

# Comparative morphology of mandibular structures in lycid larvae and its phylogenetic implications (Polyphaga, Hexapoda)

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## Abstract

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The morphology of the larval mandibular structures of the family Lycidae (Polyphaga) is characterized by facultative dicondyly, posterior articulation with long mandibular rods, lateral location of the anterior condyle and its articulation with a paired non-cranial structure. It is compared to that of Eucrustacea, Chilopoda, Entognatha, Microcoryphia and Zygentoma and found to be more reminiscent of the Entognatha. The phylogenetic implications of this conclusion are discussed, with the Pterygota and Dicondylia hypothesized to be non-monophyletic.

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## Introduction

The larval mandibular structures of Lycidae have long been known to be very different from those of any other beetle (e.g. Perris 1846; Bourgeois 1882). However, most entomologists who dealt with immature stages of the Coleoptera were at best acknowledging the bizarre composite nature of such structures, not venturing into further details (Böving and Craighead 1930–31; Gardner 1947; Crowson 1972, 1981; Lawrence 1991; Beutel 1995, etc.) – and for good reason: nothing indeed seemed to even remotely resemble them in all pterygote orders. The only exception was the treatise by Rosenberg (1943), where the mandible of a *Platerodrilus* (= *Duliticola*) larva was demonstrated to be articulated not with the cranium, but with a thin rod presumed to represent the tentorial arm, while the bi-segmented upper blade of the *Mandibelorgan* attached to the mandible proper by a fossa–condyle articulation was considered to be the clypeus and the labrum combined. However, Cicero (1994) insisted that the latter sclerite in lycid larvae is but a piece of the divided labrum. Shortly afterwards the lycid ‘mandible’ was found to be actually made of three sclerites, the above-mentioned rod again homologized with a tentorial structure (Kazantsev 2003) first, but after a more detailed study, which showed that it has nothing to do with the tentorium, hypothesized to

be homologous with the stipes of the mandible (Kazantsev 2005). The latter paper also emphasized that the lycid mandibular structure has what is called the ‘facultative dicondyly’, reported also in *Zygentoma* (Staniczek 2000) and characterized by the anterior location of the second (dorsal) articulation of the mandible proper, in the case of Lycidae connecting it to a paired dorsal blade, hypothetically the labral lobe. Such organization of mandibles occurring nowhere else in the higher insects was compared to that of a *Lithobius* sp. (Chilopoda). As most other characters of lycid larvae of any importance, including their filtration feeding mode and six-segmented legs with conspicuous first and second trochanters, are arguably in the primitive condition, it is very unlikely that such a mandibular structure could be apomorphic, so the Coleoptera were hypothesized to be non-monophyletic, with the Archostemata–Adephaga and the Polyphaga representing two independent lineages (Kazantsev 2005). However, the Microcoryphia and *Zygentoma*, which have somewhat similar types of mandibular apparatus (Fürst von Lieven 2000; Staniczek 2000, etc.) and are evidently closer to the ‘pterygote’ Coleoptera than the Chilopoda, were not used for comparative purposes.

To re-analyse and, possibly, reinterpret the larval mandibular structures of Lycidae on the basis of comparison with homologous organs of a wider range of arthropods, a further study

has been undertaken, in which the larva of the lycid genus *Platerodrilus* Pic, in addition to Chilopoda, was compared to representatives of Eucrustacea, Entognatha, Microcoryphia and Zygentoma.

### Materials and Methods

The larval *Platerodrilus* material was cleared with 10% KOH and dissected for the examination. All sutures, sulci, sclerites and appendages were studied on such KOH-treated specimens.

The Hexapoda taxonomy is given in accordance with its most recent revision by Kluge (2000) – later works, including the study on the evolution of the insects by Grimaldi & Engel (2005), do not address the taxonomic problems discussed by Kluge – with some modifications. The following names are used instead of the more widely known synonyms: Eucrustacea Kingsley, 1894 = Crustacea auct., nec Crustacea Pennant, 1777, which includes also Pantopoda and Polychaeta; Microcoryphia Verhoeff, 1904 = Archaeognatha Börner, 1904; Oligoneoptera Martynov, 1923 = Holometabola auct., nec Holometabola Burmeister, 1835, which does not include all insects with complete metamorphosis; and Amyocerata Remington, 1955 = Ectognatha Hennig, 1953, nec Ectognatha Stummer-Traunfels, 1891, which does not include Pterygota (Kluge 2000).

The relevant morphological data were extracted from various literature sources on the following taxa:

*Tricholepidion gertschi* Wygodzinsky (Zygentoma, Triplura);  
*Dilta* sp. (Microcoryphia, Triplura);  
*Isotoma viridis* Boulez (Collembola, Ellipura, Entognatha);  
*Lithobius* sp. (Chilopoda); and  
*Aegla prado* Schmitt (Anomura, Eucrustacea).

### Comparative Morphology

The females of *Platerodrilus* have a simple metamorphosis, without the pupal stage, and are externally inseparable from the larvae (Mjöberg 1925; Wong 1996), so their characters may be considered both larval and imaginal. The mandibular structures of a female/larva of *Platerodrilus paradoxus* (Mjöberg) are non-opposable, basally approximate, medially attached and apically divergent (Figs 1–3), at rest projected slightly backward proximally and forward distally (Figs 3, 4).

