

# Phylogenetic Relationships of the Suborders of Coleoptera (Insecta)

Rolf G. Beutel\* and Fabian Haas†

\*Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena, D-07743 Jena, Germany; and

†Sektion für Biologisch-Systematische Dokumentation, Universität Ulm, Helmholtzstraße 20, 89081 Ulm, Germany

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One hundred seven external and internal characters of larval and adult representatives of 28 genera of the coleopteran suborders were analyzed cladistically. Four groups of Neuropterida were introduced as outgroup. The analysis yielded 18 trees with a minimum of 194 steps (CI 0.691). All trees support the monophyly of all four suborders and a branching pattern (Archostemata + (Adephaga + (Myxophaga + Polyphaga))). The presence of elytra with meso- and metathoracic locking devices, the specific hind-wing folding, the close connection of exposed sclerites, the absence of the mera, the absence of eight thoracic muscles, the reduced abdominal sternite I, and the invagination of terminal segments are autapomorphies of Coleoptera. The monophyly of Coleoptera excl. Archostemata is supported by further transformations of the thoracic sclerites such as absence of the mesothoracic discriminial line and katapisternal joint, by an internalized or absent metathoracic trochantin, by the presence of a bending zone in the hind-wing, and by eight further muscle losses. Fusion of tibia and tarsus and presence of a single claw are larval synapomorphies of Myxophaga and Polyphaga. Adults are characterized by fusion of prothoracanthin and propleura and by the rigid connection of the meso- and metathoracic ventrites. The eucinetoid lineage of Polyphaga is characterized by the secondary absence of the bending zone of the alae.

This results in a distinctly simplified wing folding mechanism. The monophyly of Cucujiformia (+ Bostrichoidea) is supported by the presence of cryptonephric Malpighian tubules. Transformations of fore- and hind-wings, reinforcement and simplification of the thoracic exoskeleton, and an efficient use of a distinctly reduced set of thoracic muscles play an important role in the early evolution of Coleoptera. Many different larval character transformations take place in the earlier Mesozoic within the suborders. © 2000 The Willi Hennig Society

## INTRODUCTION

With approximately 360,000 described extant species, Coleoptera are by far the largest group of Insecta and Metazoa. Numerous studies were published on the biology, morphology, and classification of the group (see Crowson, 1955, 1981; Lawrence, 1982; Lawrence and Newton, 1982, 1995). However, despite strong interest in coleopteran phylogeny, interrelationships between the currently accepted suborders (Lawrence and Newton, 1995) are still controversial. Different branching patterns were proposed by several authors: ((Archostemata + Adephaga) + (Myxophaga

+ Polyphaga)) by Baehr (1979), (Polyphaga + (Archostemata + (Myxophaga + Adephaga))) by Kukalová-Peck and Lawrence (1993), and (Archostemata + (Adephaga + (Myxophaga + Polyphaga))) by Klausnitzer (1975) and Beutel (1997). In these studies, phylogenetic conclusions were based either on few selected features (Klausnitzer, 1975; Beutel, 1997) or on one character complex (Kukalová-Peck and Lawrence, 1993, hind-wing; Baehr, 1979, prothorax). Mostly or exclusively external features were evaluated in a traditional, Hennigian manner with a priori determination of character polarity and non-numerical tree building.

This contribution presents an evaluation of a broad spectrum of external and internal features of larval and adult representatives of all suborders: 3 genera of Archostemata, 3 genera of Myxophaga, 9 genera of Adephaga, 13 genera of Polyphaga, and 4 neuropterid genera as outgroup (*Agulla*, *Sialis*, *Corydalus*, *Myrmeleon*). Emphasis is placed upon muscular features which were largely or completely neglected in most previous studies. Detailed and comprehensive works on the skeletomuscular system of Coleoptera (e.g., Larsén, 1966; Baehr, 1975) and other groups of insects (see Matsuda, 1965, 1970) are available, but were never analyzed cladistically. Another important character set is the articulation, venation, and folding of the alae. Several characters presented in a comprehensive study by Kukalová-Peck and Lawrence (1993) are also included in this analysis. In addition, numerous measurements and experiments concerning wing folding were carried out (Haas, 1998). Further data concerning wing articulation were extracted from Hörnscheyer (1998).

It is evident that well-founded phylogenetic hypotheses are a necessary prerequisite for the development of evolutionary scenarios. Therefore, this study may contribute to a better understanding of the early evolution of Coleoptera.

## MATERIALS AND METHODS

For a list of taxa examined for skeletal and muscular features see Appendix II.

Larval and adult representatives of Myxophaga, Adephaga, and Polyphaga were embedded in Histo-resin for serial microtome sections (3  $\mu\text{m}$ ). The sections were

stained with methylene-blue and acid fuchsin. Other larvae (Gyrinidae, Haliplidae, Trachypachidae, Carabidae) were embedded in Paraplast, cut at 7  $\mu\text{m}$ , and stained with hemalaun and eosin (see Appendix II).

Scanning electron microscopy was carried out after specimens were cleaned in warm water, detergent, and ultra-sonic sound. They were dried at critical point (only larvae) and coated with gold.

One hundred and seven representatives of 37 families of Coleoptera were examined morphometrically for features of the hind-wing (for a list of species see Haas, 1998). Microscope slides with folded and unfolded hind wings of the same individuals were recorded with a video camera (JVC KY 55F 3CCD), stored (Macintosh Power PC 8500/120, AvidVideoshop 3.0.2.D), and manually digitized. Lengths of veins and surface areas of wings were calculated using self-developed software.

Additional data were extracted from the literature (e.g., thoracic muscles of adults of Coleoptera, Larsén, 1966; muscles of Neuropterida, Matsuda, 1956, 1970; Maki, 1936, 1938; Hasken, 1939; Korn, 1943; Czihak, 1953; Kelsey, 1954, 1957; Mickoleit, 1973; etc.).

## List of Characters

### Larvae, Head

1. Dorsal endocarina: (0) absent; (1) present (Lawrence, 1982). A distinct endocarina is present along the dorsal wall of the head capsule of larvae of Archostemata (Lawrence, 1991; Costa *et al.*, 1988). It has a very short common stem and diverges anteriorly in larvae of *Omma* (Lawrence, 1999).

2. Lateral horizontal ridge of the head capsule: (0) absent; (1) present (Ruhnau, 1986). A temporal horizontal keel is present in larvae (at least in first instars) of Amphizoidae, Hygrobiidae, and Dytiscidae (Ruhnau, 1986). It is absent from larvae of other groups under consideration.

3. Caudal tentorial arms: (0) absent or short; (1) present, elongated, attached to posteroventral part of head capsule (Beutel, 1991; Ruhnau, 1986). Elongated caudal tentorial arms which are attached to the ventral wall

of the head are present in larvae of Amphizoidae, Hygrobiidae, and Dytiscidae. Short caudal arms are present in larvae of Trachypachidae but their apices are not connected with the head capsule.

4. Number of antennomeres: (0) more than 13; (1) 5; (2) 4; (3) 3; (4) 2. Multisegmented antenna are present in some larvae of Neuroptera (Myrmeleontidae; *Sisyra*; Tauber, 1991). A four-segmented antenna is present in larvae of Raphidioptera (Tauber, 1991), Megaloptera (Neunzig and Baker, 1991; Röber, 1942), Polystechotidae (Tauber, 1991), Cupedidae and Ommatidae (Lawrence, 1991, 1999), Adephaga (at least in first-instar larvae), and a few taxa of Polyphaga such as Paederinae and Staphylininae (Kasule, 1970; Frank, 1991). The antenna is five-segmented in the scarabaeid larvae examined (see also Crome, 1957) and three-segmented in larvae of Chrysopidae (Tauber, 1991), in larvae of Micromalthidae (Costa *et al.*, 1988), and in the vast majority of polyphagan larvae. Only two antennomeres are present in myxophagan larvae. The primary four antennomeres are secondarily subdivided in second- and third-instar larvae of Dytiscinae (Bertrand, 1972) (scored as 2 for *Cybister*).

