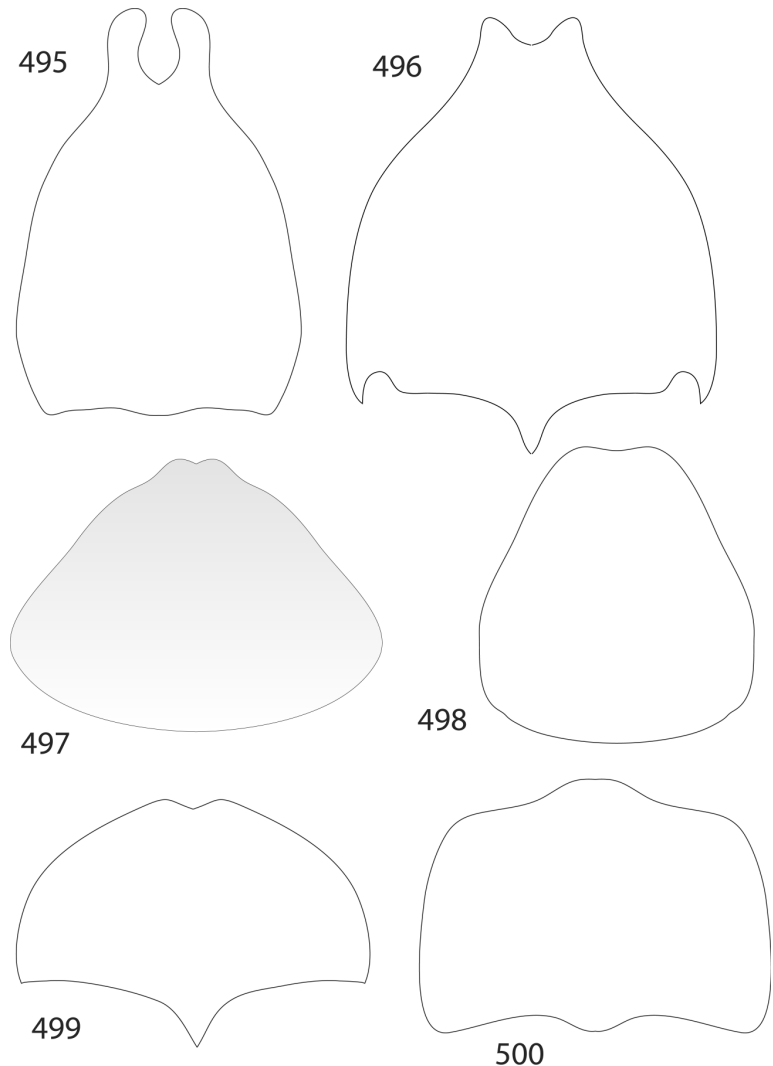
Figs 495-500: Imaginal terminal female ventrite, ventral view: *Lycostomus praeustus* (Fabricius) (495); *Macrolycus flabellatus* (Motschulsky) (496); *Calopteron reticulatum* (Fabricius) (497); *Caenia kirschi* Bourgeois (498); *Taphes brevicollis* Waterhouse (499), *Metriorrhynchus thoracicus* (Fabricius) (500).

Most of the above-mentioned features of the lycid hind wing do not refer to *Alyculus*, which has a very peculiar wing venation (Fig. 419). Its hind wing does not have cells or loops, and the few veins the wing has do not fork and hardly curve. The size of this beetle, which is 2.6 mm, is great enough to be comparable to other lycids with regular hind wing venation (e.g. 2.3 mm long *Microeron* Kazantsev or 3.1 mm *Miniduliticola*) and cannot account for such pattern. The non-folding hind wing of *Alyculus*, with RA attaining to the apex, demonstrates some parallels with the barely folded wing of *Phengodes*, while its venation pattern is similar to

Rhipiphorus (Kukalova-Peck & Lawrence, 1993). It is interesting that venation pattern of the hind wing of *Alyculus* is close to venation pattern of a typical lycid elytron, which, as it had not underwent modifications due to the evolution of a folding mechanism, may have retained some features of a primitive wing. And, as it is fairly obvious that the early Coleoptera could not have a derived hind wing folding mechanism, and development of most or many of the wing venation patterns is presumably correlated with development of such folding mechanism, there is a possibility that some of the wing venation features of *Alyculus* may be in primitive condition.

   • It is recognized that the simple wing-folding mechanism of the Cantharoidea is the most primitive in the Coleoptera (Hammond, 1979); among the Cantharoidea the Lycidae appear to have the most primitive folding pattern.

   • The primitive condition of most of the hind wing venation patterns does not appear obvious. The usually accepted views considering the coleopteran hind wing developing only in the direction of simplification (e.g. Kukalova-Peck & Lawrence, 1993) do not take into account possible polyphyly of the Coleoptera, when certain groups, such as the Polyphaga may have emerged at a stage when the insect flying wing was still developing in the opposite direction. These views are based on Kukalova-Peck's (1991) hypothesis assuming that the hind wing of the Pterygota, including the Coleoptera, evolved exclusively in the direction of oligomerization (decrease in number) of homologous organs, with the archetype pterotergum consisting of 11 sclerites, both assumptions appearing not very plausible. Among the few more or less clear primitive characters are parallel running of the C, Sc and RA veins and the anal cell closure with a transverse brace.

Articulation of the wing: The pteralia typically include the inconspicuous humeral plate, the basal sclerite, a group of axillaries and two membrane plates (e.g. *Lycostomus*, Fig. 393). A rudiment of the tegula is sometimes also present (e.g. *Lycostomus*, Fig. 393).

   • Primitive condition of pteralia is unknown.

Leg: The leg consists of the coxa, trochanter, femur, tibia and 5-segmented tarsus. In *Dexoris* and *Mimolibnetis* the trochanter is clearly divided into two parts, trochanter 1 and trochanter 2 (Fig. 429), whereas in such taxa as *Caenia*, *Ceratoprion*, *Lycostomus* or *Lampyrolycus* the trochanter has a conspicuous suture separating the basal part from the rest of the trochanter (Figs 422, 438-440); the two trochanteral segments separated by a suture are also manifest in *Lampyris* (Fig. 446). The pseudotrochanter, which in fact belongs to the femur, is noticeable in a number of lycid taxa (e.g. *Lycostomus*, *Calopteron*, *Ceratoprion*, *Caenia*, *Platerodrilus*, *Plateros*, Figs 422, 432, 433, 434, 438-440), some of them having a subdivided trochanter as well.

   The joint between the coxopodite and coxa is monocondylic, with the distal end of the trochantin attached to the coxa; joint between the coxa and trochanter 1 is dicondylic; trochanter 1, trochanter 2, if present, and femur are attached more or less rigidly; joint between the femur and tibia is dicondylic again the joint between and the tibia and the basitarsus monocondylic. *Thilmanus*, *Lampyris*, *Phengodes* and *Cantharis* have similar articulation of joints (Figs 445-448).

   Unlike in many Coleoptera, including the Archostemata, that have both sternal and pleural, including trochantinal, articulations of the pro- and mesocoxae

(Crowson, 1981: 31), the lycid imaginal pro- and mesocoxae have only pleural and trochantinal articulation.

• The single (pleural and trochantinal) articulation of the front and middle coxae, widespread in many lower Hexapoda, is considered primitive.

• Division of the trochanter into two segments, trochanter 1 and trochanter 2, is considered primitive.

Pro- and mesotrochantin: The pro- and mesotrochantins are free, setiferous, articulated proximally with the pleuron and distally with the condyle of the coxa. Indication of glabrous middle trochantins in *Calochromus perfacetus* (Say) (Calochrominae) (Branham & Wenzel, 2003) has not been confirmed.

Metatrochantin: The metatrochantin is represented in all lycids as a glabrous sclerite separated by a suture on the exterior wall of the hind coxa (Figs 449-463). Externally the metatrochantinal suture is not noticeable in *Lampyris* (Fig. 227), and may be inconspicuous in some lycid taxa (i.e. *Platerodrilus*, *Scarelus*, Figs 208, 219). It may occupy the entire anterior area of the coxa (*Dexoris*, 449), or be restricted to about half its length (e.g. *Caenia*, *Metriorrhynchus*, Figs 454, 463). In the latter case it may be more conspicuous medially (i.e. in *Lyroneces*, *Platerodrilus*, Figs 455, 457) or be located almost entirely proximally (i.e. in *Plateros*, *Metriorrhynchus*, Figs 460, 463).

As far as the metatrochantin of the Archostemata (*Priacma*, Fig. 232) is concerned, it is questionable that the sclerite usually referred to as such is a trochantin, as it is not articulated to the base of the episternum-epimeron suture, whereas the pro- and mesotrochantins are, and distally stretches beyond limits of the metacoxae; additionally, there is another sclerite, lying proximally at the anterior edge of the metacoxa, which more plausibly represents the metatrochantin (*Tenomerga*, Fig. 233). The two fused sclerites of the Archostemata lying between the metaventrite and metacoxa are quite separate from both, with the metendosternite arising from their base medially.

Pro- and Mesocoxae: The lycid pro- and mesocoxae are always elongate (Figs 422, 429, 434, etc.). The trochanteral insertion is apical with very profound membranous area in *Dexoris* (Fig. 429a) and more lateral in the rest of the taxa (e.g. Figs 430-435), with the membranous area in some of them, i.e. in *Lycostomus* and *Ceratoprion* (Figs 422, 440) more elongate, than in others. In *Phengodes* the apical insertion of the trochanter is combined with the absence of the membranous area (Fig. 447). *Dexoris* is the only lycid taxon to have the coxal suture in pro- and mesocoxae in the imaginal stage (Fig. 429a).

The pro- and mesocoxae are always separated at base, but may be contiguous distally, if their length is great enough (e.g. *Dexoris*, *Platerodrilus*, *Ceratoprion*, *Mimolibnetis*).

• Presence of the coxal suture in the imaginal pro- and mesocoxae is considered plesiomorphic.

Metacoxae: The metacoxae in Lycidae are more or less horizontal and transverse (Figs 207-225, 231); in Leptolycini the metacoxae are more oriented dorsoventrally due to the lateral compression of the metathorax. The distal end of the metacoxae may be somewhat prolonged in certain taxa (e.g. *Dexoris*, *Mesolycus*,

Mimolibnetis, Figs 215, 220, 231), which makes them appear similar to the pro- and mesocoxae of the same taxa. The metacoxae are often conspicuously longitudinally excavate to receive retracted femurs (e.g. in *Lycostomus*); however, this excavation is absent in many lycids, such as *Dexoris*, *Lampyrolycus*, *Mimolibnetis*, *Miniduliticola*, *Scarelus*, *Platerodrilus*, *Taphes*, *Helcophorus*, etc.

In addition to the trochantinal suture (discussed above in the Metatrochantin section), the metacoxa in *Dexoris, Mesolycus* and *Dilophotes* has a complete meral suture reaching margins of the coxa below the metatrochantin and on the inner wall of the coxa, contiguous with the distal opening (*Dexoris*, Fig. 449) or nearly so (*Mesolycus* and *Dilophotes*, Figs 450-453). The meron and the trochantin of the metacoxa of these taxa may be homologous with the subcoxa sensu Snodgrass (1935), the proximal part of the coxopodite forming the coxa proper. The pleural plates of the metathorax in this case are quite distinct from the subcoxae (e.g. Fig. 220), which suggests that Snodgrass's assumption (1935) that such pleural plates are derived from the subcostal parts of the leg bases is not correct. The meral suture in other Lycidae taxa, as well as in *Lampyris* and *Phengodes*, is vestigial, the meron typically represented by an upright flange near the distal opening (Figs 454-457, 460-465). The exceptions are *Ceratoprion* and *Calopteron*, in which it connects the trochantinal suture with the distal opening, being slightly prolonged in the other direction as well (Figs 458, 459).

• Though longitudinal excavation of the hind coxae is sometimes considered to be a primitive feature (Crowson, 1981), the opposite condition, the non-excavated metacoxae are here hypothesized to be primitive, as more agreeing with general morphological tendencies of the Hexapoda.

• Subdivision of the imaginal metacoxae by sutures into coxal, meral and trochantinal parts is considered plesiomorphic.