Each ‘mandible’ is tripartite (Figs 5–8), consisting of:

- (a) a sheath, or the mandible proper, constituting the interior and exterior/distal surface of the mandibular structure, bearing a condyle articulated to the fossa on the mandibular rod and a dorsal acetabular fossa received by a condyle on the shutter (Fig. 6);
- (b) a stiletto, hypothesized to be the paired hypopharyngeal suspensorium, or the superlinguae, at rest hidden within the cavity formed by the sheath and the shutter (Figs 5 and 7); and

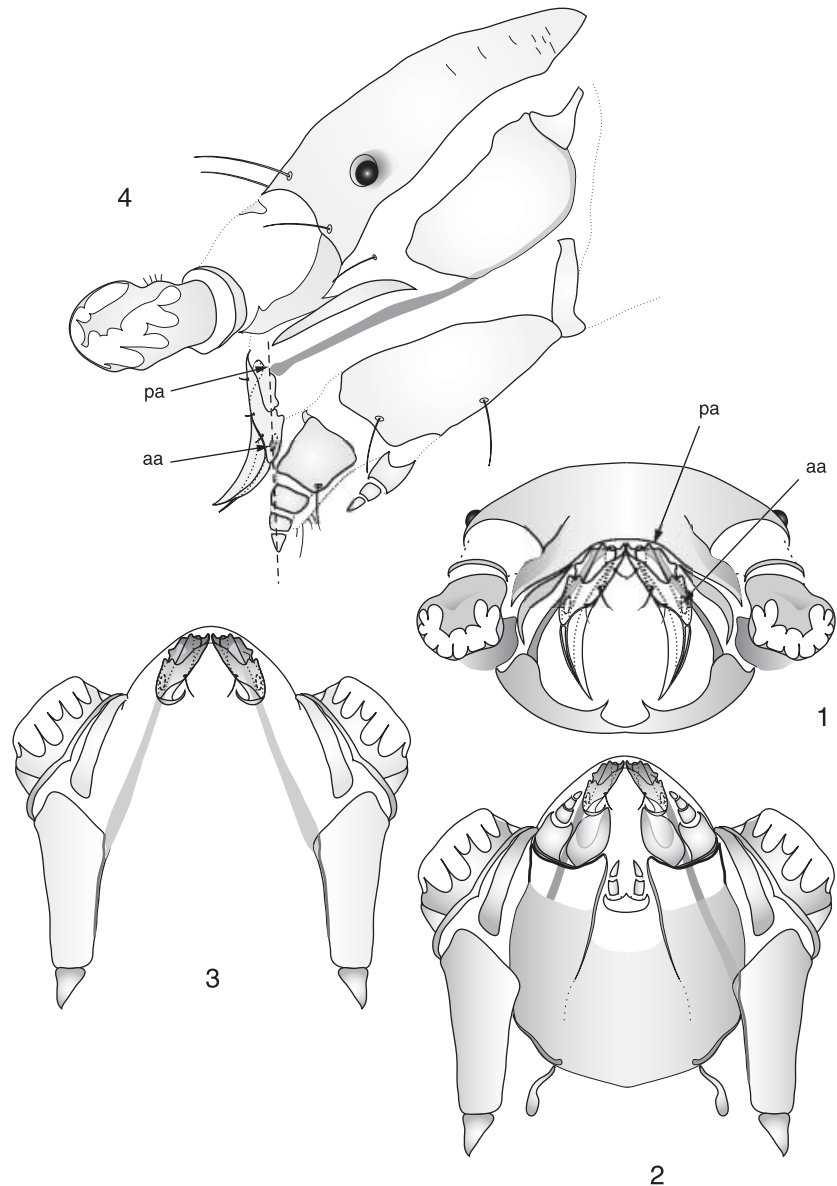
- (c) a shutter, presumed to be the bi-segmented labral lobe, loosely attached to the cranium by its posterior edge, with a wide basal sclerite constituting the basal portion of the exterior surface and articulated by a condyle to the mandible proper and a long and narrow apical sclerite, partly covering the sheath opening distally; the exterior surface of the basal sclerite bears three prominent setae (Figs 5, 7 and 8).

The shutter, according to the prekatatrepsis embryo studies (Cicero 1994), originates as a separate limb located anteriorly of the mandible proper. Presuming it to be the labral lobe effectively rejects the homology of the larval and imaginal mandibles in the family Lycidae, as well as the larval mandible in Lycidae and the rest of the Polyphaga (Kazantsev 2005). To avoid such a rejection, the shutter should be considered homologous with, probably, the second antenna and the labrum, as the secondary derivation of the cranium, deemed totally absent in the lycid larvae.

Two muscles are attached on the mandible, the anterior cranial muscle (M1) and the posterior cranial muscle (M2) (Fig. 6). Ventral adductor muscles are absent. The only mode of mandibular movement in lycid larvae is the limited rotation around the longitudinal axis by the action of abductor (M2) and adductor (M1) muscles, which splits the tripartite structure and opens the channel for suction.

In addition to the posterior (primary) articulation (*pa*) the mandible proper has the secondary anterior, or dorsal, articulation near its lateral edge (*aa*) fitting into a kink of the ventrolateral margin of the labrum, with the anterior cranial muscle inserted close to it, slightly anteriorly of the articulation point (Figs 6 and 7). The longitudinal axis of swing lies in the plane of the proximal portion of the mandibular structure (Figs 1 and 4). In neither of the conspicuously separated articulation points is the mandible articulated to the cranium: posteriorly it is hinged with the long mandibular rod and anteriorly it is loosely attached to the divided labrum. The mandibular rod, in its turn, is attached to a sclerite that does not constitute the cranium either and continues to its posterior edge, separating this sclerite from a smaller posterior sclerite (Fig. 4). The mandibular rod does not have musculature and, though profoundly invaginated, makes part of the cranial wall, being connected to the cranial and maxillary sclerites by membrane.