5. Exposure of mouthparts: (0) partly internalized, labrum laterally fused with triangular genal lobe; (1) mouthparts exposed, lateral margin of labrum free. The mouthparts are partly internalized in larvae of Hydroscaphidae (Fig. 8) and Microsporidae. The labrum is laterally fused with a triangular genal lobe (Beutel and Haas, 1998). A similar condition is not found in larvae of other groups under consideration.

6. Mandibular apex: (0) three blunt and strong teeth; (1) slender, with one or several pointed teeth; (2) blunt, with more than three apical teeth. Three blunt and strong apical teeth are present on the mandibles of archostematan larvae (Costa *et al.*, 1988; Lawrence, 1991, 1999). Blunt mandibles with more than three teeth are found in larvae of Chrysomelidae (e.g., *Leptinotarsa*, Lawson, 1991). A more or less slender apical part with or without pointed subapical teeth is present in most larvae of other groups of Coleoptera.

7. Mandibular mola: (0) present; (1) absent. A mandibular mola is present in larvae of Archostemata (Costa *et al.*, 1988; Lawrence, 1991), Myxophaga, and many groups of Polyphaga (e.g., Hydraenidae, Leiodidae, Staphylinidae part., Scarabaeidae, Tenebrionidae). It is absent from larvae of other taxa under consideration.

8. Prosthema: (0) absent; (1) present, rounded and semimembranous; (2) present, slender. A rounded, semimembranous prosthema with small, posteriorly directed spines is present in larvae of Torridincolidae and Hydroscaphidae (Beutel *et al.*, 1999), whereas a more or less slender prosthema with one or several apices is found in larvae of Hydraenidae, Agyrtidae, Leiodidae (part., Newton, 1991; Beutel and Molenda, 1997), Derodontidae, and others. It is absent from larvae of Archostemata, Adephaga (excl. Paussini), and many larvae of Polyphaga.

9. Intramaxillary moveability: (0) fully retained; (1) reduced, no maxillolabial complex; (2) reduced, maxillolabial complex present; (3) reduced, maxilla forms sucking apparatus together with mandible. A moveability between cardo and stipes of at least 45° is found in larvae of Megaloptera (Crampton, 1921; Das, 1937; Röber, 1942), Archostemata (Böving and Craighead, 1931; Costa *et al.*, 1988; Lawrence, 1991), Myxophaga (Beutel and Haas, 1998), Gyrinidae, and many groups of Polyphaga (e.g., Hydraenidae, Leiodidae, Silphidae, Staphylinidae, Scarabaeidae, Byrrhidae, Coccinellidae, Tenebrionidae, Chrysomelidae; Bitsch, 1966; Das, 1937; Jösting, 1942; Beutel, 1995b; Beutel and Molenda, 1997). The moveability is reduced to a degree of maximally 20° in larvae of Raphidioptera, Adephaga (excl. Gyrinidae), Hydrophiloidea, and Histeroidea (Beutel, 1993, 1994a, 1999). The intramaxillary moveability is also strongly restricted in the elateriform larvae with a maxillolabial complex (Beutel, 1995b). The grooved maxillary lacinia is connected with the grooved and elongated mandibles in larvae of Neuroptera, thus forming characteristic suctorial jaws (Tauber, 1991).

10. Separate galea: (0) present; (1) absent. A separate galea is present in larvae of Raphidioptera, Megaloptera (Neunzig and Baker, 1991), Adephaga, and many larvae of Polyphaga (e.g., Spercheidae, Hydrophilidae, Histeridae, Hydraenidae, Leiodidae, Silphidae, Scarabaeidae, Elateriformia). A divided apex of the mala is still recognizable in some staphylinid larvae (Leschen, pers. comm.). A separate galea is absent from larvae of Neuroptera (Wundt, 1961; Tauber, 1991), Myxophaga, and most Staphylinidae and from the cucujiform larvae examined.

11. Ligula: (0) sclerotized, wedge-shaped, and enlarged; (1) ligula not enlarged and unsclerotized (Lawrence, 1982). The ligula is distinctly enlarged, sclerotized, and wedge-shaped in larvae of Archostemata

(Lawrence, 1991, 1999). A similar condition is not found in larvae of other taxa under consideration.

### Larvae, Thorax

12. Leg segments: (0) six; (1) five, tibia fused with tarsus. Legs with coxa, trochanter, femur, tibia, tarsus, and claws are present in most larvae of Neuroptera (e.g., Chrysopidae, Myrmeleontidae; pers. obs. Beutel; Tauber, 1991), Raphidioptera (Tauber, 1991), Megaloptera, Archostemata (Costa *et al.*, 1988; Lawrence, 1991), and Adephaga. Five-segmented legs (including tarsungulus) with fused tibia and tarsus are present in some larvae of Neuroptera (Ithonidae; Tauber, 1991), all larvae of Myxophaga, and the majority of polyphagan larvae (Lawrence, 1982). The tibiotarsal muscles, which are present in larvae of Adephaga, are absent from the larvae of Myxophaga and Polyphaga examined (pers. obs. Beutel; Grassé, 1949). Fewer than five segments are found in Paussini (v. Emden, 1922) and some polyphagan larvae with adaptations toward burrowing in plant tissue (e.g., Cerambycidae part., Chrysomelidae part., Curculionidae).

13. Claws: (0) double; (1) single. A double claw is present in most larvae of Neuroptera (e.g., Chrysopidae, Myrmeleontidae; Tauber, 1991), Raphidioptera (Tauber, 1991), Sialidae, Corydalidae, Ommatidae, Micromalthidae (Lawrence, 1991, 1999), and Adephaga. Legs with a single claw are present in larvae of Haliplidae, Myxophaga, and Polyphaga and first-instar larvae of *Priacma* (Lawrence, 1999).

### Larvae, Abdomen

14. Abdominal tergal ampullae: (0) absent; (1) present. Transverse tergal ampullae are present on the abdominal tergites of larvae of Cupedidae, Ommatidae, and Micromalthidae (Lawrence, 1991, 1999). Similar structures are found in some larvae of Oedemeridae and Cerambycidae (Lawrence, 1991).

15. Abdominal segment IX: (0) well developed, tergum present; (1) largely reduced, tergum absent. The abdominal segment IX is almost completely reduced in larvae of the dytiscoid lineage (Beutel, 1995a), whereas it is well developed in other larvae under consideration.

16. Enlarged terminal spiracles VIII: (0) absent; (1)

present; (2) closed, ventral gills present. Larvae of Noteridae, Amphizoidae, and Dytiscoidae are characterized by exposed terminal spiracles VIII. They were secondarily replaced in larvae of Hygrobiidae by ventral gills according to Ruhnau (1986) (coded as 2). Large terminal spiracles were not found in other larvae under consideration.

17. Spiracular gills: (0) absent; (1) present (Lawrence, 1982; Beutel *et al.*, 1999). Spiracular gills are present in larvae of Myxophaga (Lepiceridae?) (Fig. 9).

18. Pointed sclerotized process of tergum IX: (0) absent; (1) present. A pointed, median sclerotized process of tergum IX is present in larvae of Cupedidae and Micromalthidae (Lawrence, 1991), but not in a larva of *Omma* described by Lawrence (1999). It is also absent from all other larvae examined.