Trochanters: Trochanters are always elongate and rigidly connected to femurs. The shape of metatrochanters varies from triangular to cylindrical, and the insertion of the femur may be set off or oblique. Typically the femur insertion is set off (e.g. *Ceratoprion*, *Aferos*, Figs 436, 440), but in rare instances it may be oblique, as in *Dexoris* or *Mimolibnetis* (Figs 231, 429). In other Cantharoidea taxa, as in *Cantharis*, *Phengodes* and *Lampyris*, the femurs are inserted obliquely (Figs 446-448), but in *Thilmanus* they are set off (Fig. 445). The length of the trochanter may exceed one third (*Caenia*, *Ceratoprion*, Figs 438, 440) or, rarely, half of pertinent femur (*Leptolycus*, Fig. 430); especially long and sometimes modified, i.e. acquiring a spine distally, may be the hind trochanters (e.g. *Punicealis* Kazantsev, Fig. 431).

• Primitive condition of the trochanteral length and the type of femur insertion is unclear.

Femora and Tibiae: The femora and tibiae appear to be equally compressed, with few exceptions, for example in *Calochromus* and *Lycus*, where the femora may be considerably thicker than the tibiae. The femora are typically straight, though may have a tooth or a spine-like appendage on its internal surface (e.g. *Cavoplateros* Pic, Fig. 441), while the internal margins of the tibiae vary from straight (e.g. *Taphes*, *Caenia*, Figs 437, 438) to conspicuously sinuate (e.g. *Lycostomus*, *Aferos*, Fig. 422, 436) or bisinuate in case the femur has, as in the male of *Cavoplateros*, an elevation thereon (Fig. 441). In *Thilmanus, Phengodes* and *Cantharis* the femurs and tibiae are not compressed (Figs 445, 447-448), while in *Lampyris* they are (Fig. 446).

Tibial spurs: All lycid taxa examined, with the exception of *Ceratoprion*, *Leptolycus*, *Dexoris*, *Scarelus*, *Dilophotes* and *Mesolycus* (Figs 425, 429, 430, 440, 444), appeared to possess tibial spurs (e.g. Figs 422-424), though indication of possible absence of spurs was given by Miller for all Leptolycini (1991). The absent tibial spurs were also reported for *Leptoceletes basalis* (Leconte) (Calopterini, Lycinae) (Branham & Wenzel, 2003), while in fact this species does have them. Sometimes the tibial spurs do not exceed in length the hairs of the surrounding pubescence and are only slightly thicker (as in *Taphes*, Fig. 437; *Leptoceletes basalis*), which makes it hard to notice them. In *Scarelus*, however, they are either absent, or literally indistinguishable from the apical setation that is definitely thicker than the rest of the tibial pubescence (Figs 425-426).

The tibial spurs may be dissimilar in all tibiae, as in *Lucaina*, or just in the metatibia, as in *Neolycus* Bourgeois, while in *Calcaeron* Kazantsev (2004a) it is the protibiae that are armed with a large unpaired inner spur each (Fig. 442-443), the rest of the tibiae lacking spurs at all.

Tibial spurs have been found to be absent in *Thilmanus* and *Phengodes* (Figs 445, 447) and present in *Lampyris* and *Cantharis* (Figs 446, 448). Absent tibial spurs are also signaled for Omalisidae, Drilidae and some genera of Lampyridae (Branham & Wenzel, 2003).
- The absence of tibial spurs is considered primitive.

Tarsi: The tarsomeres in Lycidae are typically more or less dilated, especially distally (e.g. *Lycostomus*, Fig. 422). They may, however, be narrow and not dilated, as in *Alyculus*, *Miniduliticola*, *Sinodulia*, *Atamania*, *Lampyrolycus*, *Mimolibnetis*, *Dexoris*, *Platerodrilus*, *Lyropaeus*, *Lyroneces*, *Taphes*, *Ceratoprion*, etc. (e.g. Figs 427, 428, 429, 432, 437, 440), being usually deeper than wide. The narrowness of the tarsi is correlated with the absence of plantar pads, though sometimes apical plantar pads may occur in tarsomeres 3 and/or 4 in some of the taxa with non-dilated tarsi (e.g. *Lyroneces*, *Platerodrilus*, *Taphes*, Figs 428, 432, 437).
- Non-dilated tarsi and absence of plantar pads is considered primitive.

Claws: Claws are generally simple and uniform in the Lycidae. The exceptions are *Dexoris* and *Lyroneces*, where they are provided with series of minute teeth on their inner surface (Figs 428, 429b), and the tribe Macrolycini, where the claws are cleft (e.g. *Dilophotes*, *Calcaeron*, Figs 443, 444; *Macrolycus*, *Mesolycus*).
- Primitive condition of the claws is unclear.

Abdomen: The abdomen of adult Lycidae is sexually dimorphic, having eight visible sternites (ventrites) in male and seven in female, neither of them interrupted or otherwise affected by the metathorax. In *Flagrax* there are seven ventrites in male and seven in female, with the male ultimate abdominal segments not reduced, but completely retracted into the abdomen (Fig. 468). The ventrites are extended so they cover the lateral edges of abdominal segments, slightly encroaching of the dorsal surface, but never having a distinct edge separating ventral and dorsal parts of sternites. There are always ten tergites in male lycid abdomen (Figs 84, 466), though in *Flagrax* two apical tergites are retracted (Fig. 469). Laterally the lycid abdomen is not coadapted to the elytral margin and proximally not coadapted with metasternal structures (Fig. 85). *Thilmanus* was found to have seven ventrites in the male (and unknown number in the undescribed female).
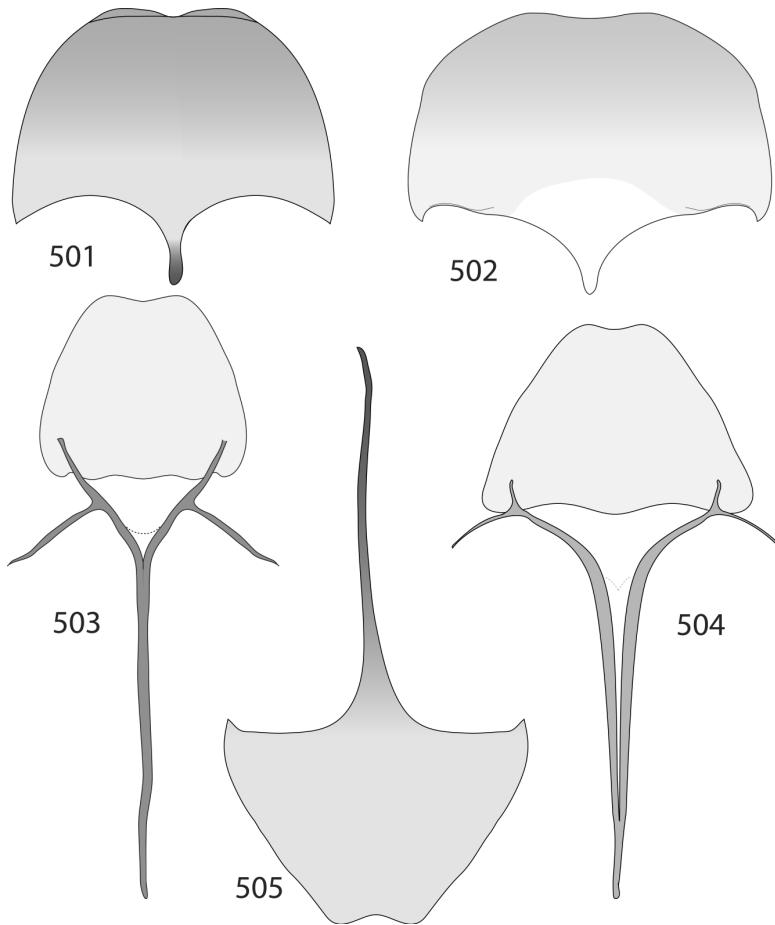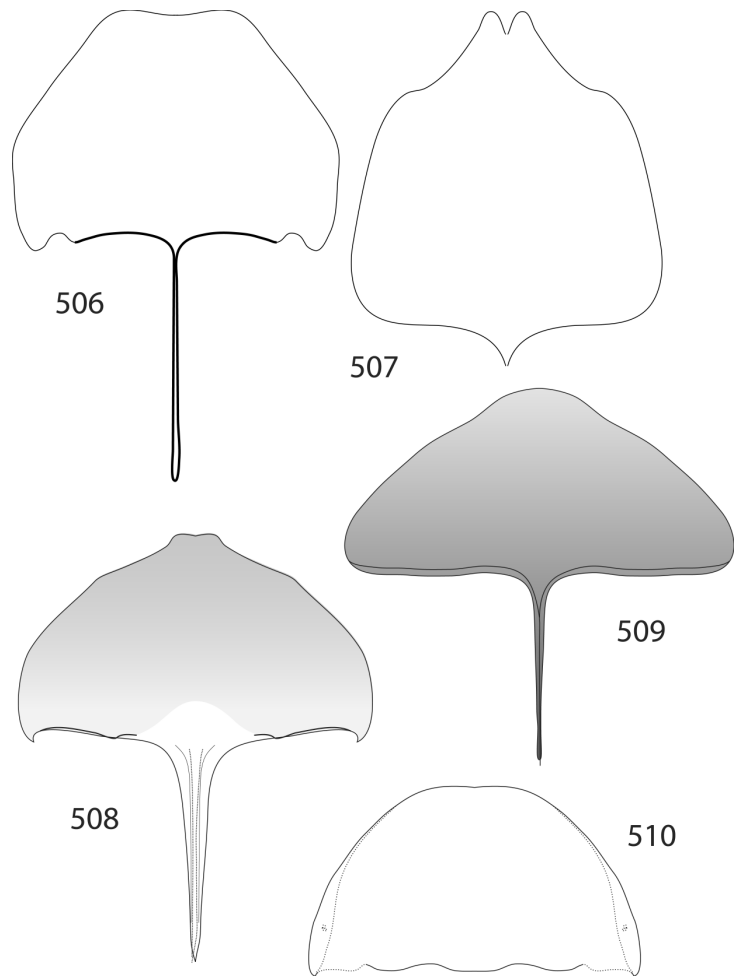
Figs 501-505: Imaginal terminal female ventrite, ventral view: *Aferos* sp. (501); *Lopheros rubens* (Gyllenhal) (502); *Platycis minuta* (Fabricius) (503); *Eros humeralis* (Fabricius) (504); *Pyropterus nigroruber* (Degeer) (505).

The male abdomen in Phengodidae (*Phengodes* sp.) typically consists of eight and that of Omalisidae (*Omalisus fontisbellaquei* Fourcroy) of seven ventrites. Male Cantharidae and Lampyridae may have both seven and eight ventrites. In the female abdomen, when it is not larviform, there is usually one segment less. Telegeusidae have seven ventrites in the male, with unknown number in the female, as no females have yet been discovered in the family.

•   As the general trend is the reduction of abdominal segments (Snodgrass, 1935), it is here hypothesized that eight male and seven female abdominal ventrites is primitive.

•   Not coadapted laterally abdomen is considered primitive.

Tergites: *Dexoris*, *Dilophotes* and *Lyroneces*, as well as *Pyractomena* (Lampyridae), have a median longitudinal suture in all tergites, which may

Figs 506-510: Imaginal terminal female ventrite, ventral view: *Flagrax auberti* (Bourgeois) (506); *Conderis signicollis* (Kirsch) (507); *Dictyoptera aurora* (Herbst) (508); *Pyrotes* (509); *Mesolycus shelfordi* (Bourgeois) (510).

sometimes be substituted by a longitudinal groove (e.g. in *Ceratoprion*). Typically Lycidae do not have explanate margins at the posterior angles in tergites, but some (e.g. *Lycostomus*) may have.

• Median longitudinal suture in all tergites is considered plesiomorphic.

Sternites: In a number of lycid taxa (*Lycostomus*, *Lygistopterus*) there are 9 ventrites visible from below in male and 8 in female, with the first sternite/ventrite completely separated by the metacoxae. On the other hand, in *Lygistopterus* the metacoxae may conceal sternite II medially. Normally Lycidae do not have explanate margins on the posterior angles in sternites, but some (e.g. *Lycostomus*) do.