Unlike *Platerodrilus*, *Tricholepidion gertschi* Wygodzinsky (Zygentoma, Triplura) is characterized by the transverse (with respect to the mandible plane) axis of swing (Fig. 10). Anteriorly its mandible is articulated with the laterodorsal angle of the clypeus (Figs 10 and 11), forming the so-called facultative dicondyly, whereas the mandible proper of *Platerodrilus* is articulated with the labral segment. Posteriorly, the *Tricholepidion* mandible is attached to a separate, but inconspicuous, sclerite (Fig. 10). Unlike those of lycids, the *Tricholepidion* mandibles are provided with a transverse ligament and ventral muscles (Fig. 11). The mandibles of another zygentom, *Lepisma saccharina* Linnaeus, on the other hand, do not have the transverse ligament (Staniczek 2000).



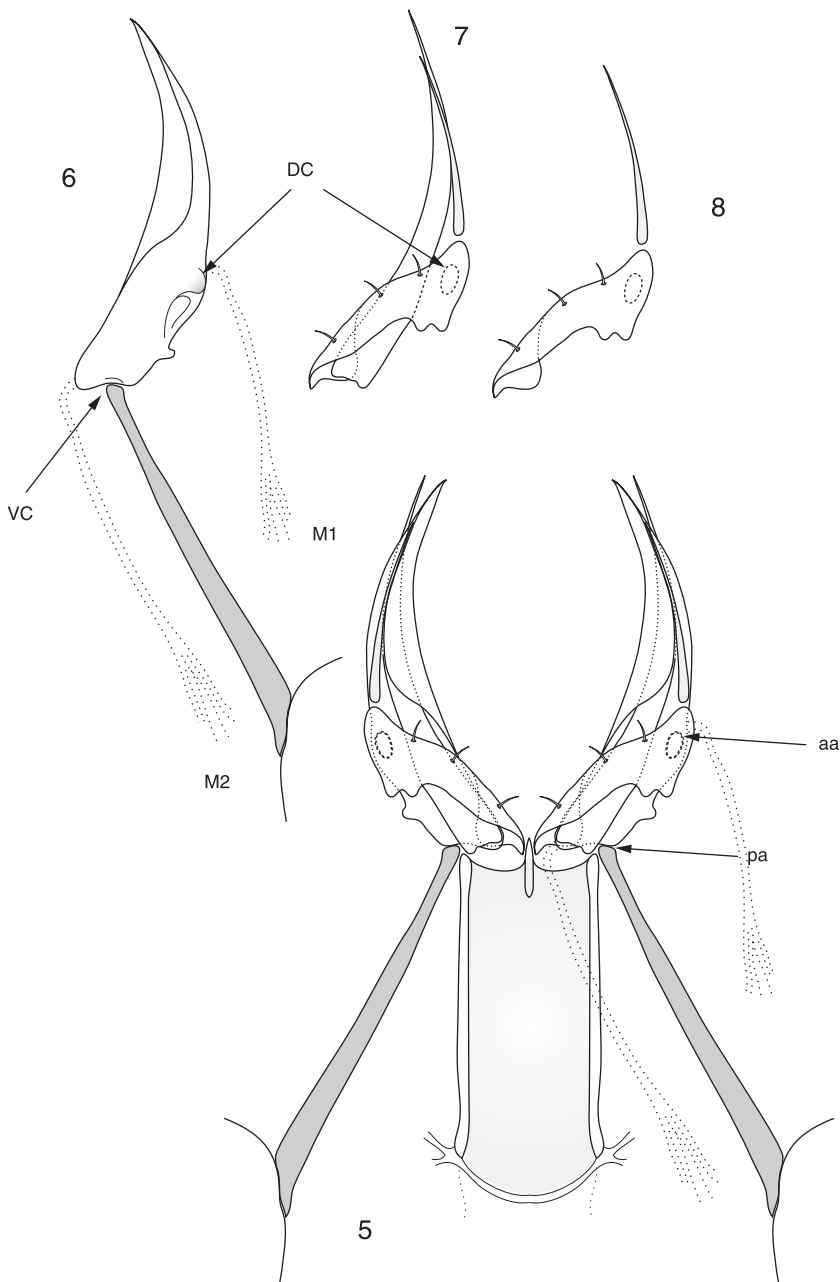
**Figs 1–4**—*Platerodrilus paradoxus* (Mjöberg), larval head. —1. Anterior view; —2. — ventral view; —3. same, labium and maxillae removed; —4. lateral view. aa, anterior articulation; pa, posterior articulation.

Somewhat more similar is the mandibular structure of a *Dilta* sp. (Microcoryphia, Triplura) (Fig. 9): in both cases the axis of swing is longitudinal, the anterior hinge being on the clypeus (in *Dilta*) or on the labrum (in *Platerodrilus*), the *Platerodrilus* labrum being a divided sclerite (Figs 4 and 5), the *Dilta* clypeus a one-piece sclerite. However, posteriorly the *Dilta* mandible is articulated with the cranium, whereas the mandible proper of *Platerodrilus* is articulated with the mandibular rod attached to a free sclerite (Figs 3–6). The microcoryphian mandibles, unlike those of lycid larvae, are also characterized by the presence of ventral muscles (Bitsch 2000).