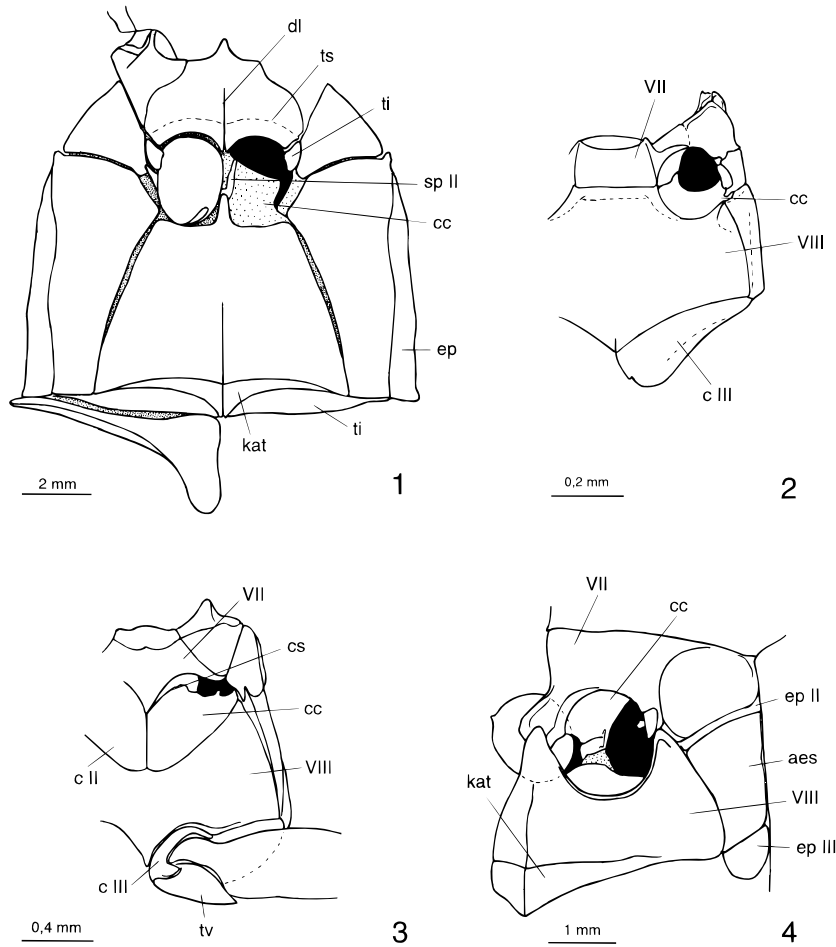
19. Urogomphi: (0) absent; (1) present. Articulated or fixed urogomphi are absent from non-coleopteran larvae; from larvae of Archostemata (Lawrence, 1991), Hydroscaphidae, and Microsporidae, and from larvae of many groups of Polyphaga (Scarabaeidae, eucinetoid lineage s. Kukalova-Peck and Lawrence, 1993). They are present in larvae of Torridincolidae, in most larvae of Adephaga (absent in Haliplidae excl. *Pelto-dytes*), and in larvae of several basal groups of Polyphaga such as Staphylinioidea, Histeroidea, and Hydrophiloidea.

### Adults, General

20. Sclerites: (0) connected by extensive, externally exposed membranes; (1) firmly connected, no membranes exposed externally (Lawrence, 1982). The sclerites which are not covered by the elytra are closely attached to each other in adults of all coleopteran suborders. No membranes are visible externally (Figs. 1–4). The presence of exposed ventral membranous areas in adults of *Chauliognathus* (Campau, 1940) is almost certainly a secondarily derived feature, as the typical condition (with weakly sclerotized cuticle) is found in most other adults of Cantharidae (e.g., *Cantharis* spp.).

### Adults, Head

21. Gula: (0) absent; (1) present, broad (Lawrence and Newton, 1982). A broad sclerotized gula is present



FIGS. 1–4. Pterothorax. (1–3) Ventral view. (1) *Omma stanleyi*; (2) *Torridincola rhodesica*; (3) *Catops* sp.; and (4) *Pterostichus niger* ventrolateral view. Abbreviations used: aes, anepisternum; c, coxa; cc, coxal cavity; cs, connecting suture; dl, discriminal line; ep, episternum; kat, katepisternum; sp, spinasternum; ti, trochantinus; ts, transverse suture; v, ventrite (preepisternum).

in most adults of Coleoptera (Doyen, 1966; Schneider, 1981; Beutel, 1986, 1989a; Belkaceme, 1991; Figs. 10 and 11), Raphidioptera (Fig. 2c in Achtelig, 1967), and Megaloptera (Crampton, 1921; Maki, 1936). A gula or postgenal bridge is absent from adults of Neuroptera (e.g., Myrmeleontidae; Fig. 5 in Sundermeier, 1940; Ferris, 1940a; hypostomal bridge in adults of Nemopteridae; Acker, 1958).

22. Scale-like cuticular structures: (0) absent; (1) absent. Scale-like surface structures are found in adults of Cupedidae and Ommatidae (Fig. 12; Lawrence, 1982). Similar structures were probably also present in adults of Permian and mesozoic fossils assigned to Archostemata by Ponomarenko (1969).

23. Compound eyes: (0) undivided; (1) completely divided. Completely divided compound eyes, with an above-and a below-water component, are found in adults of Gyridae, but not in representatives of other taxa examined.

24. Number of antennomeres: (0) more than 13; (1) 11; (2) fewer than 11. Antennae with a multisegmented flagellum are found in adults of Neuroptera (Theischinger, 1991; Aspöck and Aspöck, 1991; New, 1991) and adults of other endopterygotan groups (e.g., Mecoptera; Heddergott, 1939). Thirteen antennomeres are present in adults of Protocoleoptera and Permocupedidae (Kukalová-Peck, 1991). The antennae are 11-segmented in adults of Archostemata (Lawrence, 1982),

Adephaga (excl. Paussinae and Gyrininae; Beutel, 1989a; Fig. 10), Deleveinae (Torrincolidae), Microsporidae, and many groups of Polyphaga (e.g., Staphylinidae, Eucinetoidae part., Dascilloidea part., Byrrhidae part.; Lawrence, 1982). Fewer than 11 antennomeres are present in adults of Gyrininae, Hydroscaphidae, Hydraenidae (part.), Hydrophiloidea, and Scarabaeidae.

25. Function of antenna: (0) mechano- and chemoreception; (1) accessory breathing organ; (2) perceptive organ for movements of the water surface. The antennae are used as accessory breathing organs in adults of Hydraenidae and Hydrophiloidea (Fig. 11). They are highly specialized receptors for vibrations of the water surface in adults of Gyrinidae. Similar conditions are not found in adults of other groups of Endopterygota.

26. Mandibular mola: (0) absent; (1) present. A mandibular mola is absent from adults of Neuropterida (Maki, 1936, molar area with three teeth but not a true mola; Sundermeier, 1940; Ferris, 1940a; Ferris and Pennebaker, 1939; Röber, 1942; Achtelig, 1967), Archostemata, Adephaga, and several groups of Polyphaga (e.g., Staphylinidae part., Scarabaeidae, Elateroidea, Cantharoidea; Blackwelder, 1936; Lawrence, 1982). A mola is found in adults of Myxophaga and in adults of polyphagan families such as Hydraenidae, Leioididae, Silphidae, Hydrophiloidea, Byrrhidae, Coccinellidae, Tenebrionidae, and Chrysomelidae (Lawrence and Newton, 1982).

27. Single mandibular preapical tooth: (0) absent; (1) on left mandible (Reichardt, 1973). An articulated tooth is found on the left mandible of adults of Myxophaga (Reichardt, 1973; Lawrence, 1982). A similar condition was not found in adults of other groups under consideration.