• Visible first sternite is considered plesiomorphic.
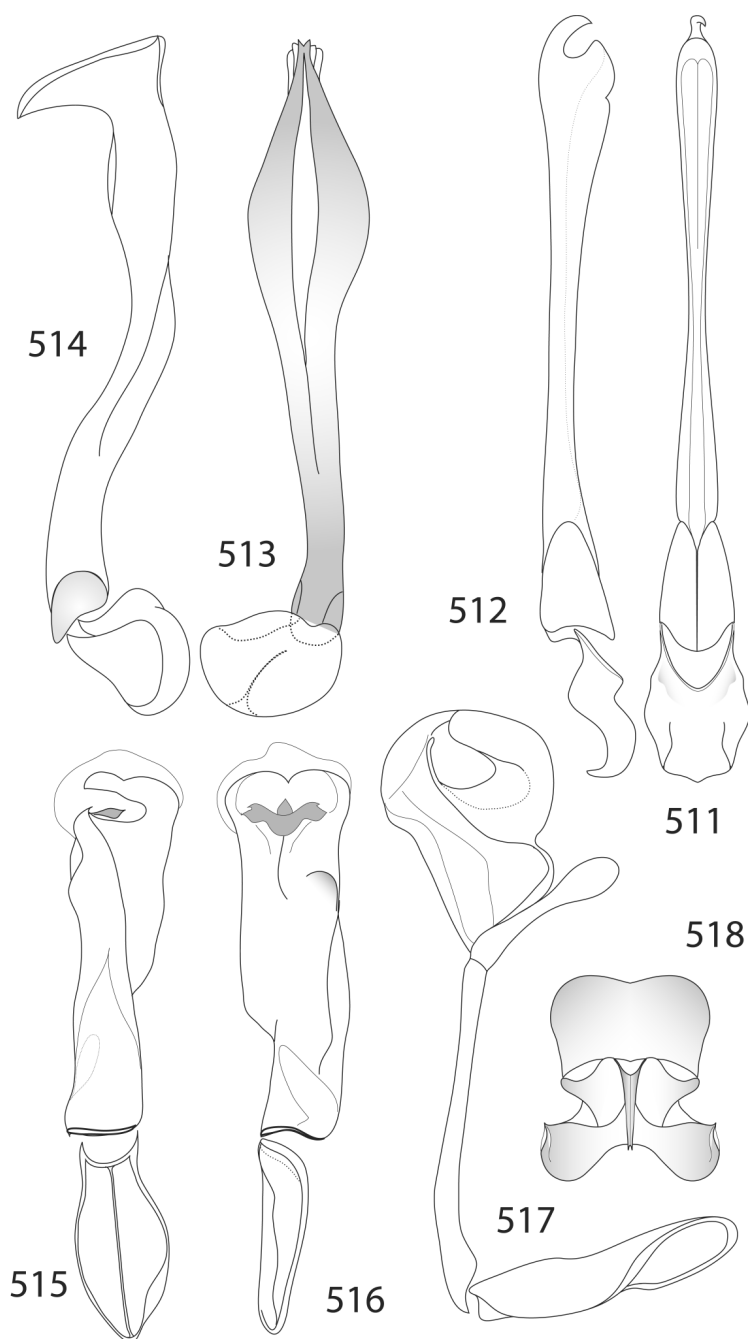
Figs 511-518: Aedeagus: *Lycostomus similis* (Hope), ventral view (511); same, lateral view (512); *Macrolycus flabellatus* (Motschulsky), ventral view (513); same, lateral view (514); *Dilophotes testaceus* Pic, ventral view (515); same, lateral view (516); *Mesolycus vitalisi* Pic, lateral view (517); same, inner sac structures, apical view (518).
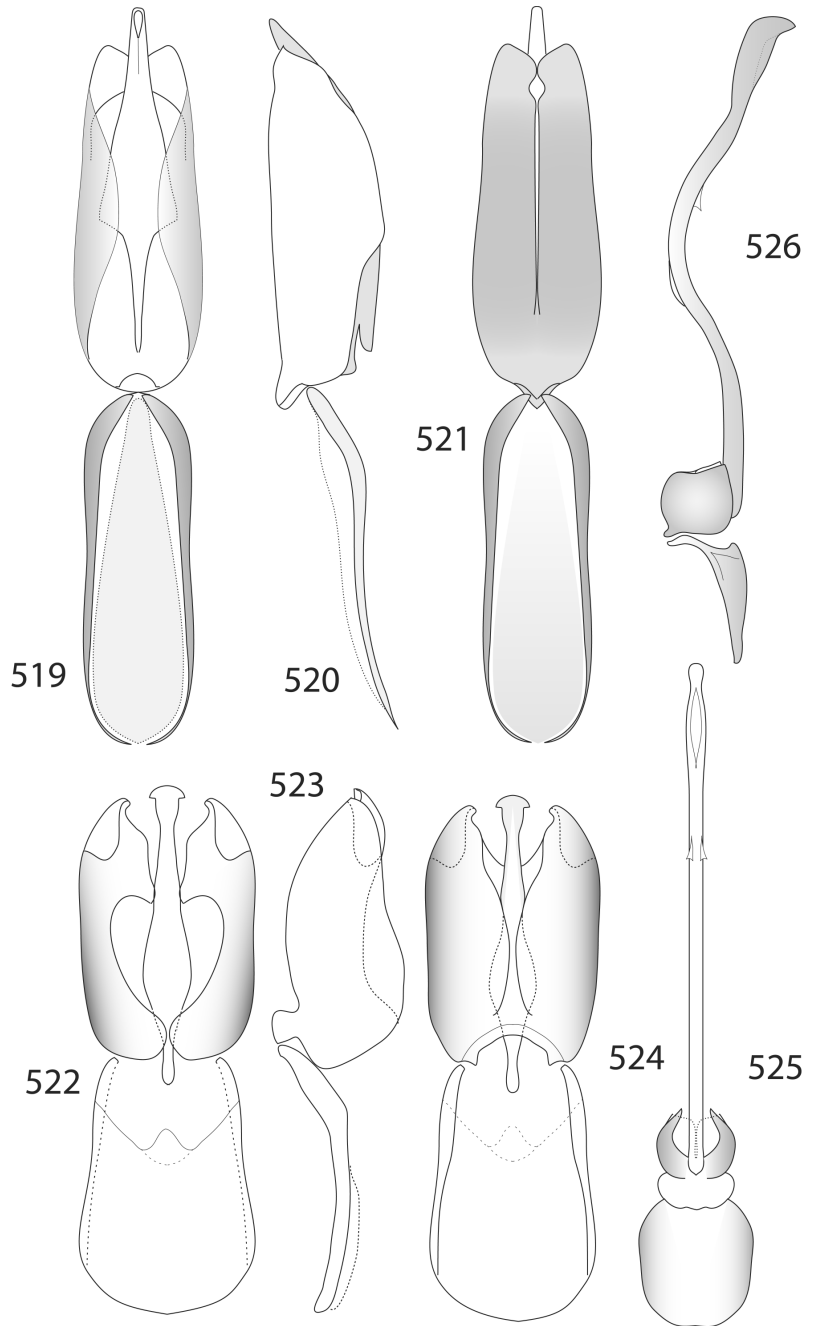
Figs 519-526: Aedeagus: *Pyrotes sculpturatus* (Waterhouse), ventral view (519); same, lateral view (520); same, dorsal view (521); *Dictyoptera gansuensis* Kazantsev, ventral view (522); same, lateral view (523); same, dorsal view (524); *Propyropterus plateroides* Kazantsev, ventral view (525); same, lateral view (526).
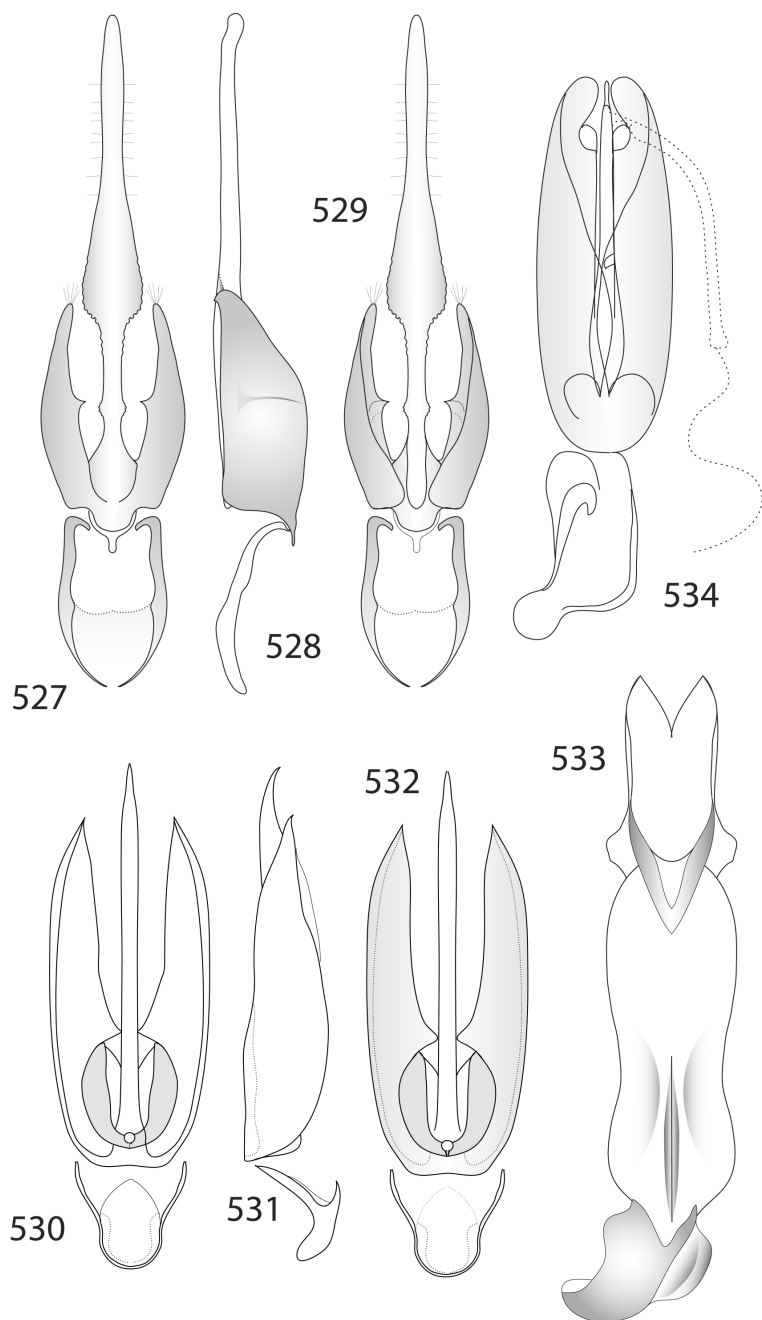
Figs 527-534: Aedeagus: *Proteros sempiternus* Kazantsev, ventral view (527); same, lateral view (528); same, dorsal view (529); *Eropterus glebulus* Kazantsev, ventral view (530); same, lateral view (531); same, dorsal view (532); *Aferos aethiops* (Kleine), ventral view (533); *Calochromus glaucopterus* (Guerin-Meneville), dorsal view (534).
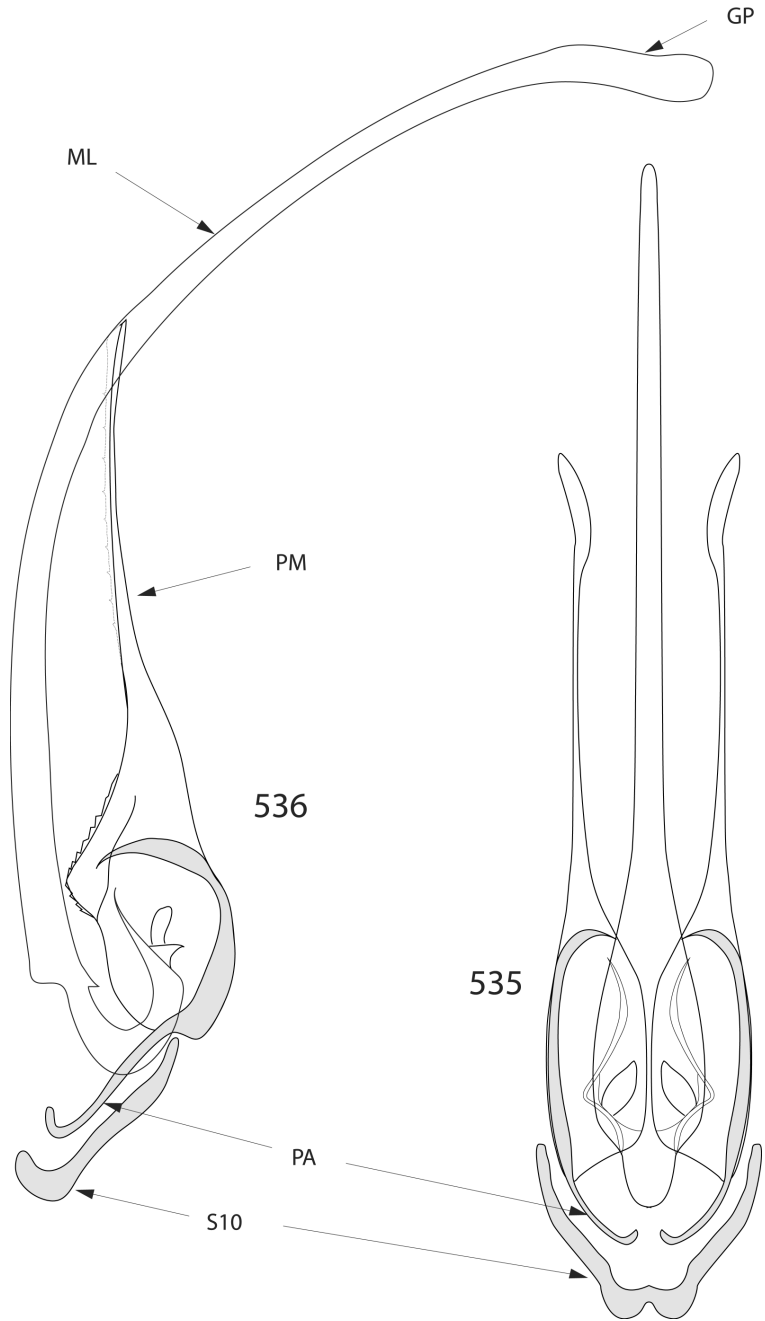
Figs 535-536: Aedeagus: *Platerodrilus* sp., dorsal view (535); same, lateral view (536).