Yet more reminiscent of the lycid larval mandibular structures are those of the Collembola (Ellipura, Entognatha),

where the posterior mandibular articulation is connected to the cranium by a thin rod (Bitsch 2000; Koch 2001) and a rudimentary anterior articulation in the form of a hump-like protrusion of the mandibular wall meets a boss near the base of the anterior tentorial apodeme (Fig. 12). As in *Platerodrilus*, the mandibles of some Collembola (such as *Neoarthropleona*), as well as all Protura (also *Ellipura*, *Entognatha*) are not chewing, stiletto-like and lacking mola (Kluge 2000).

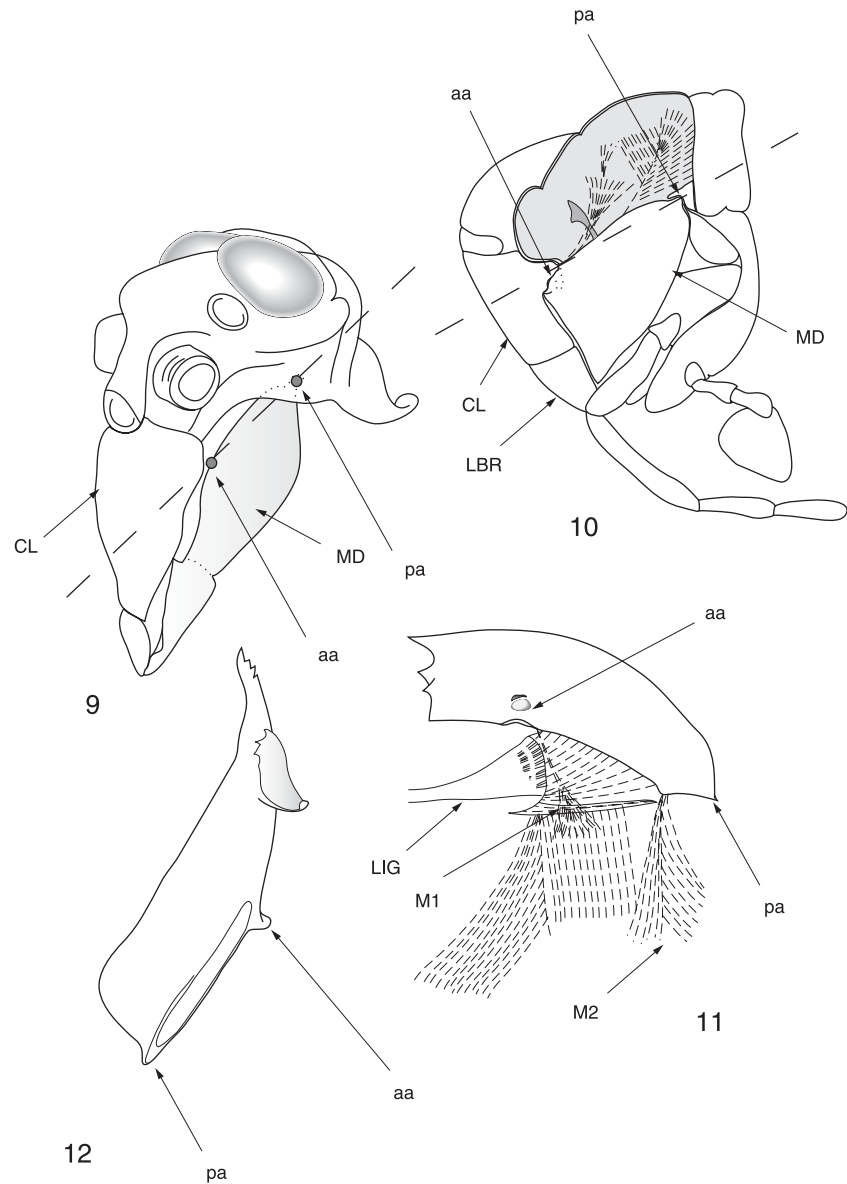
Comparing the lycid larval ‘mandibles’ with those of a *Lithobius* sp. (Chilopoda) (Figs 13, 14) reveals that the mandible in both cases is posteriorly articulated with a thin ‘mandibular’ rod attached on a separate sclerite and the labrum is similarly represented by a paired structure. The sclerite, to which the mandibular rod is attached, is free in *Platerodrilus*



**Figs 5–8**—*Platerodrilus paradoxus* (Mjöberg), larval mandibular structures, dorsal view. —5. Mandibular structures with hypopharynx; —6. right mandible proper with mandibular rod; —7. right labral lobe with stiletto; —8. right labral lobe. aa, anterior articulation; DC, dorsal condyle; M1, anterior cranial muscle; M2, posterior cranial muscle; pa, posterior articulation; VC, ventral condyle.

and rigidly connected to the cranium in *Lithobius*. The pre-mandible proper in both taxa has a dorsal acutabular fossa near its lateral edge making a joint with the condyle – on the labral segment in *Platerodrilus* (Fig. 6) or on the fultura in *Lithobius* (Fig. 14). Similarly arranged are the mandibles of a *Cambarus* sp. (Decapoda) (Bitsch 2000). The myriapods appear to be the only terrestrial arthropods that also have lateral location of the anterior mandibular articulation. The apparent distinction between *Platerodrilus* and *Lithobius* is the division of the mandible of the latter into two sclerites, as well