28. Galea: (0) round, unsclerotized, covered with short hairs; (1) fairly broad, proximally sclerotized, with apical brush; (2) with narrow stalk and apical brush; (3) fimbriate; (4) two-segmented, palp-like; (5) vestigial, part of corpus maxillare; (6) absent. A more or less rounded, unsclerotized galea covered with short hairs is present in adults of Neuropterida (Maki, 1936; Ferris and Pennebaker, 1939; Ferris, 1940a; Röber, 1942; Theischinger, 1991). A fairly broad galea with a more or less distinct basigalea and a dense apical brush is found in adults of most families of Polyphaga (e.g.,

Leioididae, Silphidae, Scarabaeidae, Byrrhidae, Cantharidae, Coccinellidae, Tenebrionidae, Chrysomelidae; Williams, 1938). A galea with a narrow stalk and apical brush is characteristic of adults of Cupedidae (Williams, 1938). The galea is vestigial in adults of Micromalthidae, fimbriate in adults of Hydraenidae and Hydrophiloidea, two-segmented and palp-like in most adults of Adephaga (Fig. 10), and absent in Myxophaga.

29. Lateral lobes of mentum: (0) absent; (1) present (Beutel, 1997). The mentum of adults of Adephaga is characterized by large lateral rounded lobes which enclose the prementum (Fig. 10; Beutel, 1997). A similar condition is not described for other adults examined.

30. Presternal cervical sclerites: (0) absent; (1) present; (2) vestigial. Cervical sclerites are absent from Archostemata, Adephaga (Larsén, 1966; Baehr, 1979), and Myxophaga. Lateral cervical sclerites which are derived from the prothoracic presternum (Matsuda, 1970) are present in most adults of Polyphaga (e.g., Hydraenidae, Hydrophilidae, Leioididae, Derodontidae). They are absent in adults of some groups of Polyphaga, such as Tenebrionidae and Curculionidae, and very small or vestigial in adults of Chrysomelidae and related families (Larsén, 1966).

31. Preepisternal cervical sclerites: (0) absent; (1) present. Cervical sclerites of preepisternal origin are present in adults of Mecoptera and Neuropterida, but absent from adults of other groups of Endopterygota (Matsuda, 1970).

### **Adult, Prothorax**

32. Lateral margin of pronotum: (0) without inflected part; (1) inflected part present (Lawrence, 1982). The pronotum of Coleoptera is large and it extends to the ventral surface of the prothorax (Figs. 10- and 11; Lawrence, 1982). A distinct lateral edge is present in adults of most taxa (obsolete in *Micromalthus*; Lawrence, 1982). A similar condition is not found in adults of the other groups examined.

33. Protibial apex: (0) without antenna-cleaning organ; (1) antenna-cleaning organ present. A characteristic protibial antenna-cleaning organ is present in adults of Trachypachidae and Carabidae but absent from adults of other taxa examined.

34. Prothoracic trochantin: (0) large, completely visible externally; (1) partly visible externally, not fused

with propleura; (2) fused with propleura; (3) notum, sternum, pleura, and trochantin fused. A fairly large prothoracic trochantin is completely visible externally in adults of Cupedidae and Ommatidae (Baehr, 1975: “. . . Trochantinus bei *Priacma* noch ziemlich groß, und im Unterschied zu den Adephega, gänzlich von außen sichtbar”; Fig. 3; pers. obs. Beutel) and also in adults of Neuropterida (Matsuda, 1970). It is partly concealed but moveable in adults of Adephega (Baehr, 1979; pers. obs. Beutel). The trochantin is fused with the propleura in all adults of Myxophaga and Polyphaga (Hlavac, 1972, 1975). The prothoracic notum, sternum, pleura, and trochantin are completely fused in adults of *Micro-malthus* (Lawrence and Newton, 1982).

35. Propleura: (0) part of external body wall; (1) concealed, reduced in size. The pleura is greatly reduced in size and length and is almost always concealed in adults of Polyphaga (Hlavac, 1972, 1975; Lawrence, 1982; Fig. 11).

36. Spinasternum I: (0) well developed; (1) vestigial or absent. A well-developed spinasternum I is present in adults of Neuropterida (excl. Sialidae; Matsuda, 1970) and Cupedidae (pers. obs. Beutel; Baehr, 1975), but absent or strongly reduced in the adults of non-archostematan Coleoptera examined (Campau, 1940; Doyen, 1966; Baehr, 1975; Beutel, 1986, 1989b, 1990a, b, 1994b). A narrow strip anterior to the preepisternum of Meloidae has been interpreted as a possible remnant of a spinasternum I by Larsén (1966).

37. Apical part of procoxa: (0) without condyle; (1) condyle present. A ventral procoxal condyle and a corresponding socket of the prosternal process is present in adults of Adephega (excl. Gyriminae). It is partly reduced but still recognizable in adults of Dytiscidae (coded as 1).

38. Prothoracic defensive glands: (0) absent; (1) present. Prothoracic defensive glands are present in adults of Hygrobiidae and Dytiscidae (Beutel, 1995a), but absent from adults of other taxa under consideration.

39. *M. pleuro-occipitalis* (M. 7; Matsuda, 1970, op-p 2): (0) present; (1) absent. Present in adults of *Chrysopa* (53; Miller, 1933), *Sialis*, and *Corydalus* (Matsuda, 1970), but absent from adults of *Agulla* (Matsuda, 1956), *Myrmeleon* (Korn, 1943), and Coleoptera (pers. obs. Beutel; Larsén, 1966; Baehr, 1975).

40. *M. cervicale-occipitalis torquatus* (M. 8; Matsuda, 1970, op-cv 1, 2): (0) present; (1) absent. This muscle, which connects the dorsolateral angle of the

postocciput and the lateral cervical sclerite, is absent from adults of *Chrysopa* (Miller, 1933) and all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966).

41. *M. mesonoto-postpleuralis* (M. 19; Matsuda, 1970, t-p 17): (0) present; (1) absent. Absent from adults of Neuroptera and all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966; Baehr, 1975).

42. *M. cervicale-coxalis* (M. 26; Matsuda, 1970, cv-cx 3): (0) present; (1) absent. Absent from adults of *Agulla* (Matsuda, 1956), Neuroptera (Matsuda, 1970), Strepsiptera (Kinzelbach, 1971), and all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966; Baehr, 1975, 1979).

43. *M. sterno-coxalis* (M. 27; Matsuda, 1970, s-cx 5; Larsén, 1966, M 18; Baehr, 1975, 18): (0) present; (1) absent. Absent from adults of Gyriminae (Larsén, 1966; Beutel, 1989b), adults of Haliplidae, and most adults of Polyphaga (Baehr, 1979; Larsén, 1966).

44. *M. pleura-trochanteralis* (M. 31; Matsuda, 1970, p-tr 3; Larsén, 1966, M 20; Baehr, 1975, 20): (0) present; (1) absent. Present in adults of Coleoptera (Larsén, 1966; Baehr, 1975, 1979; Beutel, 1986, 1989b), but absent from adults of *Agulla* (Matsuda, 1956), Neuroptera, and Megaloptera (Matsuda, 1970).

### Adult, Pterothorax

45. Ventrites of meso- and metathorax: (0) meso- and metaventrite clearly separated; (1) connected by an intersegmental membrane, metasternal process articulates with posterior part of mesoventrite; (2) both sclerites directly connected between and within mesocoxal cavities, intersegmental membrane absent. The ventral sclerites of the meso- and metathorax, often erroneously referred to as sterna (Campau, 1940; Matsuda, 1970; Beutel, 1992), are clearly separated from each other in adults of Neuropterida, in extant adults of Cupedidae and Ommatidae (Fig. 1; Baehr, 1975), and also in fossils assigned to Archostemata by Ponomarenko (e.g., *Platycupes*; Ponomarenko, 1969). The metasternal process articulates with the posterior mesoventrite in adults of Adephega (Fig. 4; Beutel, 1986, 1992, 1994b; Belkaceme, 1991). Both parts are connected by an intersegmental membrane within the mesocoxal cavity and can be separated easily. Meso- and metathoracic ventrites are directly attached to each other within the mesocoxal cavities in all adults of Myxophaga (Fig. 2) and Polyphaga examined. A ventral intersegmental

membrane is absent (Fig. 3; e.g., *Ochthebius*, *Catops*, *Silpha*, *Hydrobius*, *Pachnoda*, *Byrrhus*, *Leptinotarsa*; Fig. 16 in Rivnay, 1928; Fig. 3A in Blackwelder, 1936; Campau, 1940; Fig. 35, "transverse thickening," in Doyen, 1966).