GP - gonopore; ML - median lobe; PA - posterior apodemes; PM - parameres; S - sternite.

Spiculum gastrale: Some lycid taxa possess developed spiculum gastrale, a median strut of male sternite 9 (e.g. *Flagrax*, *Proteros*, Figs 469, 470), whereas most of them do not have it (e.g. *Macrolycus*, *Calopteron*, *Ceratoprion*, Figs 473, 485, 487).
   • Plesiomorphic condition of spiculum gastrale (absent vs. present) is unclear.

Spiculum ventrale: Certain lycids are characterized by long conspicuous spiculum ventrale, a median anterior strut of female sternite 8. In many Erotini and Dictyopterini a long spiculum ventrale is a typical condition (e.g. *Platycis*, *Eros*, *Pyropterus*, *Dictyoptera*, *Pyrotes*, Figs 503-506, 508-509). Some taxa are characterized by conspicuous lateral arms of the spiculum ventrale (e.g. *Platycis*, *Eros*, Figs 503, 504). On the contrary, some lycids do not have any trace of this structure (e.g. *Lycostomus*, *Calopteron*, *Ceratoprion*, *Mesolycus*, Fig., 495, 497, 498, 510).
   • Plesiomorphic condition of spiculum ventrale (absent vs. present or provided with lateral arms) is unclear.

Abdominal spiracles: In Lycidae abdominal spiracles are always located dorsally [vs. *Lampyris* where they are located ventrally on sternites]. However, their position varies: they may be located dorsally on the folded dorsal portion of sternites at their very edge (*Dexoris*, *Lycostomus*, *Calochromus*, *Pyrotes*, *Metriorrhynchus*, *Dilophotes*), on the sternite rather distant from the edge (*Plateros*, *Macrolycus*, Fig. 568, *Mesolycus*, *Aferos*), or dorsally on the pleural membrane (*Lyroneces*, *Conderis*, *Calopteron*, *Caenia*, *Platycis*, also *Cantharis* and *Phengodes*), or dorsally at the posterior angle of the tergite (*Ceratoprion*, Fig. 488). In *Taphes* and *Conderis* the spiracle located on the membrane is equipped with a conspicuous setiferous peritreme (e.g. Fig. 579), making it somewhat similar to the thoracic spiracles.
   • Location of the abdominal spiracles on the pleural membrane is considered plesiomorphic.

Paraproct: In male lycids the paraproct (tergite 9) is undivided dorsally (Figs 466, 469, 470, 472, etc.), unlike, for example, in *Cantharis*, where it is divided. In females the paraproct is also often present as a distinct sclerite in the external genitalia (e.g. *Lycostomus*, *Calopteron*, *Aferos*, *Macrolycus*, Figs 562, 563, 567, 572). In Lampyridae the paraproct appears to be fused with tergite 8 (*Lampyris*, Fig. 489).
   • Free and undivided paraproct is considered plesiomorphic.

Proctiger: The male proctiger (tergite 10) is medially attached to the paraproct in all lycid taxa examined, except *Platerodrilus*, where it is not medially articulated (Fig. 478). In Lampyridae the proctiger is absent altogether (*Lampyris*, Fig. 489).
   • Presence of the proctiger is deemed plesiomorphic.

External male genitalia: The external male genitalia of Lycidae consist of an unpaired intromittent organ and paired lateral accessories. Structurally, the aedeagus is typically trilobate, consisting of a phallobase, a median lobe and parameres, and in most cases is strictly symmetric (e.g. *Lyroneces*, *Ceratoprion*, *Scarelus*, *Platerodrilus*, *Calopteron*, *Proteros*, Figs 527, 535, 537, 539, 545, 546, 548).

However, sometimes the parameres may be absent (*Dexoris*, *Plateros*, Fig. 537-538, 549), and in a number of taxa the phallobase may be conspicuously asymmetric (e.g. *Calochromus*, *Mesolycus*, *Aferos*, Figs 517, 533, 534) or slightly asymmetric (e.g. *Metriorrhynchus*, Fig. 550). The median lobe and parameres may also be asymmetric, as in *Dilophotes* (Fig. 515-516), while some lycids may have all of the aedeagal structures slightly asymmetric (e.g. *Macrolycus*, Figs 513-514).

What is usually referred to as the phallobase (e.g. in Bocák & Bocáková, 1990) appears to be a composite structure that includes sternite 10, possibly represented by its coxites (Kluge, 2000), as an unpaired proximal sclerite, and a paired distal sclerite, probably representing the apodemes of the phallobase proper. Typically they are effectively fused with each other, but in certain cases remain free (e.g. in *Platerodrilus*, *Lyropaeus*, Figs 535-536, 542-544). As the sclerite hypothesized to be the coxite of sternite 10 is evidently separate from the aedeagus in the above two taxa, it is unlikely to be homologous with the aedeagal apodemes. The somewhat annuliform phallobase of *Metriorrhynchus* (Fig. 550), as well as the completely annuliform phallobase of *Phengodes* (Fig. 559), seem to be a result of reduction of sternite 10. The seemingly paired phallobase of *Proteros* and *Pyrotes* is probably a combination of the weakly sclerotized sternite 10 fused with the heavily sclerotized posterior apodemes (Figs 519-521, 527-529). The proximal paired sutures of the phallobase (e.g. in *Lycostomus*, Fig. 511) appear to be a transitional condition to the phallobase divided by a median suture (such as in *Ceratoprion*, *Macrolycus*, *Dilophotes*, *Calopteron*, Figs 513, 515, 545, 546). The true phallobase, which appears structurally hardly separable from the median lobe (phallus), seems to lack posterior apodemes in *Dexoris* and *Lyroneces* (Figs 537-541), the former taxon lacking any parameres and the latter taxon having the phallobase continuous with the parameres.

The median lobe is typically elongate and straight, acute or rounded apically, being in general not modified (Figs 537-543). Sometimes, though, it acquires asymmetric shape and may develop additional lobes (e.g. *Plateros*, Figs 548, 592, 594), become hooked apically (e.g. *Lycostomus*, *Macrolycus*, Figs 512, 514) or get fused with the parameres (e.g. *Dilophotes*, Figs 515-516). The inner sac, usually membranous, may acquire sclerotic exterior structures (e.g. *Metriorrhynchus*, *Lyponia*, Figs 550, 593).

The parameres are sometimes outwardly hooked (*Lyropaeus*, Fig. 542, 544). They are individually (e.g. *Platerodrilus*, *Lyropaeus*, Figs 535-536, 542-544) or jointly (e.g. *Scarelus*, *Pyrotes*, Figs 519-521, 548) articulated to the base of median lobe. The absent parameres in the symmetric aedeagus of *Dexoris* (Figs 537-538) apparently are not homologous with the absent parameres in the asymmetric aedeagus of *Plateros* (Figs 548, 592, 594), the latter probably being the result of its reduction. In *Lampyris* the parameres appear to be attached to the phallobase (Fig. 557). In Cantharidae both the parameres, forming the ventral arms of the paired lateral accessory structure, and the epimeres, or the dorsal lobes, are typically well-developed, with additional secondary processes, the laterophyses, often present (e.g. *Ancistronycha*, Fig. 561).

The general trend in evolution of the male copulatory organs in Lycidae seems to be development of paired lateral accessories, both distad (parameres) and proximad (posterior apodemes) of the articulation of the phallobase with the median lobe, with consequent fusion of the apodemes with the phallobase and occasional reduction of the parameres (e.g. in *Plateros*). The modified phallobase

incorporating the posterior apodemes appears to gradually lose its proximal portion (sternite 10) in certain lineages, such as *Metriorrhynchus*. Another hypothesized evolution trend is development of asymmetry independently in separate parts of the aedeagus, i.e. in the phallobase and the median lobe, or in all of the aedeagal structures. Yet another obvious evolutionary tendency is the basal fusion of the parameres.

• As the parameres are paired lateral accessories (Snodgrass, 1935), it is here hypothesized that individually articulated parameres are primitive.

• A composite phallobase composed of two separate pieces is considered primitive.

• Absent parameres, when the phallobase is simple, are considered primitive; on the contrary, absent or greatly reduced parameres, when the phallobase is modified having absorbed the paired parameral structure, are considered derived.

External female genitalia: The external female genitalia are probably absent in *Leptolycus* (Miller, 1991) and *Platerodrilus*, as the descriptions of females of the latter genus do not mention any (Mjöberg, 1925; Wong, 1996). The female genitalia, when present, are typically composed of paired valvifers, coxites and styli. The valvifers may be free (e.g. *Macrolycus*, *Taphes*, *Pyrotes*, *Mesolycus*, *Eros*, *Eulopheros*, *Conderis*, Figs 565, 567, 569, 571, 573, 576, 578) or may be distally fused (*Lopheros*, *Dilophotes*, *Calopteron*, *Caenia*, Figs 563, 564, 570, 574). When fused distally, they may be divided longitudinally by a suture (*Lopheros*, Fig. 574). They may also appear to be separately fused to the bases of the coxites (e.g. *Lycostomus*, *Phaneros*, *Metriorrhynchus*, Figs 562, 566, 575). In some cases there occur one or two additional sclerites between the apices of the valvifers and the bases of the coxites, which, with the paraproct and the valvifers associated with, respectively, the tergite and sternite of segment 9 (Crowson, 1981), appear to be sternite 10 and 11 incorporated in the female genitalia (e.g. *Macrolycus*, *Aferos*, *Taphes*, Figs 567, 571, 572). Sternite 10 may have participated in fusion of the valvifers in at least some of the taxa (e.g. *Lopheros*, Fig. 574). On the other hand, it is possible that the divided sternite 10 is attached to bases of the coxites (as in *Dictyoptera* or *Pyrotes*, Figs 573, 577). The only taxon found to possess what seems to be sternite 11 is *Macrolycus* (Fig. 567).

The coxites sometimes appear fused, though the degree of sclerotization of the area of fusion is typically low (e.g. *Eulopheros*, Fig. 565), or nearly contiguous proximally (e.g. *Phaneros*, Fig. 575).

The styli vary from long and slender (e.g. *Caenia*, *Dilophotes*, Figs 564, 570) to short and stout (e.g. *Calopteron*, *Taphes*, Figs 563, 571), but in general they seem to be subject to little variation.

Internal female genitalia: The internal female genitalia are quite variable in Lycidae. A pair of accessory glands is often present (e.g. *Lycus*, *Taphes*, *Pyropterus*, *Metriorrhynchus*, Figs 580, 582, 586, 589), being completely absent in other taxa (e.g. *Platycis*, *Dictyoptera*, *Calopteron*, Figs 581, 584, 585). Some lycids seem to possess just one accessory gland (e.g. *Plateros*, *Conderis*, Figs 587, 588). The seminal duct varies from extremely long (e.g. in *Taphes*, Fig. 582) to very short (e.g. *Platycis*, *Metriorrhynchus*, *Conderis*, Figs 585, 587, 589). In some taxa the vagina is provided with a conspicuous vaginal pouch (e.g. *Lycus*, *Lygistopterus*, Figs 580, 583). Snodgrass (1935) suggests that the absence of accessory glands is a derived condition.