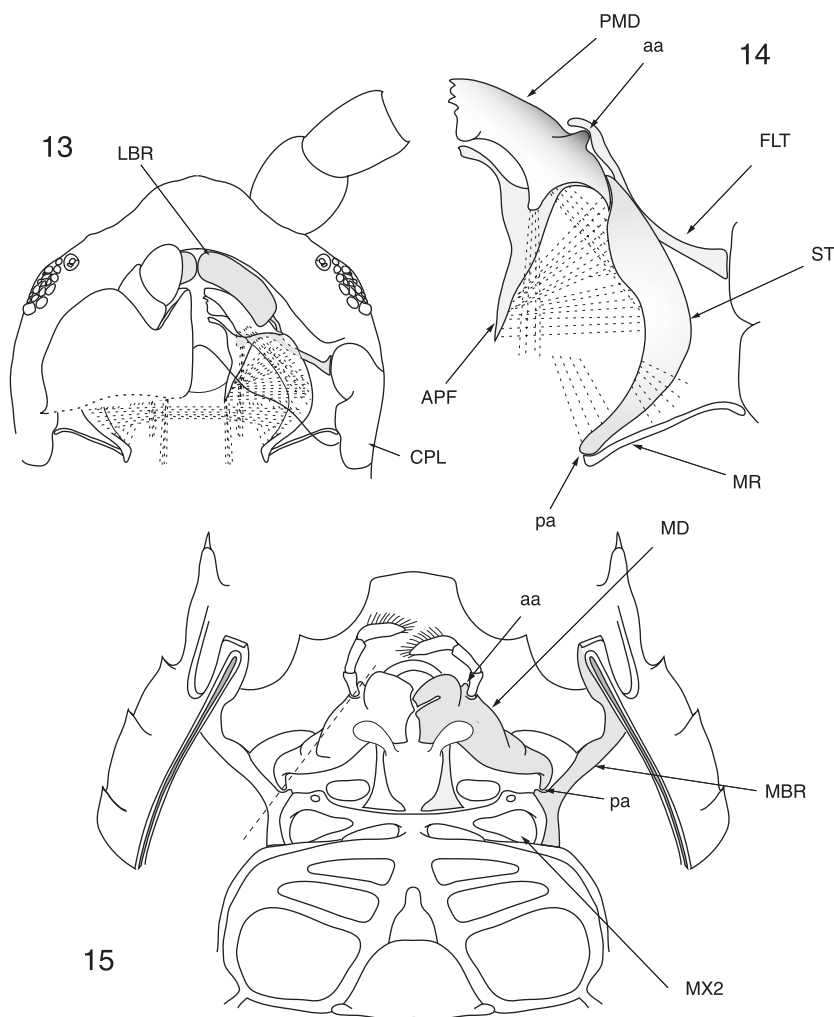
as the presence of ventral muscles and fultura. Despite the similarity of location of the secondary/anterior condyle of the mandible proper and its articulation with a paired non-cranial structure, the possibility of homology of the divided labral segment of *Platerodrilus* with the fultura is doubtful: the prekatatrepsis embryo studies demonstrate the independent origin of the lycid larval labral lobe as a separate limb anterior of the mandible proper (Cicero 1994), while the fultura in chilopods is believed to be related to the hypopharynx (Snodgrass 1935).



**Figs 9–12**—Details of Microcoryphia, Zygentoma and Collembola. —9. *Dilta* sp. (Microcoryphia), head, latero-anterior view (after Manton 1977 and Fürst von Lieven 2000); —10. *Tricholepidion gertschi* (Zygentoma), head in lateral view, antenna removed (after Staniczek 2000); —11. same, right mandible (after Staniczek 2000); —12. *Isotoma viridis* Boulez (Collembola), left mandible (after Kluge 2000). aa, anterior articulation; CL, clypeus; DC, dorsal condyle; LBR, labrum; LIG, ligament; M1, anterior cranial muscle; M2, posterior cranial muscle; MD, mandible; pa, posterior articulation; VC, ventral condyle.

The eucrustacean mandible typically has one point of articulation, though obtaining a second point in the higher lineages (Snodgrass 1950); in most cases it is articulated to the relevant tergum, with rare exceptions, as in Anomura and Brachyura (Fig. 15), where it is hinged with the maxillary bridge. This maxillary bridge may be homologous with the hexapod mandibular rod, as it is unlikely that the mandible, the coxopodite of an independent limb, could acquire its primary articulation on a sclerite belonging to the maxilla, another independent limb. Examples of when the ‘maxillary’ bridge is not attached to the cranium, being connected just with the maxilla (as in *Petrolesthes erimerus* Stimpson – Snodgrass 1950: p. 42) seem to be secondary modifications.

Thus, the closest approach to the mandibular structure of the lycid larvae, among the known hexapods, seems to be in the Collembola and Protura, which also have the facultative dicondyly and the posterior mandibular articulation also connected to the cranium by a thin rod. However, the collembolan and proturan mandible is hinged anteriorly with the cranial/tentorial apodeme, and in this respect the *Platerodrilus* mandibular apparatus appears to more resemble that of Microcoryphia or Zygentoma with their non-cranial anterior articulation. Obviously, the non-cranial location of the anterior articulation of the coxopodite part of a free limb, which has become the mandible, is plesiomorphic. On the other hand, in Microcoryphia and Zygentoma the clypeus, to



**Figs 13–15**—Details of Chilopoda and Eucrustacea. —13. *Lithobius* sp. (Chilopoda), head, ventral view, second maxillae and left maxilla 1 removed; —14. same, right mandible, dorsal view (after Snodgrass 1950 and Kluge 2000); —15. *Aegla prado* Schmitt, ventral skeleton of anterior body region, ventral folds of carapace removed (Anomura, Eucrustacea) (after Snodgrass 1950). aa, anterior articulation; APF, apodeme of fultura; CL, clypeus; CPL, coxopleurite; FLT, fultura; LBR, labrum; LIG, ligament; MBR, maxillary bridge; MD, mandible; MR, mandibular rod; MX, maxilla; pa, posterior articulation; PMD, premandible; ST, stipes.