46. Katepisternal mesocoxal joint: (0) present; (1) absent. A ventral mesocoxal joint is present in adults of Mecoptera (Fig. 4 in Mickoleit, 1967), Neuropterida (Fig. 15 in Acker, 1958; sternacoila, Fig. 15 in Maki, 1936; Fig. 63 in Ferris and Pennebaker, 1939; Fig. 13 in Ferris, 1940a; Czihak, 1953; Matsuda, 1956), Cupedidae, and Ommatidae (Fig. 1; Baehr, 1975; pers. obs. Beutel), but absent from the adults of Adephaga, Myxophaga, and Polyphaga examined (Larsén, 1966; pers. obs. Beutel).

47. Mesoventrite: (0) internalized, discriminal line present; (1) internalized, discriminal line absent. A mesothoracic median discriminal line which results from the internalization of the sternum (Campau, 1940; Ferris, 1940b, median line of contact of the subcoxae) and a corresponding internal median ridge is present in adults of Neuropterida (Ferris and Pennebaker, 1939; Ferris, 1940a; Matsuda, 1970), Cupedidae (Fig. 5), Ommatidae (Baehr, 1975; pers. obs. Beutel), and Gyrininae (Larsén, 1966). It is absent in adults of *Spanglerogyrus* (Beutel, 1990a) and all other Coleoptera.

48. Mesothoracic transverse ridge: (0) present; (1)

absent. A mesothoracic transverse ridge which separates the katepisternum from the preepisternum is present in adults of Panorpidae (Figs. 34 and 35 in Issiki, 1933), Neuropterida (Ferris and Pennebaker, 1939; Ferris, 1940a; Fig. 15 in Acker, 1958; Matsuda, 1956, 1970), Cupedidae, and Ommatidae examined (Fig. 1; Baehr, 1975). It is absent from adults of Micro-malthidae and all other groups of Coleoptera (Blackwelder, 1936; Larsén, 1966; Doyen, 1966).

49. Mesofurcae: (0) arise between mesocoxae with common stem; (1) mesofurcal arms distinctly separated at base. The mesofurcae arise with a common base between the mesocoxae in adults of Neuropterida (Maki, 1936; Ferris and Pennebaker, 1939; Fig. 15 in Acker, 1958; pers. obs. Beutel), Cupedidae, and Ommatidae (pers. obs. Beutel; Baehr, 1975). The arms are separated from each other at their base with individual invaginations in adults of Adephaga (excl. Gyrinidae part.), Myxophaga, and Polyphaga examined (e.g., *Ytu*, *Satonius*, *Hydroscapha*, *Microsporus*, *Ochthebius*, *Catops*, *Silpha*, *Pachnoda*, *Byrrhus*, *Tenebrio*; pers. obs. Beutel; Larsén, 1966; Doyen, 1966).

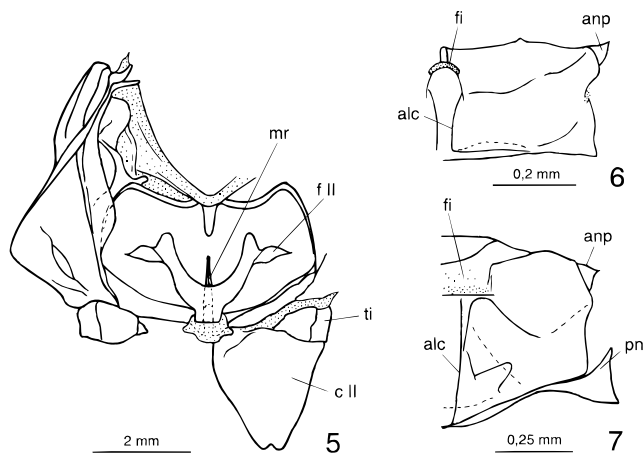
50. Mesothoracic meron: (0) present; (1) absent (Whiting *et al.*, 1997). A mesothoracic meron is absent in hemimetabolous insects, Coleoptera, and Hymenoptera. It is present in other groups of Endopterygota (Kristensen, 1981; Whiting *et al.*, 1997).

51. Fore-wings: (0) unsclerotized; (1) partly sclerotized, with reticulate pattern; (2) fully sclerotized. Fore-wings which are transformed into elytra with lateral epipleura are present in all extant Coleoptera (Lawrence and Newton, 1982). The elytra of adults of Proto-coleoptera (Kukalová-Peck, 1991), Cupedidae (extant and fossil species), and Ommatidae are characterized by a reticulate pattern. They are not fully sclerotized like in other adults of Coleoptera.

52. Mesothoracic elytra-locking device: (0) absent; (1) present. The median part of the mesoscutellum is transformed into a triangular elytra-locking device in adults of Coleoptera (Heberdey, 1938). It is not exposed in some adults of Coleoptera (e.g., Noteridae excl. Phreatodytinae; Belkaceme, 1991).

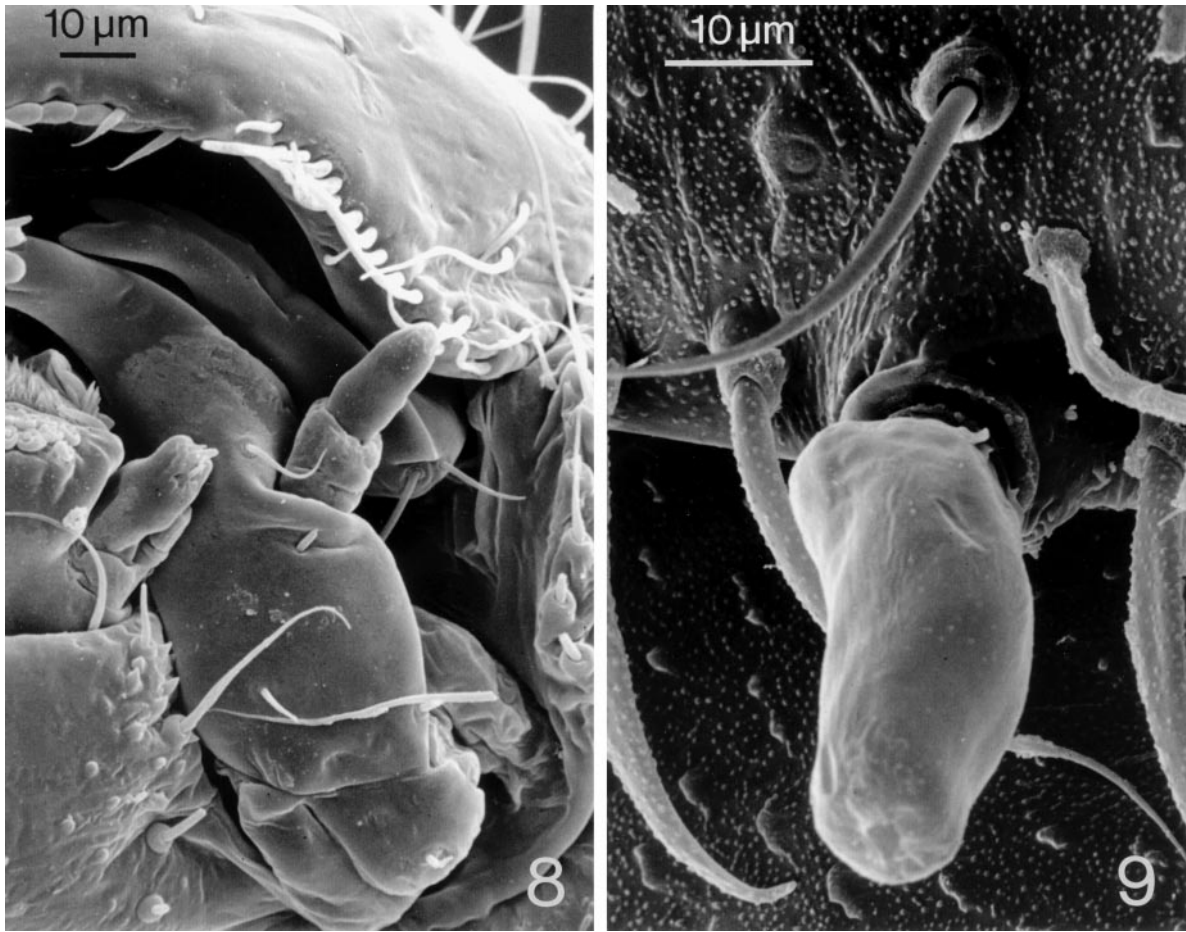
53. *M. scutello-postnotalis* (M. 41; Matsuda, 1970, t-13): (0) present; (1) absent. Absent from all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966; Baehr, 1975).