• Plesiomorphic condition of internal female genitalia is unclear.

BIOLOGY

The life history of members of Lycidae is still obscure. The number of larval instars and the total length of larval development remain unknown. No full cycle of any lycid has ever been documented. Eggs laid by both mated and unmated females in captivity do not hatch (Mjöberg, 1925; Wong, 1996). In rare instances when first instars hatch from eggs taken in nature they die before undergoing their first ecdysis (Burakowski, 1990; Wong, 1996). Fortunately, at least some later instars taken from nature pupate or otherwise turn into mature adults, after being kept in captivity without ecdysis for up to eight months (e.g. *Platerodrilus*, Wong, 1996; *Metriorrhynchus*, Bocák & Matsuda, 2003). The maximum time a lycid larva was being observed in captivity before pupation was five years (*Pyropterus nigroruber* Degeer - Bourgeois, 1882).

Most of the lycid larvae are associated with decaying wood. They prefer red or, more seldom, white rotten wood, with generally no preference to any particular group of trees. They may be found in the soft rotten wood or under the loose bark of such trunks, often being noticeable on their surface or surrounding low strata foliage. At least some species demonstrate marked tendency to make aggregations inside crevices of decaying trunks. At the same time the larvae of some Lycidae appear to be associated with plant debris of the forest or bush floor, and some are reported to prefer the underground parts of the decaying trunks (i.e. *Plateros*, *Calopteron*, Miller, 1997). The activity of lycid larvae does not seem to be restricted by nocturnal or diurnal patterns.

Older instars often crawl on relatively intact decaying logs or stumps, lowering their head and probing the surface with their antennae, from time to time jamming head and mouthparts into crevices in the act of feeding. The tripartite mandibles of the Lycidae larvae allow sucking of the juices of decaying wood with further consumption of the microfauna and other organic substance associated with them. This mode of feeding appears similar to that of water-dwelling ancestors of Mandibulata that did not have chewing mandibles and were presumably water filtrators, and to that of Recent Pseudognatha or certain Eucrustacea. Another mode of feeding was reported by Miller (1988) who described foraging of *Calopteron* larvae on small mollusks.

In the larvae of Lampyridae, the closest relatives of the Lycidae, the mandibles are perforated by channels opening at their bases, through which a liquid is injected into the body of their prey. This liquid comes from their stomach and converts the tissues of their victims into a «bouillon nutritif» (Bugnion, 1929). But the ingestion takes place directly through the mouth and by way of mandibular channels.

One group of Lycidae (*Platerodrilus*) has been documented to have paedomorphic development in females. The paedomorphosis is the phenomenon of retention of immature features in imagines. The paedogenesis is the phenomenon of acquiring or retention by larvae of the reproduction capability. The ultimate form of paedomorphosis, when all characters of the female, except the ability to reproduce, are larval and the pupa phase is absent in its development, is thus inseparable from the paedogenesis. This extreme condition has been found in one lycid genus, but probably occurs in a number of others, where females are not discovered yet. It is also reported in Micromalthidae and some Phengodidae, and probably represents a plesiomorphy. Transitional conditions of this character, when larval features are retained in females to a lesser degree, are widespread in a number of families of
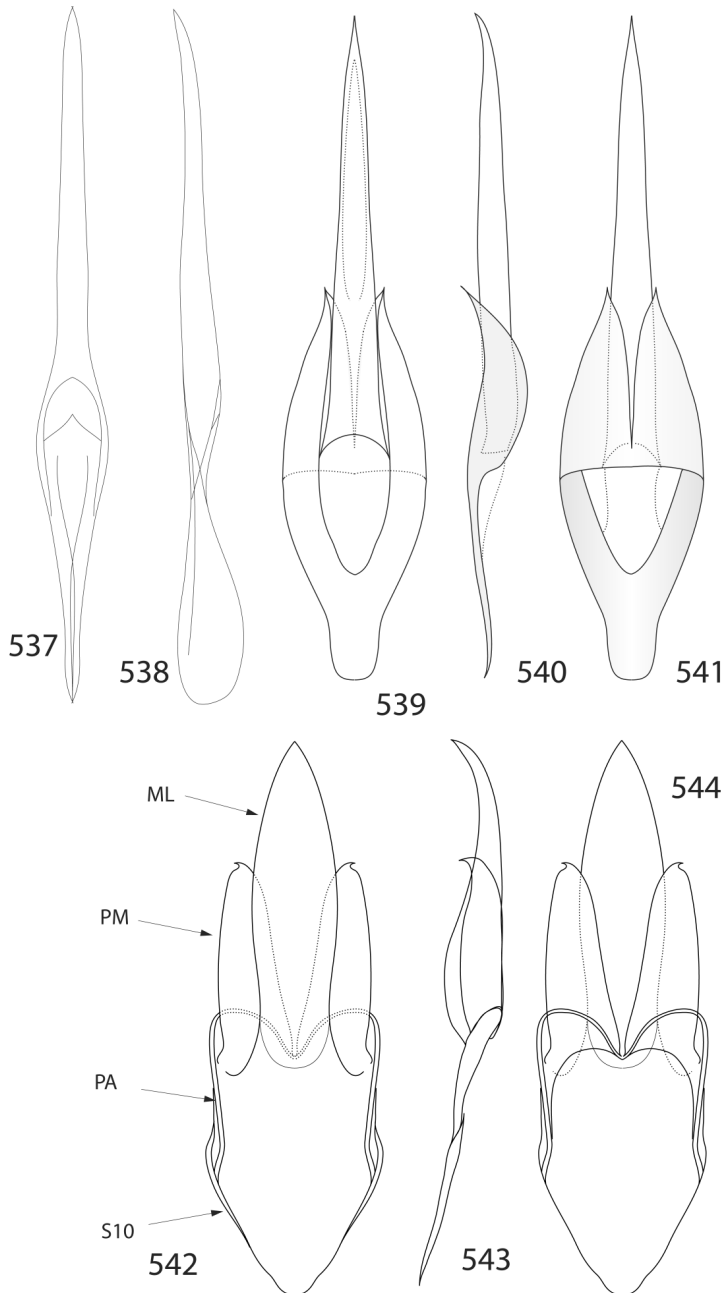
Figs 537-544: Aedeagus: *Dexoris tessmani* Bocák & Bocáková, ventral view (537); same, lateral view (538); *Lyroneces optabilis* (Kleine), ventral view (539); same, lateral view (540); same, dorsal view (541); *Lyropaeus fallax* (Walker), ventral view (542); same, lateral view (543); same, dorsal view (544).

ML - median lobe; PA - posterior apodemes; PM - parameres; S - sternite.

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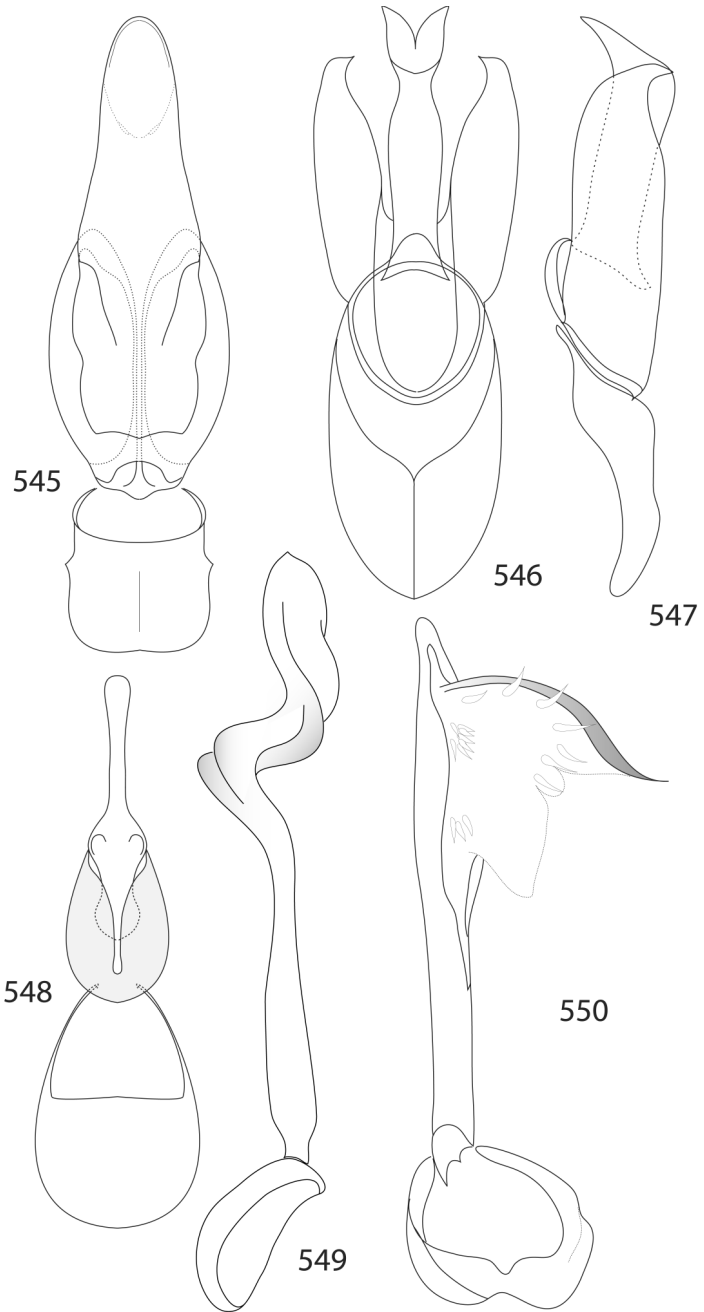
Figs 545-550: Aedeagus: *Calopteron reticulatum* (Fabricius), ventral view (545); *Ceratoprion* sp., ventral view (546); same, lateral view (547); *Scarelus umbrosus* Kleine, ventral view (548); *Plateros dentifer* Kazantsev, lateral view (549); *Metriorrhynchus* sp., ventral view, after Bocák, 1998 (550).
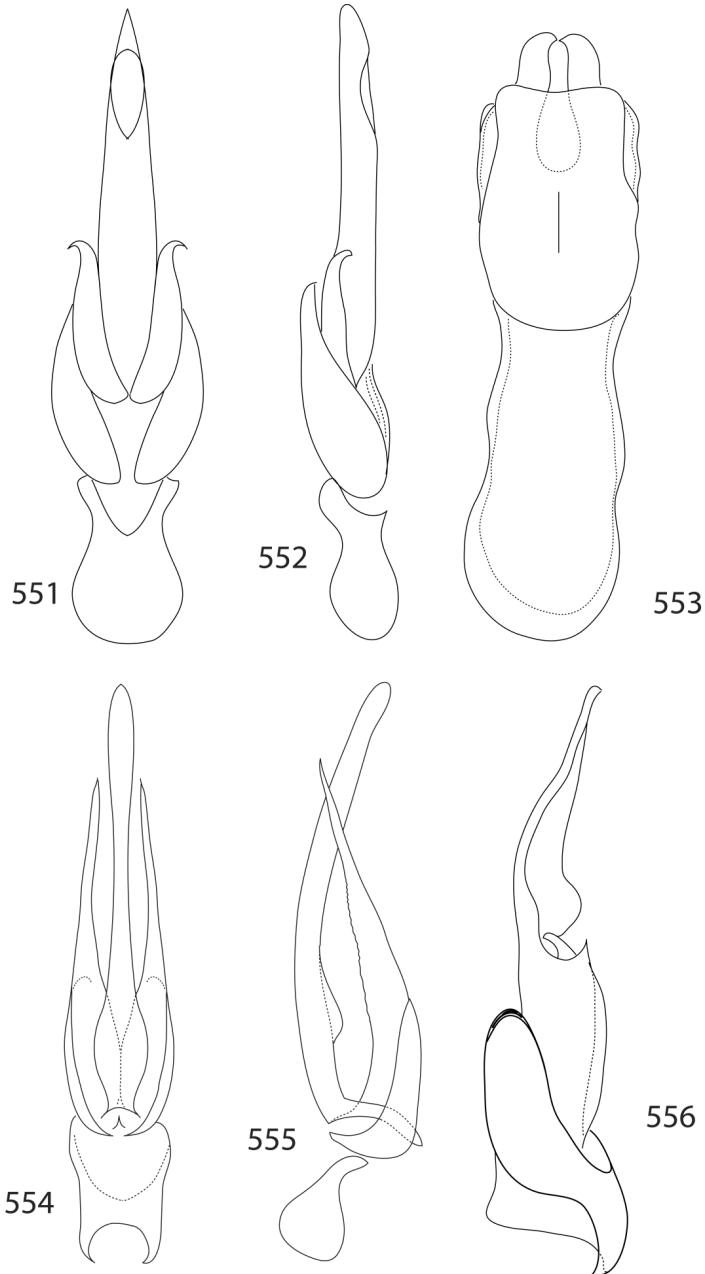
Figs 551-556: Aedeagus: *Microeron verae* Kazantsev, ventral view (551); same, lateral view (552); *Dihammatus poringianus* Kazantsev, dorsal view (553); *Atamania tembeling* Kazantsev, ventral view (554); same, lateral view (555); *Libnetis bousqueti* Kazantsev, lateral view (556). Scale: 0.5 mm.
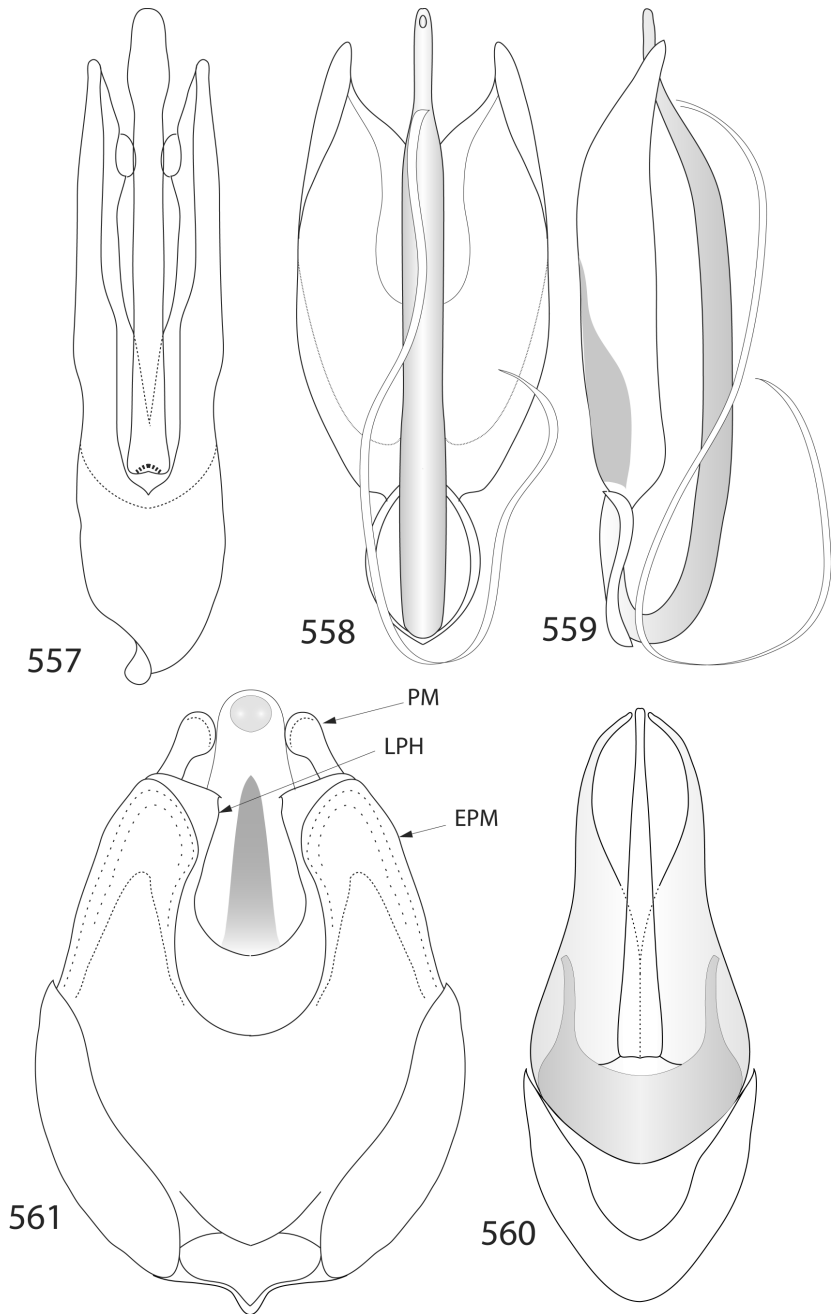
Figs 557-561: Aedeagus: *Lampyris* sp., ventral view (557); *Phengodes* sp., ventral view (558); same, lateral view (559); *Thilmanus obscurus* (Baudi), ventral view (560); *Ancistronycha violacea* (Paykull), lateral view (561).