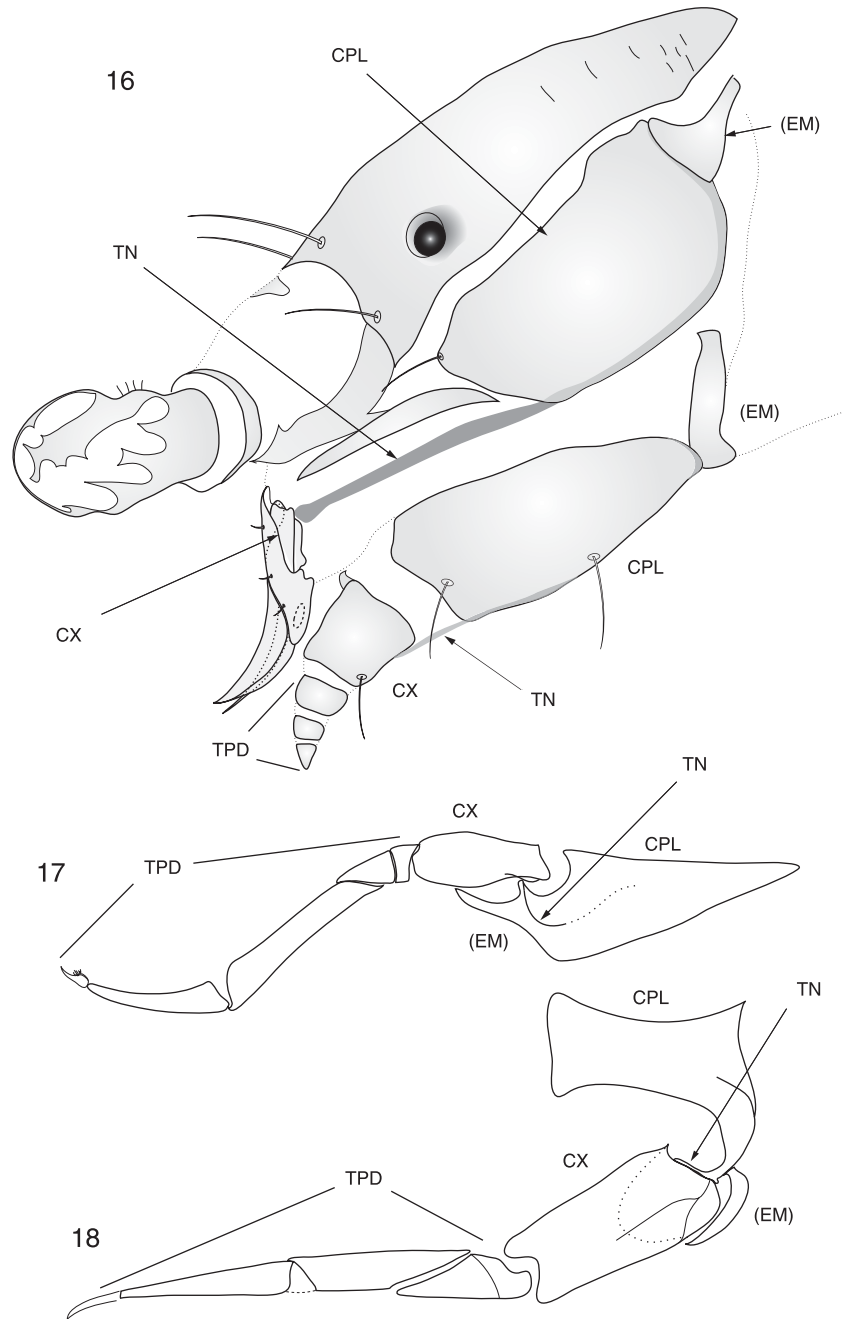
which the mandible is anteriorly articulated, is rigidly attached to the cranium, whereas in *Platerodrilus* the divided labrum is attached only loosely. Microcoryphia and *Zygentoma* also differ by the non-divided labrum and the direct posterior articulation of the mandible with the cranium, the divided labrum and posterior articulation with a free sclerite most probably representing another plesiomorphy of *Platerodrilus*. It is noteworthy that some of the features of the lycid larval mandibular structures that distinguish them from both triplurans and ellipurans appear to be plesiomorphic.

That said, it is necessary to acknowledge that a yet closer match with the lycid larval mandibular apparatus, though possibly achieved through homoplastic development, is found in chilopods, which share the lateral location of the secondary/anterior condyle of the mandible proper and its articulation with a paired non-cranial structure.

The mandible, as it is generally agreed, represents part of a modified limb, presumably the coxopodite (Snodgrass 1950; Bitsch 2000, etc.). The non-cranially attached larval

mandibular structures in *Platerodrilus* allow the following interpretation of their components. The two posterior sclerites divided by a strong suture are hypothetically pieces of the coxopleurite, the episternum and the epimeron. The elongate sclerite derived from the anterior part of the coxopleurite and articulated anteriorly/ventrally to the coxa, is hypothetically the trochantin. Finally, the mandible is the coxopodite of the primitive limb, its telopodite absent (Fig. 16). Whereas the elongate condition of the trochantin is apparently apomorphic, developed from a shorter state, the muscle initially inserted on it lost in the course of such transformation, a similar condition is shared by the Collembola and Protura, as well as some Chilopoda, and in some cases may represent synapomorphies.