54. *M. mesosterni secundus* (M. 43; Matsuda, 1970, s-12; Larsén, 1966, M 31; Baehr, 1975, 26): (0) present;



FIGS. 5–7. (5) *Priacma serrata*, metathorax, opened dorsally, muscles removed. (6 and 7) Metanotum, dorsal view, (6) *Torridincola rhodesica* and (7) *Catops* sp. Abbreviations used: alc, alacrista; anp, anterior notal process; c, coxa; f, furca; fi, metanotal fissure; mr, median ridge of ventrite II; pn, postnotum; ti, trochantinus.





FIGS. 8 and 9. SEM micrographs. (8) Larval head of *Hydroscapha natans*, labrum and triangular genal fold; (9) *H. natans*, prothoracic spiracular gill.

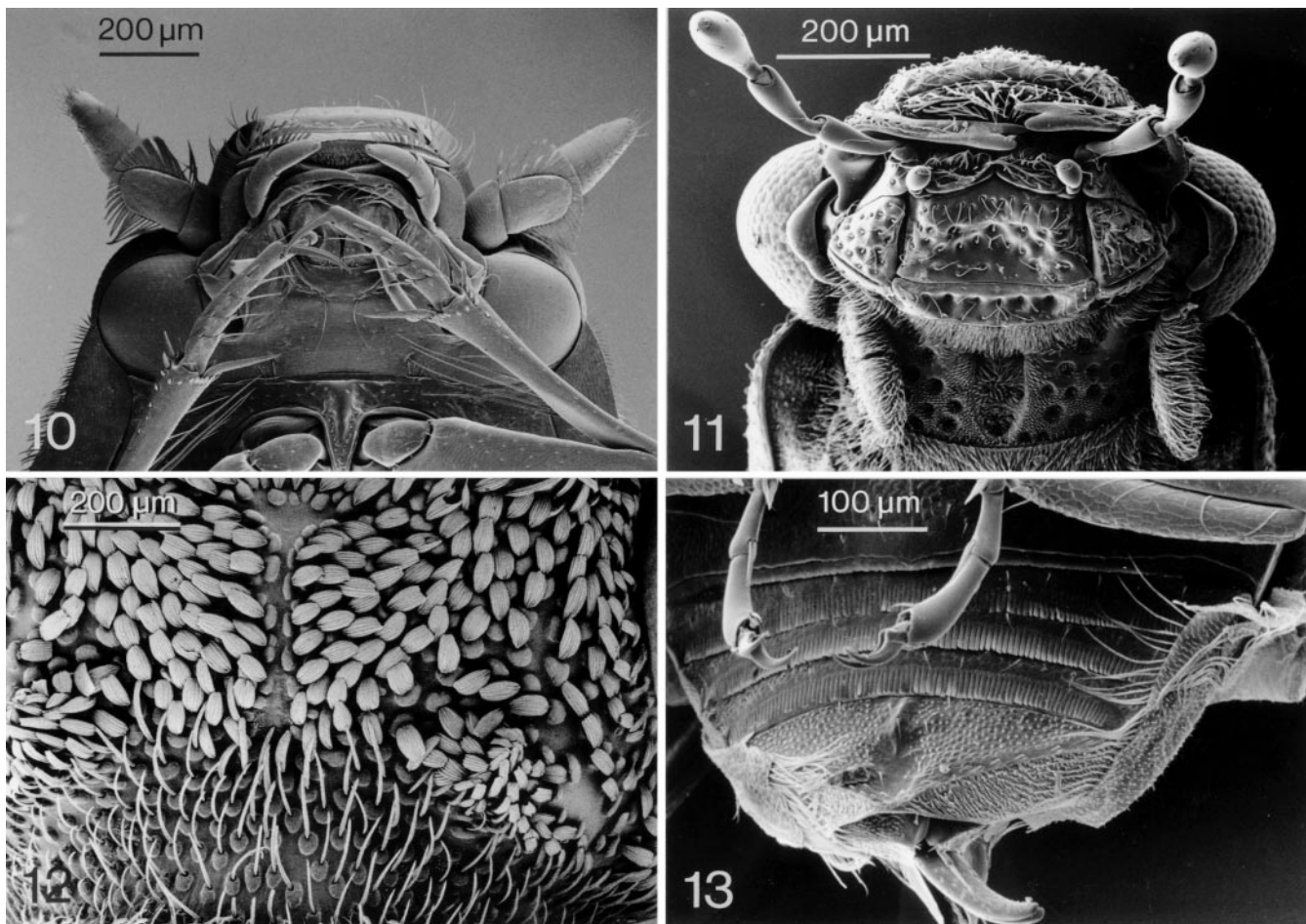
(1) absent. This muscle, which connects the mesofurca and the spina I, is well developed in adults of *Corydalus*, *Sialis* (Kelsey, 1957; Czihak, 1953), and *Priacma serrata* (Baehr, 1975). It is also present but very thin in most adults of Adephaga (absent in Haliplidae, Noteridae, Hygrobiidae, Dytiscidae part.; Larsén, 1996; Beutel, 1986, 1989b; Belkaceme, 1991). It is absent from all adults of Polyphaga examined (Larsén, 1966), with the exception of *Lytta* and *Meloe*, and from adults of *Myrmeleon* (Korn, 1943). A relatively strong mesal component of *M. mesosterni primus*, which arises between the profurcae, is present in adults of *Hydroscapha* and *Microsporus*. It is not homologous with *M. mesosterni secundus* as it is clearly different in terms of shape and insertion.

55. *Mm. notosternales II* (M. 44; Matsuda, 1970, t-p 5/6; Baehr, 1975, 27): (0) present; (1) absent. Very strong

in adults of Neuropterida (Matsuda, 1956; Maki, 1936; Czihak, 1953; Kelsey, 1957; Matsuda, 1970) and *Priacma* (Baehr, 1975), but absent from adults of Myxophaga, Adephaga, and Polyphaga (pers. obs. Beutel; Larsén, 1966; Baehr, 1975; Beutel, 1986, 1990a; Belkaceme, 1991).

56. *M. noto-pleurocostalis longus II* (M. 46; Matsuda, 1970, t-p 12/15; Baehr, 1975, 28): (0) present; (1) absent. This broad muscle, which is not homologous with the thin anterior notopleural muscle described by Larsén (1966, M 33), is present in adults of Neuroptera (*Myrmeleon*; Korn, 1943), Megaloptera (Maki, 1936; Czihak, 1953; Kelsey, 1957; Matsuda, 1970), and *Priacma* (Baehr, 1975), but absent from adults of *Agulla* (Matsuda, 1956) and non-archostematan Coleoptera (Larsén, 1966; Baehr, 1975; Beutel, 1986; Belkaceme, 1991).