EPM - epimere; LPH - laterophyse; PM - parameres.

Cantharoidea, especially in Lampyridae, and in some Polyphaga. The only other Neoptera order where both simple and complete metamorphoses occur is Copeognatha (= Psocoptera) (Kluge, 2000). On the other hand, at least in one lycid group certain fundamental characters of a seemingly fully imaginal female are in a state suggestive of its fairly recent paedomorphic past, providing more evidence of possible plesiomorphic nature of the paedomorphosis in the Polyphaga. In *Helcophorus* the female metendosternite consists of a pair of widely separated transverse bars, comparable to the mesendosternite or to the condition characteristic of the larvae. As it is not very probable that it has regained its ancestral state, it is more plausible to assume that the female acquired complete metamorphosis considerably later than the male.

The pupal stage, when present, is typically short in lycids. According to various authors, it lasts between one and three weeks (Korschefsky, 1951; Burakowski, 1988).

Lycidae are one the most speciose models for many Batesian and Müllerian mimicry complexes in the animal kingdom. The typically broad elytra, aposematic coloration, gregarious habits and sluggish behavior well suit them for this role. The family is considered perhaps the most ancient living group of models for mimicry purposes (Linsley *et al.*, 1960). They are resembled in colour and pattern by every order of Insects whose habitats yield the relevant foundation: the Lepidoptera, Hymenoptera, Diptera, Hemiptera, numerous Coleoptera, etc. (e.g. Carpenter and Ford, 1933). Predators, both vertebrate and invertebrate, apparently seem to avoid lycids and members of their mimicry assemblages alike (Linsley *et al.*, 1960).

• The paedomorphosis found in one lycid genus, but probably occurring in a number of others, is hypothesized to be a plesiomorphy.

PHYLOGENY

The Lycidae, along with the Cantharoidea, had been traditionally placed close to the root of the Coleoptera (e.g. Lameere, 1900), mostly until Böving and Craighead (1931) suggested that the Archostemata are the most primitive Coleoptera. Despite some resistance (i.e. in Crowson, 1938, where they were again placed at the root of the Polyphaga), the cantharoids were gradually moved to the very top of the coleopteran phylogeny tree as a derived clade of Elateriformia, and most contemporary authors regard them as «terminal elements of the malacodermization sequence» (Hlavac, 1975).

Regarding this family as «terminal elements of the malacodermization sequence» might indeed seem justified, if the Archostemata were confidently established as the stem coleopterans. However, there are certain doubts about this hypothesis. The Lycidae are among the least malacodermized Cantharoidea in terms of undersclerotization of their cuticle, but greatly surpass the more soft-bodied members of the superfamily, e.g. Cantharidae or Lampyridae, in acquiring more diverging characters from those of the alleged stem coleopterans. The Melyridae (Cleroidea), or Pyrochroidae and Oedemeridae (Tenebrionoidea), for instance, being no less soft-bodied than the cantharoids, retain the dorso-lateral compression of the body, five ventrites of their abdomen, prominent gula, sclerotized flanges of the elytral suture margin, transverse folding of the hind wing, etc., their larvae

show none of the modifications characteristic of the lycids (Böving & Craighead, 1931). The same refers to the soft-bodied Meloidae, which have perhaps the most inedible features among the Coleoptera. The soft-bodied *Thylodrias* in Dermestidae, Rhipidiinae in Rhipiphoridae, Karumiinae in Dascillidae, Cebrioninae in Elateridae, exhibiting some degree of neoteny as well, with females either brachypterous or almost larviform, have not gained conditions even distantly approaching those of the Lycidae.

Böving & Craighead (1931: 6), though obviously a priori convinced of the archaic nature of the reticulated beetles (Cupedidae), had to acknowledge the primitiveness of the larval types to which the Polyphaga could be traced. Nevertheless, the Archostematan larvae separated from the Polyphagan larva by the distinct tarsus with one or two distinct claws and the hypopharyngeal and paragnathal structures fused with prementum into «a strong, hard unit», were suggested to be primitive, though this opinion was not supported with sound arguments. The mentioned features, however, can hardly be regarded plesiomorphic. While there is obviously no need to comment on the larval ligular sclerome, the simple dactylopodite-like end-segment of the leg has been demonstrated to be characteristic of the primitive hexapods, the lateral, i.e. paired, claws being secondary structures developed from the base of the pretarsus (Snodgrass, 1935: 198). The crustacean dactylopodite, a simple claw-like segment, is shared by many Hexapoda, a simple dactylopodite-like end-segment of the leg occurring in the Protura, in some Collembola, which is considered among the most ancient hexapod groups, and in a number of Pterygote insects. The earliest known Archostemata date back to the Permian and they are already derived Coleopterans: their elytra have dove-tailed suture margins, they have elytral epipleures and locking flanges; their elytra, thorax and abdomen are perfectly coadapted with each other; their thoracic segments are accordingly modified to receive legs in their grooves; they already have extremely sophisticated folding of the metathoracic wing; the number of their abdominal segments is already greatly reduced (to 5 from 10). Consequently, the first beetles should date back at least to the Carboniferous (or Devonian), which makes a search for plesiomorphic conditions of the morphological characters of the order in the most primitive arthropod stock, including the Trilobitomorpha, a natural choice. Looking in that direction suggests accepting plesiomorphies outlined in the Morphology section above.

Nevertheless, the first scenario envisaged that the Lycidae, being the terminal elements of the malacodermization sequence, evolved from the common stock with the Lampyridae, their closest relatives from the morphological standpoint, and keeping in mind that the two of them evolved from the common stock with the Omalisidae, Drilidae, Cantharidae and other Cantharoidea, which in their turn evolved from the common stock with Elateroidea, and all of them with other Polyphaga, from the common stock with Archostemata.

Scenario 1

The first transformation the larvae of net-winged beetles underwent in correlation with highly derived feeding habits, i.e. after they had switched from feeding on snails and other soft prey, characteristic of their ancestors and persisting among Lampyridae and Cantharidae, to sucking juice from moist decaying wood,

was the splitting of mandible into three separate sclerites. It was accompanied, first, by separation of the hypostomal margin from the cranium and its transformation into another separate sclerite, similar to the myriapod stipes of mandible, providing articulation to the lower piece of the mandibular structure, the premandible, or the mandible proper. Secondly, all lycid larvae completely lost any trace of tentorium, with the anterior tentorial arms transformed into a pair of sclerotic hypopharyngeal lobes, also reported in some Entognatha and Myriapoda, articulated anteriorly to hypopharyngeal suspensorium, which became the median part of the mandibular structure, the stiletto. Third, the cranial dorsal condyle and relevant mandibular articulation completely disappeared; instead, the labrum acquired division into a pair of sclerites and each sclerite developed a fossa to receive the condyle on the anterior/dorsal surface of the mandible proper. In more derived forms (e.g. *Platerodrilus*, Fig. 16) the labral segment acquired secondary segmentation. Initially the stiletto was distally attached to the labral segment (as in *Lygistopterus*), but in more derived forms (*Lycus*, *Platerodrilus*) the two became separate from each other.

All of the functional thoracic and abdominal spiracles of a number of Lycidae larvae lost any trace of the closing apparatus. Many Lycidae, probably because of the abundance of wet decaying wood in larval habitats, regained their metathoracic spiracles as functional ones, and some derived forms acquired a condition when these spiracles became identical to those of the mesothorax and abdomen (e.g. *Platerodrilus*, Fig. 20). The transition to low-in-calories wood juice, which inevitably considerably increased the larval life-span, due to unknown reasons led to broadening of the ventral opening of head. Some derived forms developed division of the cranium into segments, which, however, as not related to ecdysis, cannot be recognized as a derivation of ecdysial lines/sutures. Such division independently occurred in unrelated lineages (e.g. *Platerodrilus*, Figs 10-11, *Xylobanus*, *Lyponia*, *Plateros*, Fig. 60, etc.).