Such interpretation of the mandibular structures is supported by the similar arrangement of the maxillary sclerites, the presumed telopodite of a primitive limb represented by the maxillary palps (Fig. 16). Unlike in the mandibular sclerites, however, the maxillary trochantin is interrupted



**Figs 16–18**—Details of larval Polyphaga. —16. *Platerodrilus paradoxus* (Mjöberg), head, lateral view; —17. same as in 16, anterior leg; —18. *Pyractomena* sp., posterior leg. CPL, coxopleurite; CX, coxa; EM, epimeron; MD, mandible; TN, trochantin; TPD, telopodite.

between the middle and the posterior edge of the presumed episternum, where the suture disappears, probably as a result of the fusion of the two episterna into the ventral plate (Fig. 2). In the leg of the *Platerodrilus* larva the trochantin is rudimentary, manifest just as a suture separating the epimeral and episternal parts at the base of the coxopleurite (Fig. 17), whereas in *Pyractomena* (Lampyridae, Polyphaga) it is distally produced to form an additional articulation point for the leg (Fig. 18).

**Phylogenetic Implications**

The following two hypotheses may be suggested to interpret the above-discussed morphologies:

Hypothesis 1: These morphological peculiarities are apomorphic modifications of the Lycidae that occurred as a result of the change in the feeding mode and the family is the terminal element of the Cantharoidea lineage of the Elateriformia.

## Assumptions:

- Transition to primitive feeding mode (filtration of liquids associated with decaying plant debris in damp habitats);
- Transition to simple female metamorphosis;
- Complete loss of ventral closure of cranium by the larvae, with almost complete loss of ventral closure of cranium by the imago, including males;
- Division of larval cranium into separate sclerites, presumably related to gnathal segments;
- Loss of cranial articulation of mandibles;
- Division of mandible into three sclerites;
- Acquisition of facultative dicondylly by the mandible proper;
- Division of labrum, both larval and imaginal, into two sclerites;
- Separation of hypostomal margin from the cranium;
- Complete loss of tentorium;
- Acquisition of similarity with thoracic spiracles by cervical sclerites;
- Acquisition of functionality by metathoracic spiracles;
- Acquisition of similarity with mesothoracic spiracles by metathoracic and abdominal spiracles;
- Loss of coxal articulation by trochantin;
- Division of trochanter into trochanter 1 and trochanter 2; and a number of other reverse morphological changes (Kazantsev 2005).

Hypothesis 2: These morphologies are plesiomorphic, the Lycidae are basal Polyphaga and the Polyphaga evolved as a basal group of the Neoptera.

## Assumptions:

- Independent development of dicondyllic mandibles in the Neoptera and the Palaeoptera (Ephemeroptera and Odonata), and, consequently,
- Independent development of flight and wings in the Neoptera and the Palaeoptera.

The assumptions of the first hypothesis envisage regaining numerous ancestral conditions in unrelated lineages: e.g. transition to simple female metamorphosis in various Lycidae, as well as in most cantharoid families and in such groups, as Dermestidae (*Thylodrias*), Rhipiphoridae (Rhipidiinae), Dascillidae (Karumiinae), Elateridae (Cebrioninae); division of the larval trochanter into trochanter 1 and trochanter 2 in *Platerodrilus*, *Lycus*, *Calopteron*, *Lyponia*, *Xylobanus* and *Porrostoma* (Kazantsev 2005), i.e. throughout the range of lycid lineages; loss of cranial articulation of the mandibles, their transformation into the mandibular structure composed of several separate sclerites and acquisition of facultative dicondylly by the mandible proper, etc. These are quite unlikely events, perhaps, equivalent to regaining by the mammal jaw of the ancestral gill arch condition as a reversal adaptation to the aquatic environment. On the other hand, this hypothesis appears to be supported by the ‘total evidence’ trees (Wheeler 1997; Wheeler *et al.* 2001); however, the data matrices used therein conspicuously lack certain crucial characters of the ‘Coleoptera’, such as the presence of

the divided trochanter (reported by Rosenberg 1943), the larval nature of both male and female imaginal abdominal musculature in the Lycidae (described by Kasap and Crowson 1975), etc.; at the same time the used morphological characters, also according to Klass and Kristensen (2001), apparently need a much closer scrutiny.

On the contrary, the assumptions of the second hypothesis are fairly easy to make because these obviously progressive changes are very likely to have occurred independently, at least in related lineages of hexapods. This hypothesis appears to be supported by the recent reconstructions based on the 18S ribosomal DNA data analyses (e.g. Whiting 2002) that ‘disturbingly’ clearly demonstrate the non-monophyletic nature of the Coleoptera and place the Polyphaga and the Archostemata–Adephaga in different clades. In a study that specifically targeted the basal relationships of the Coleoptera (Caterino *et al.* 2002) the authors admit that adding representatives of other insect orders results in a non-monophyletic Coleoptera; they had (in accordance with their own views on hexapod evolution) to ‘constrain’ the targeted group to make it ‘monophyletic’. It is noteworthy that hexapod monophyly itself has been found to have weak support (Friedrich and Tautz 1995, 2001) in the maximum likelihood trees based on rDNA; a hexapod clade has not been supported by the parsimony analysis based on rDNA either (Wheeler 1997).