57. *M. noto-episternalis longus II* (M. 48; Matsuda,



FIGS. 10–13. SEM micrographs. (10) Head of *Spanglerogyrus albiventris*, ventral view; (11) head of *Hydrochus* sp., ventral view; (12) dorsal surface of the head of *Priacma serrata*, cuticular scales and stiff hairs; (13) posterior abdominal segments of *Torridincola rhodesica*.

1970, t-p 8): (0) present; (1) absent. Absent from adults of *Agulla* (Matsuda, 1956) and Coleoptera (pers. obs. Beutel; Larsén, 1966; Baehr, 1975; Beutel, 1986; Belkaceme, 1991).

58. *M. episterno-sternalis* II (M. 50; Matsuda, 1970, p 3; Baehr, 1975, 33): (0) present; (1) absent. Absent from adults of non-archostematan Coleoptera (pers. obs. Beutel; Larsén, 1966; Beutel, 1986; Belkaceme, 1991).

59. *M. pleura-alaris* a and b (*Mm. pleurocosta-alaris* and *episterno-alaris* II) (M. 53, M. 54; Matsuda, 1970, t-p 14, t-p 13; Baehr, 1975, 30, 31): (0) clearly separated; (1) single muscle or two branches inserting on one tendon (Larsén, 1966, M 36). Both subcomponents of the muscle have separate origins and insertions in

adults of Neuropterida (Korn, 1943; Maki, 1936; Czihak, 1953; Kelsey, 1957) and *Priacma* (Baehr, 1975), but not in adults of non-archostematan Coleoptera (Larsén, 1966; Beutel, 1986; Belkaceme, 1991). In most cases only one component is present. If two branches are present, they are attached to the 3Ax by means of a common tendon.

60. *M. intraepisternalis* II (M. 56; Matsuda, 1970, p 1): (0) present; (1) absent. Absent from all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966; Baehr, 1975; Beutel, 1986; Belkaceme, 1991).

61. *M. pleurocosto-praenotalis* II (M. 57; Matsuda, 1970, t-p 4): (0) present; (1) absent. Absent from all adults of Coleoptera examined (pers. obs. Beutel;

Larsén, 1966; Baehr, 1975; Beutel, 1986; Belkaceme, 1991).

62. *M. noto-trochantinalis* II (M. 59; Matsuda, 1970, t-ti(cx) 2; Larsén, 1966, M 39; Baehr, 1975, 36): (0) present; (1) absent. Absent from adults of some genera of Adephaga and from adults of Myxophaga and Polyphaga (pers. obs. Beutel; Larsén, 1966).

63. *M. coxa-subalaris* II (M. 64; Matsuda, 1970, t-cx 8; Larsén, 1966, M 43; Baehr, 1975, 40): (0) present; (1) absent. Absent from adults of Polyphaga (Larsén, 1966).

64. *M. episterno-trochantinalis* II (M. 68; Matsuda, 1970, p-ti(cx) 3): (0) present; (1) absent. Absent from adults of *Myrmeleon* (Korn, 1943) and Coleoptera (Larsén, 1966; Baehr, 1975; Beutel, 1986; Belkaceme, 1991).

65. *M. noto-trochanteralis* (M. 69; Matsuda, 1970, t-tr 1; Larsén, 1966, M 47; Baehr, 1975, 44): (0) present; (1) absent. Absent from adults of *Microsporus* and all adults of Polyphaga examined (Larsén, 1966).

66. Mesal metacoxal walls: (0) not fused; (1) metacoxae attached to each other along ventromedian edge; (2) mesal walls fused. The mesal metacoxal walls are fused in adults of Trachypachidae and Dytiscoidea (Beutel and Belkaceme, 1986; Beutel and Roughley, 1987, 1988) but separate in adults of all other groups of Coleoptera and Insecta. They are connected along their ventromedian edges in adults of Gyrininae.

67. Transverse metascutal fissure: (0) absent; (1) present (Brodsky, 1994). A membranous, transverse metascutal fissure or area is characteristic for Coleoptera (Figs. 6 and 7; Fig. 24 in Campau, 1940; Doyen, 1966; membranous area, Figs. 10 and 61 in Larsén, 1966; Beutel, 1986, 1988, 1990a, b, 1994b; Brodsky, 1994). The presence of this structure results in focusing of the effort from contraction of the dorsal longitudinal muscles (M. 79, 80) on the anterior notal process (Brodsky, 1994).

68. Metathoracic elytra-locking device: (0) absent; (1) present. Posteriorly converging alacristae which border a shallow median longitudinal depression are present in Coleoptera (Figs. 6 and 7; Fig. 24 in Campau, 1940; Doyen, 1966; Larsén, 1966, all Coleoptera; Beutel, 1986, 1988, 1990a, b, 1994b; Belkaceme, 1986, 1991; Brodsky, 1994). They function as an additional elytra-locking device.

69. Metapostnotum: (0) divided medially; (1) undivided medially. The metapostnotum is medially divided in adults of Neuropterida (Kristensen, 1991; Achteleg, 1975, 1981).

70. Metathoracic meron: (0) present; (1) absent (Whiting *et al.*, 1997). A metathoracic meron is absent in hemimetabolous insects, Coleoptera, and Hymenoptera. It is present in other groups of Endopterygota (Kristensen, 1981; Whiting *et al.*, 1997), even though very indistinct in adults of Strepsiptera (Kinzelbach, 1971, sutura coxomeralis).

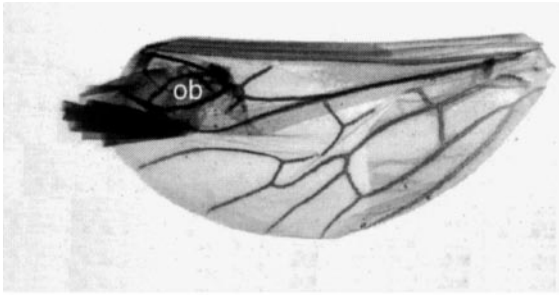
71. Metacoxae: (0) transverse, not recessed into cavities; (1) not transverse, recessed into cavities (Lawrence, 1982). The metacoxae of Coleoptera are distinctly transverse (Fig. 1), and not globular or elongated, and recessed into cavities as in other insects under consideration (Larsén, 1966; Baehr, 1975; Matsuda, 1970; Lawrence, 1981).

72. Metathoracic trochantin: (0) broad, well developed; (1) reduced, not visible externally. The metathoracic trochantin is well developed and visible externally in adults of Neuropterida (Maki, 1936; Ferris and Pennebaker, 1939; Ferris, 1940a; Acker, 1958; Matsuda, 1970), Cupedidae, and Ommatidae (Fig. 1; Baehr, 1975). It is completely absent from the external surface in all adults of Adephaga, Myxophaga (Figs. 2 and 3), and Polyphaga.

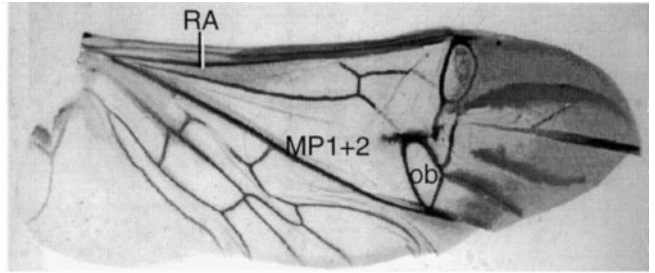
73. Number of costal cross veins: (0) fewer than five; (1) more than five. More than five costal cross veins are present in the hind-wings of adults of Raphidioptera (Aspöck and Aspöck, 1991), Neuroptera (New, 1991), and Megaloptera (part.; Theischinger, 1991; pers. obs. Beutel).