The larval trochantin lost its distal attachment to the coxa (Figs 20, 34, 41), probably due to the reduced need in fast movement, with only pleural articulation remained in the lycid coxa, as opposed to the pleural and trochantinal articulation of their ancestors. In some derived lycid taxa the prementum became divided into a pair of proximal annuli (*Calopteron*, Fig. 47, *Lycostomus*, *Lyponia*); certain derived lycids (e.g. *Platerodrilus*, *Calopteron*) acquired the alveolate cuticle structure, uniform in all body sclerites, including the head. *Platerodrilus*, *Lyponia* and *Lycus* also acquired elongate coxa making part of the limb (Figs 20, 39, 64).

In some Lycidae the evolution went in such a way that their larvae regained division of their trochanters into trochanters 1 and 2, which is not known in Pterygota other than in Odonata. The fact that these include otherwise distant morphologically *Platerodrilus*, *Lycus*, *Calopteron*, *Lyponia* (Figs 20, 39, 53, 64), and *Xylobanus* may be explained by the independent occurrence of the said condition in at least some of these taxa.

The imaginal Lycidae also underwent significant morphological changes.

Obviously, one of the first modifications that occurred in the adult Lycidae was the loss of tentorium, which first lost the corpotentorium or posterior connection between the ventral arms, then ventral arms were reduced to inconspicuous processes, even in forms with large and strong mandibles, such as *Calochromus* (Figs 127-129). In perhaps most primitive lycids the tentorium persisted in the form of relatively long ventral arms, as in *Macrolycus*, *Aferos* and *Plateros* (Figs 137, 144, 152), but certain derived lycids lost it completely (*Dexoris*, *Lyroneces*, Figs 110, 116), with the attachment of antennal muscles becoming cranial.

Another modification that occurred in all lycids, probably due to the special distasteful features of their blood (though the Lampyridae appear to possess similar, if not the same, blood qualities and are equally avoided by predators), was separation of the mesoventrite from the mesopleuron by a suture, as compared to the ancestral condition, manifest in i.e. Cantharidae, Phengodidae and Lampyridae, where these two sclerites remain fused. In presumably more derived, but obviously unrelated taxa (*Lyroneces*, *Caenia*, *Plateros*, Figs 305, 308, 315) the mesoventrite became divided into the mesoventrite proper and the sternopleural processes. The prosternum in some derived lycids, such as *Lycostomus*, *Lyroneces*, *Mesolycus* (Figs 237, 238, 254), also acquired division into the prosternum proper and sternopleural processes connecting it with the hypomeron. Yet another character distinguishing lycids from the Cantharoidea common stock and all other cantharoids was the acquisition of the non-coadapted elytron that lacks epipleuron and has unmodified ventral surface. The suture margin of a lycid elytron lost the dove-tailed sclerotized flange that ensured the locking of elytra together in their ancestors, and some derived groups (e.g. *Dexoris*, Fig. 330) have completely lost such flange. Parallel with such development of the elytron the lycid hind wing acquired simpler folding pattern (Figs 387-388), the wing folding in some of the (hypothetically) derived Lycidae becoming so insignificant that the elytron started to exceed length even of a fully unfolded hind wing (e.g. *Lyroneces*, Figs 387, 395, 396). The wing venation in some presumably derived taxa was modified in such a way that the C, Sc and RA veins separated from each other and became parallel in most of the costal area before joining the radial bar (Fig. 398). Another specific feature that acquired all Lycidae probably due to their distastefulness to potential predators was the loss of coadaptation of the abdomen, both with the metasternal and with the elytral structures; in some derived taxa the coadaptation between the elytra and other thoracic segments became equally absent (Fig. 85).

The broad ventral closure of the head behind mouthparts manifest in some hypothetically primitive lycids (e.g. *Scarelus*, *Platerodrilus*, Figs 94, 117) gave way to the absent gula, i.e. actually open ventrally head capsule, with a narrow process connecting the cranial sclerites anteriad of the posterior tentorial pits, in a number of evidently unrelated derived lineages (e.g. *Lyroneces*, *Aferos*, *Calopteron*, Figs 91, 114, 150). The prognathous head that seems to have survived perhaps in just one lycid taxa (*Platerodrilus*, Fig. 83) gave way to hypognathous condition that became characteristic of the Lycidae (Figs 82, 84, 86). The labrum evolved from the uniformly sclerotized structure rigidly attached to the epistoma (*Lygistopterus*) or fused thereto (*Lucaina*) first to a feebly sclerotized sclerite with its proximal part lying within the oral cavity, and finally to the bipartite, divided into two independent lobes labrum (e.g. *Dexoris*, *Proteros*, Figs 107, 108). The prementum became completely divided in *Calopteron* and *Ceratoprion* (Figs 186, 189), acquiring longitudinal suture in *Macrolycus* and *Caenia* (Figs 187, 191). In several obviously unrelated lycid lineages the cervical sclerites acquired condition resembling sclerites related to the thoracic spiracles, in terms of shape, position, sclerotization and pubescence (Figs 87,142).

In some presumably derived lycids the posterior process of the mesoscutellum acquired a tendency to reduction and became vestigial in such taxa as *Caenia*, *Calopteron*, *Lyroneces*, *Ceratoprion* (Figs 270, 280, 338, 342, 344), with the loss of function of locking the elytra and protecting the elytral notch. In addition to the trochantinal suture, the metacoxa in such derived groups as *Dexoris, Mesolycus*
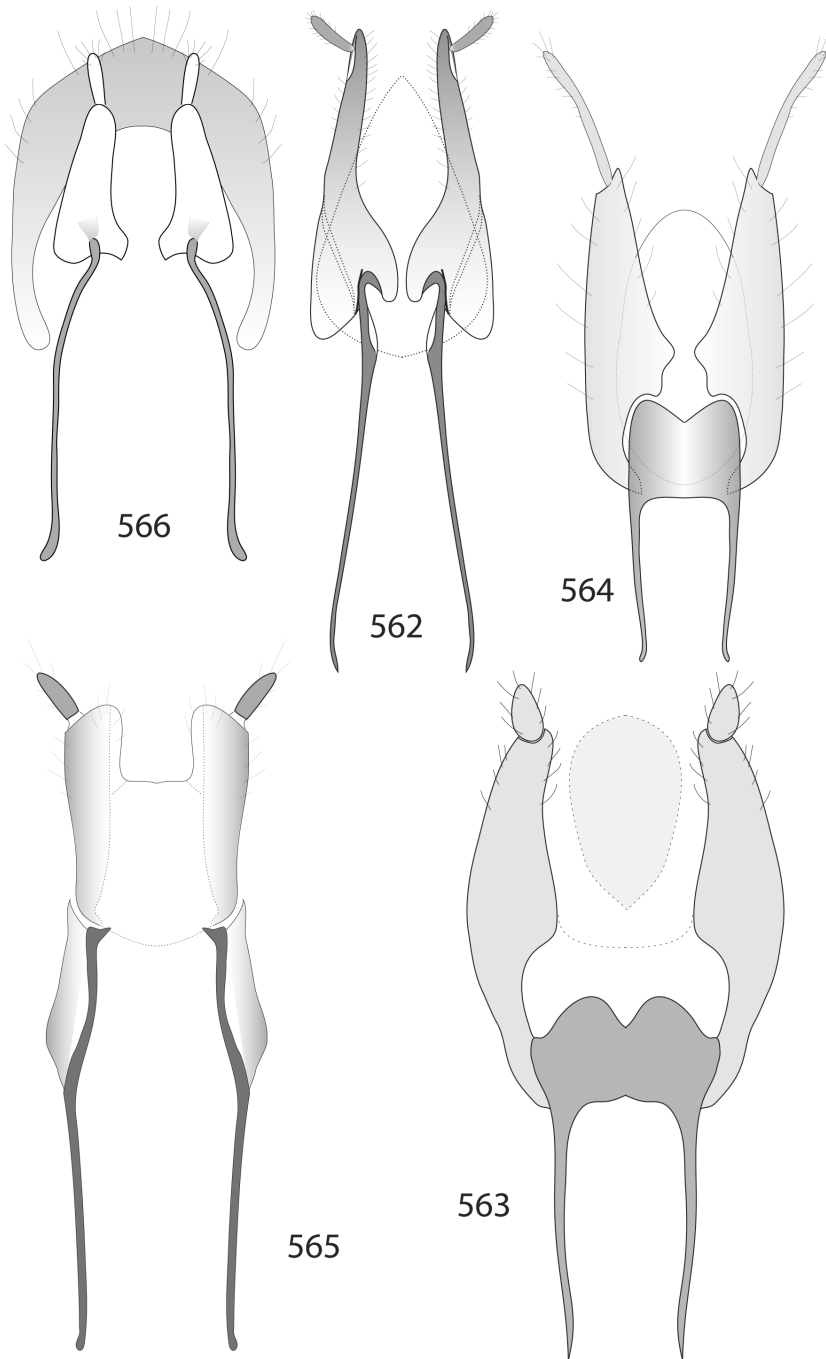
Figs 562-566: External female genitalia: *Lycostomus praeustus* (Fabricius) (562); *Calopteron reticulatum* (Fabricius) (563); *Caenia kirschi* Bourgeois (564); *Lopheros* (*Eulopheros*) *harmandi* (Bourgeois) (565); *Metriorrhynchus thoracicus* (Fabricius) (566).
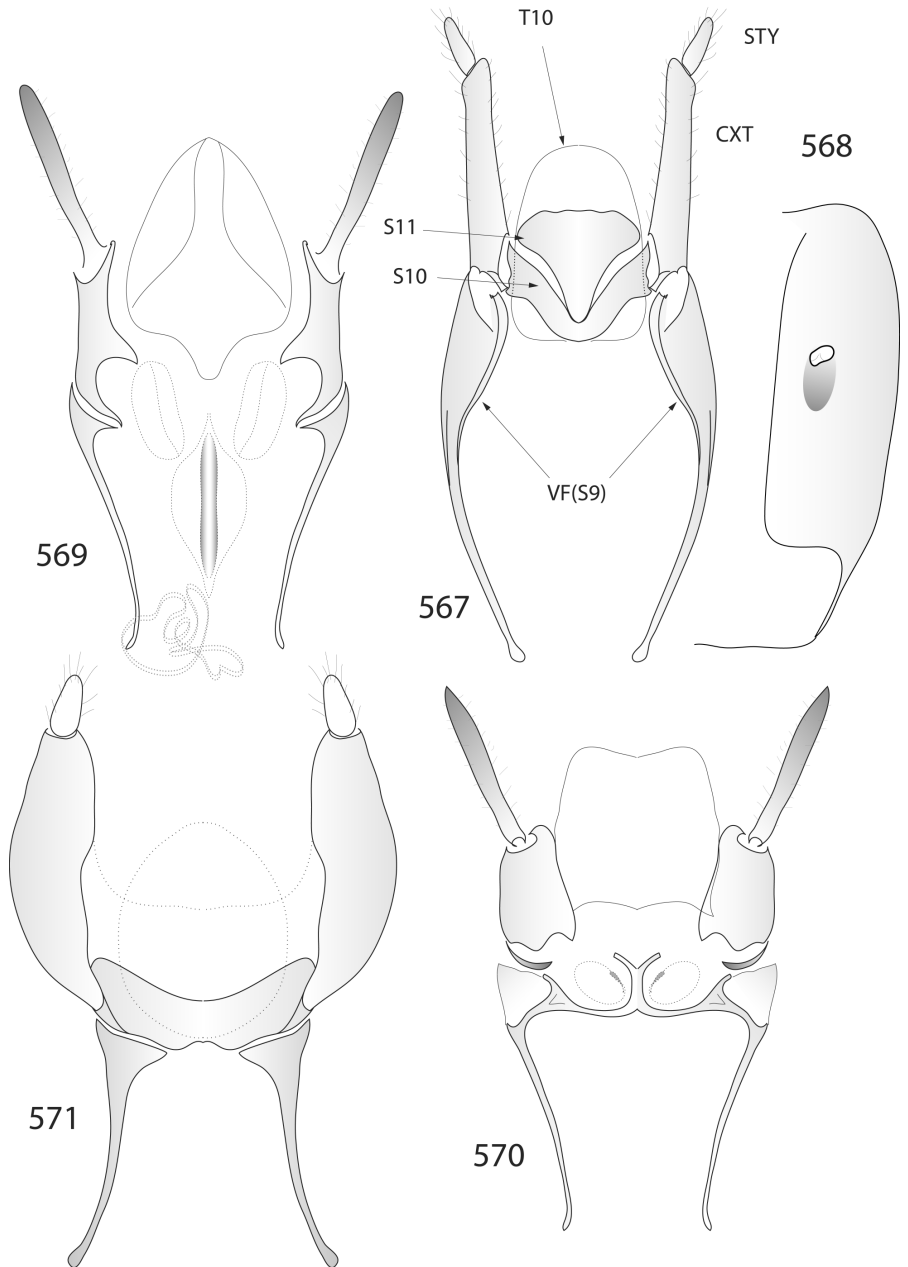
Figs 567-571: Imaginal structures: *Macrolycus flabellatus* (Motschulsky), external female genitalia (567); same, lateral margin of ventrite 6, dorsal view (568); *Mesolycus shelfordi* (Bourgeois), external female genitalia (569); *Dilophotes depressicornis* Pic, external female genitalia (570); *Taphes brevicollis* Waterhouse, external female genitalia (571).