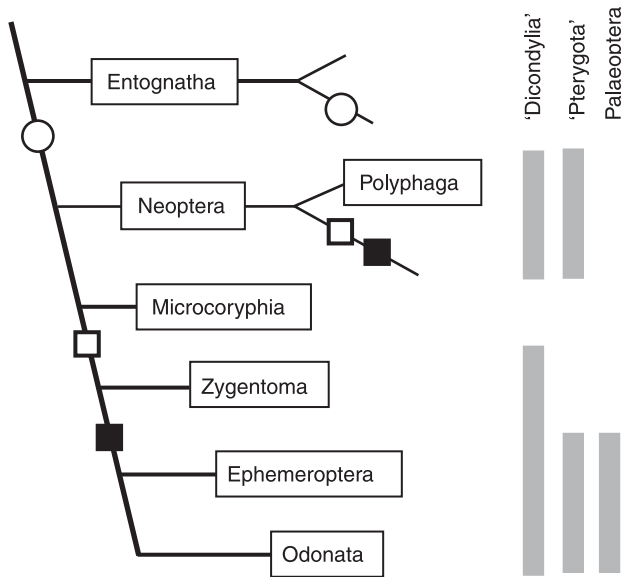
While the reader is free to make his/her own decision, the above considerations, given the weak support of the monophyly of the Pterygota, with very unclear relationships between the Palaeoptera (Ephemeroptera + Odonata), on the one hand, and the Neoptera, including the Oligoneoptera, on the other (Rasnitsyn 1980; Kristensen 1999; Kluge 2000), and the absence of ‘any known operational groundplan’ autapomorphies of the Oligoneoptera (Kristensen 1999), compel me to choose hypothesis two.

The widely accepted theory on the phylogeny of the three Amycerata (‘Ectognatha’) lineages considers Microcoryphia to be the sister group of Dicondylia (*Zygentoma* + Pterygota) (Kristensen 1981; Bitsch 2000, etc.). Dicondylia is supported by the ball-and-socket type of the anterior mandibular articulation and the transverse axis of swing. However, while the difference between the anterior mandibular articulations in Microcoryphia and *Zygentoma* has already been questioned as fairly vague (Kluge 2000; Koch 2001), the discovery of the non-ball-and-socket type anterior mandibular articulations with the longitudinal axis of swing in the Neoptera (Fig. 4) seems to seriously compromise the monophyly of Dicondylia.

The monophyly of Pterygota, which has rather weak support (see above), the real dicondylly being, perhaps, its only weighty autapomorphy (except for the very presence of wings, which yet have to be proved to have originated only once), is also compromised by the discovery of the facultative dicondylly with the longitudinal axis of swing in the Neoptera.

Thus, the *Platerodrilus* larva, an uncontested polyphagan and neopteran, because of its facultative dicondylly does not





**Fig. 19**—Hypothesized phylogeny tree of the major hexapod lineages. Blank circles indicate emergence of the secondary anterior articulation of the mandible; blank squares indicate transition from longitudinal to transverse axis of swing of the mandible; solid squares indicate transition from facultative to real dicondylia.

fit in the Dicondylia and Pterygota. Although its mandible exhibits certain ‘entognathous’ features (such as posterior articulation with a long rod, longitudinal axis of swing, a certain degree of entognathy with the mandibular apparatus at rest directed somewhat backward/inward), it cannot be included in the group characterized by the real entognathy, i.e. by presence of the oral folds and location of the posterior mandibular articulations deep inside the head. Under these circumstances it is tentatively placed in a clade near the Entognatha (Fig. 19), also bearing in mind that the latter taxon is not strongly supported as a monophyletic lineage (Kluge 2000; Klass and Kristensen 2001).

The long mandibular rods, also characteristic of certain Myriapoda and Eucrustacea, are hypothesized to be plesiomorphic both in the Entognatha and the Neoptera and possibly symplesiomorphic of the two lineages. These rods seem to have been preserved in just one lineage of the Polyphaga, the Lycidae, giving way to fusion with the genal sclerite and transformation into the hypostomal sulcus in others (Kazantsev 2005). The non-cranial attachment of these mandibular rods, which are hypothesized to be homologous with the trochantins of a primitive limb, probably represents a plesiomorphy not shared by the entognaths. Certain traits of the larval mandibular structures of Lycidae, which they have in common with the Chilopoda and which have not been reported in other hexapods, such as the lateral location of the secondary/anterior condyle of the mandible proper and its articulation with a paired non-cranial structure, also appear to be plesiomorphic.

On the other hand, while the longitudinal axis of swing of the mandible appears to be a symplesiomorphy of the Neoptera and Microcoryphia, the anterior secondary articulation of the mandible is hypothesized to have originated independently and to be apomorphic in each of the Entognatha and the (Neoptera + (Microcoryphia + (Zygentoma + Palaeoptera))) lineages, with, consequently, the real dicondylia independently developed in the Neoptera and the Palaeoptera (Fig. 19).

## Conclusion

As emphasized by Klass and Kristensen (2001), the impression that the question of hexapod origin and phylogeny is at present conclusively answered is deceptive. The estimates of the actual number of hexapod taxa show that less than one tenth of them are currently described, with only a few sufficiently studied. Moreover, myriads of forms that had been emerging and vanishing during the 400-million-year history of the class and that also have to be considered convert our modest knowledge of the group into a tiny fraction of what is minimally required for a cladistic analysis. I fully agree with Klass and Kristensen (2001) who admit that the evidence accumulation is still in an initial phase. Therefore, it is natural to expect that any contribution, such as this communication on lycid morphology, can challenge the ‘accepted’ views.

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