CXT - coxite; S - sternite; STY - stylus; T - tergite; VF - valvifer.
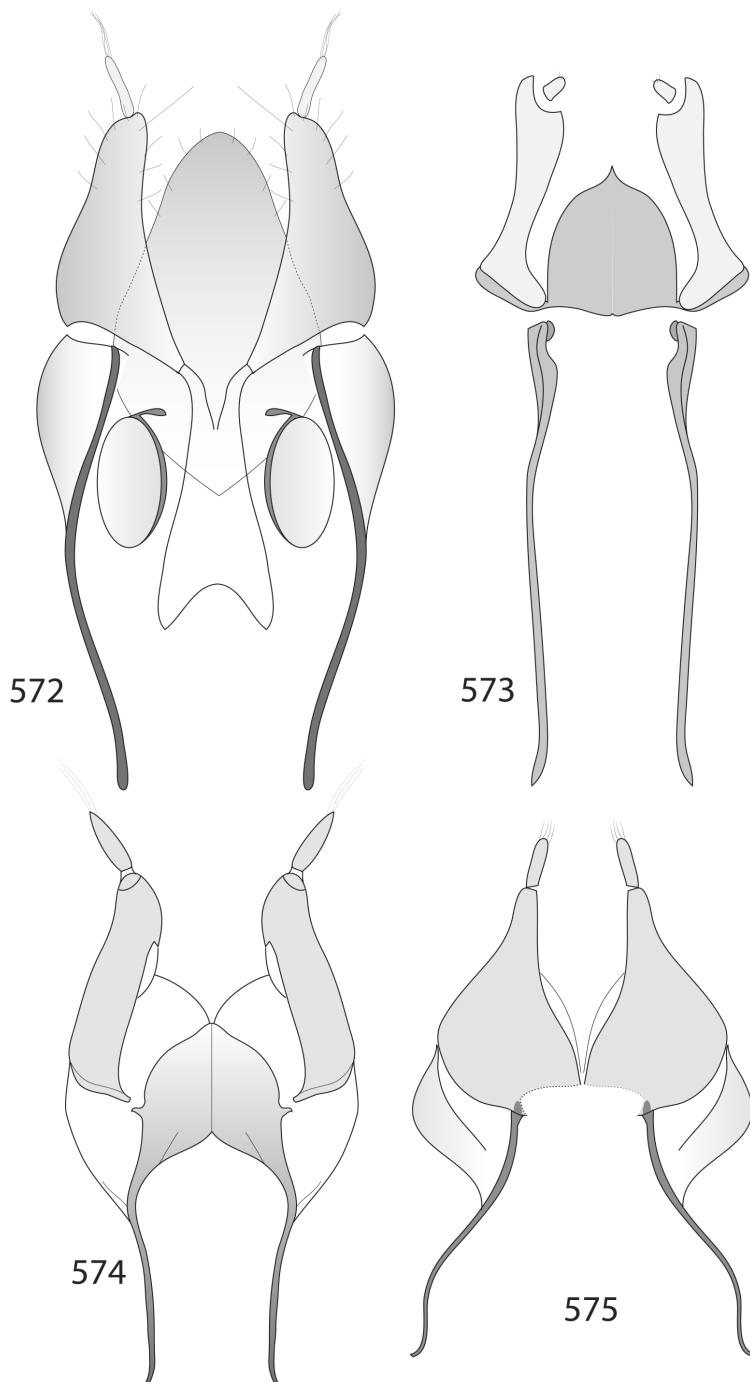
Figs 572-575: External female genitalia: *Aferos* sp. (572); *Pyrotes sculpturatus* (Waterhouse) (573); *Lopheros rubens* (Gyllenhal) (574); *Phaneros xanthopterus* (Bourgeois) (575).
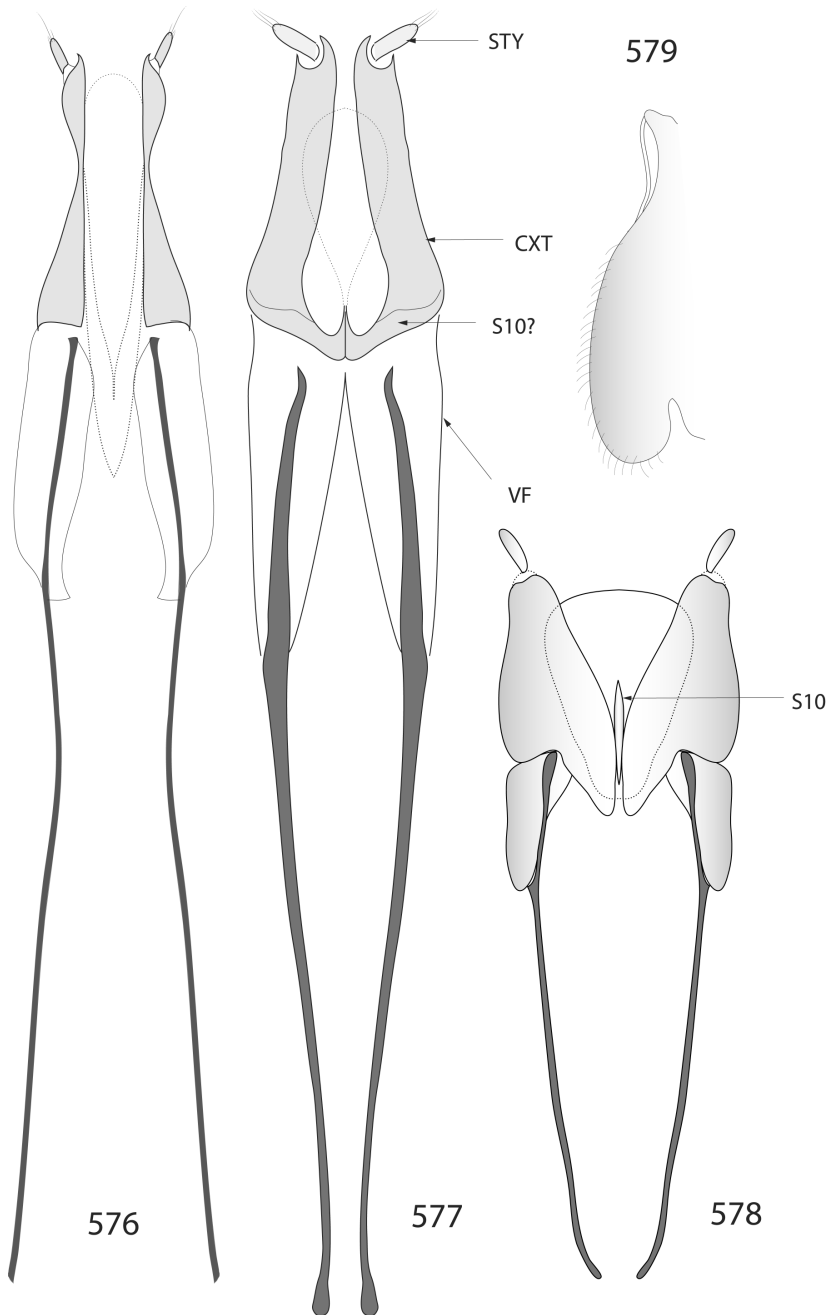
Figs 576-579: Imaginal structures: *Eros humeralis* (Fabricius), external female genitalia (576); *Dictyoptera aurora* (Herbst), external female genitalia (577); *Conderis signicollis* (Kirsch), external female genitalia (578); same, spiracle of segment 6, dorsal view (579).

CXT - coxite; S - sternite; STY - stylus; VF - valvifer.
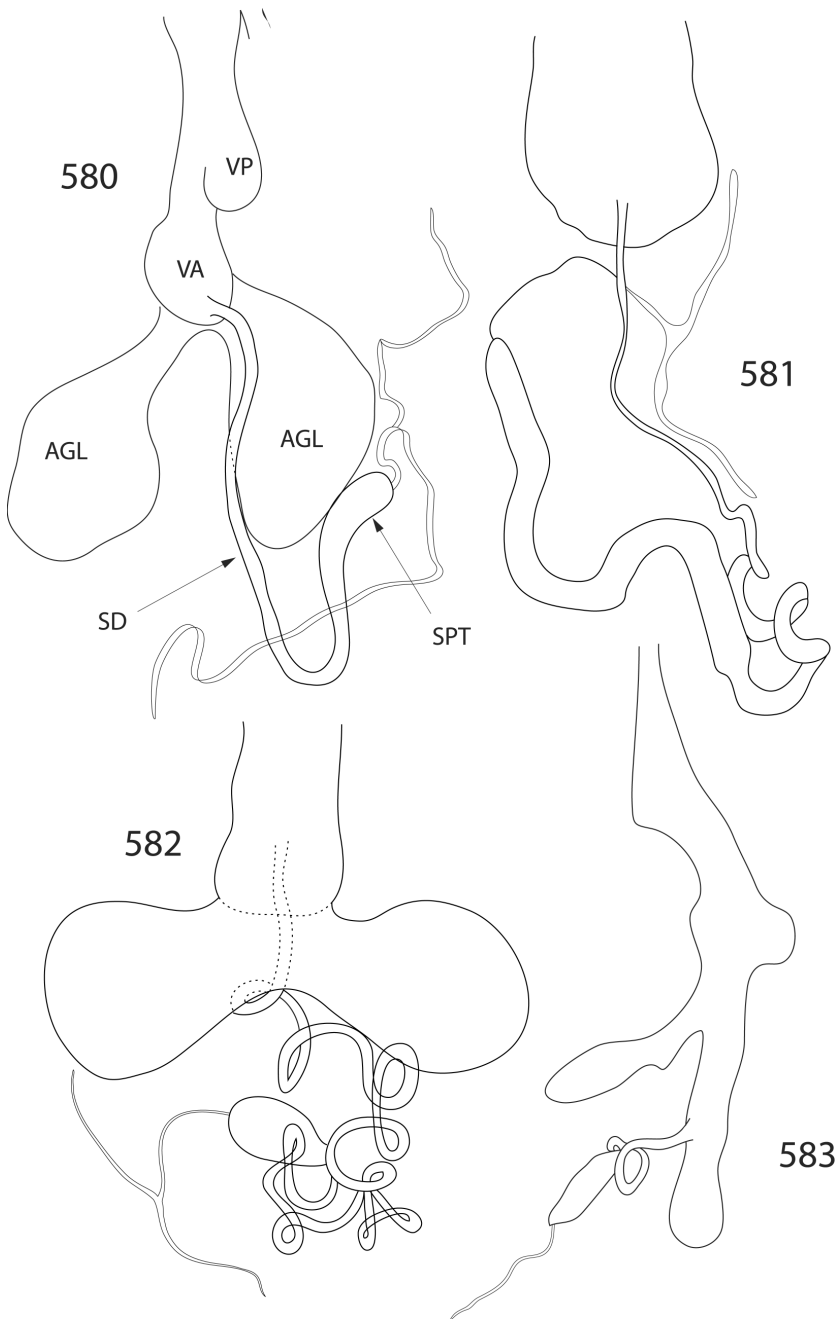
Figs 580-583: Internal female genitalia, after Bocák & Bocáková, 1990: *Lycus* sp. (580); *Calopteron terminale* (Say) (581); *Taphes brevicollis* Waterhouse (582); *Lygistopterus sanguineus* (Linnaeus) (583).

AGL - accessory gland; SD - seminal duct; SPT - spermatheca; VA - vagina; VP - vaginal pouch.