74. Hind-wing folding: (0) absent; (1) longitudinal and transverse hind-wing folding, wings completely covered under elytra in repose (Lawrence, 1982). The hind wings are folded longitudinally in adults of Proto-coleoptera (Kukalová, 1969; Haas, 1998) and not completely covered by the elytra. This is not coded as a separate character state as fossil Coleoptera are not included in the analysis. The capacity of folding the distal part of the hind-wing in order to store them under the elytra is characteristic of extant Coleoptera (Figs. 14–21). Unfolding of the alae is achieved by spreading of the longitudinal veins RA and MP 1+2 in all beetles examined (pers. obs. Haas).

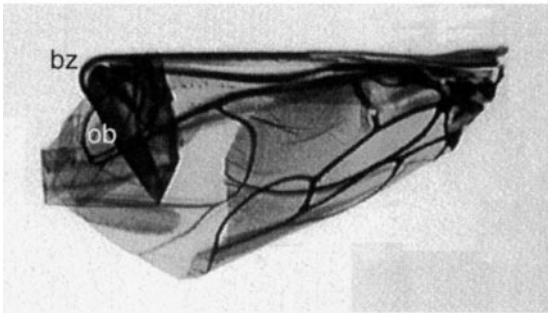
75. Apical part of hind-wing in resting position: (0)



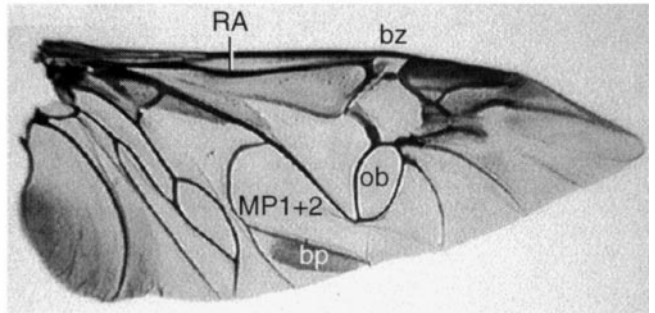
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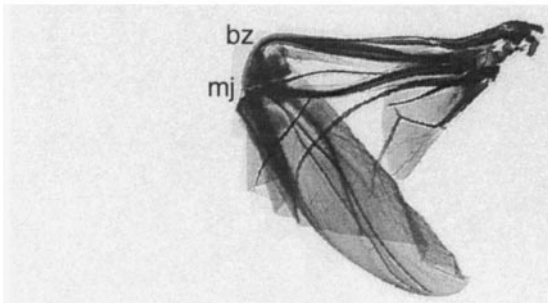
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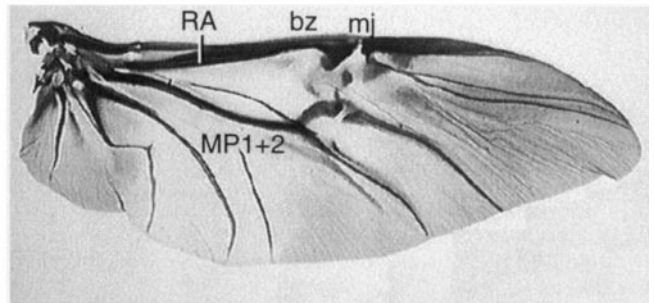
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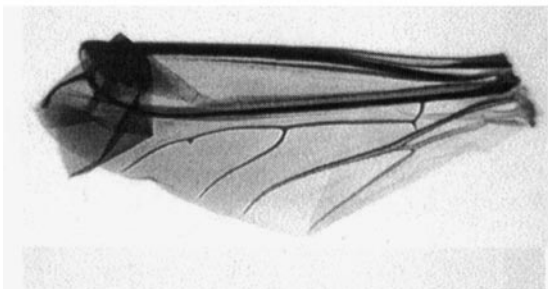
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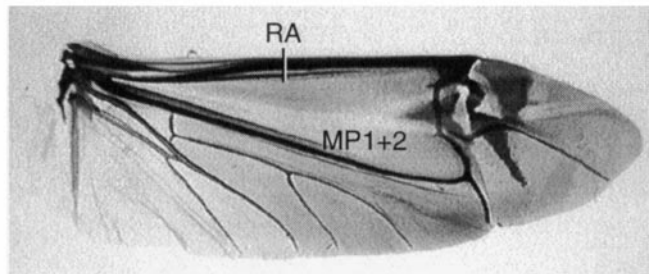
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FIGS. 14–21. The folded and unfolded alae of (14 and 15) *Priacma serrata*; (16 and 17) *Acilius sulcatus*; (18 and 19) *Aphodius fossor*; (20 and 21) *Cerambyx scopoli*. Abbreviations used: bz, bending zone; bp, binding patch; ob, oblongum cell; mj, marginal joint; MP1+2, media posterior; RA, radius anterior.

unfolded; (1) rolled; (2) folded. The apical part of the alae is rolled in the resting position in adults of Archostemata, *Spanglerogyrus*, Haliplidae, and some small dytiscids, but folded in other adults of Coleoptera examined.

76. Oblongum of hind-wing: (0) present; (1) absent. An oblongum of the hind wing, i.e., a distinct, closed cell between RP and MP1 (sensu Kukalová-Peck and Lawrence, 1993) is present in adults of Ommatidae, Cupedidae (Figs. 14 and 15), Lepiceridae, Microsporidae, Hydroscaphidae (part.), most Torridincolidae, and Adephaga (Figs. 16 and 17).

77. Subcubital binding patch: (0) absent; (1) present. A characteristic subcubital binding patch is present on the hind-wings of adults of *Trachypachus* and Dytiscoidea (excl. Hygrobiidae; Beutel and Roughley, 1988) (Figs. 16 and 17). It is absent from the alae of other groups of Endopterygota examined and from adults of most other groups of Coleoptera (katastigma present in some representatives of Polyphaga; Heberdey, 1938) (Figs. 14, 15, and 18–21).

78. Anterior margin of hind-wing: (0) not flexible; (1) flexible, bending zone absent; (2) bending zone present; (3) marginal joint (Haas, 1998). A distinct bending zone (“Biegungszone”; Schneider, 1978) is present in adults of Myxophaga, Adephaga (Figs. 16 and 17), and the hydrophiloid lineage of Polyphaga (sensu Hansen, 1997). It is absent from adults of Archostemata (Figs. 14 and 15) and from all adults of the eucinetoid lineage (sensu Hansen, 1997) (Figs. 20 and 21). The costal margin of the alae of all Scarabaeoidea is marked by a marginal joint (“Randgelenk”; Schneider, 1978) which allows the sharp bending of the costal margin (Figs. 18 and 19).

79. MP1+2: (0) bent anteriorly or straight; (1) bent posteriorly (Haas, 1998). MP1+2 is bent anteriorly or straight in adults of non-coleopteran Endopterygota, Archostemata, Hydroscaphidae, and Adephaga. It is bent posteriorly in all adults of Polyphaga examined.

80. RP3+4: (0) not crossed by folding line; (1) crossed by folding line (Haas, 1998). RP3+4 is crossed by a folding line in the alae of all adults of Coleoptera except for the eucinetoid lineage.

81. Triangular fold: (0) completely absent; (1) RA3+4 cut twice by triangular fold; (2) RA3+4 not cut twice by triangular fold (Kukalová-Peck and Lawrence, 1993). The basal portion of RA3+4 is cut twice by a triangular fold in adults of Archostemata, Myxophaga,

and Adephaga (Kukalová-Peck and Lawrence, 1993). A triangular fold crossing RA3+4 is absent from adults of Polyphaga according to Kukalová-Peck and Lawrence (1993).

82. 1Ax: (0) without caudal process; (1) caudal process present (Kukalová-Peck and Lawrence, 1993). A more or less elongated caudal process of 1Ax is present in adults of Archostemata, Adephaga, and some families of Polyphaga (Dascillidae, Buprestidae, Byrrhidae; Hörnschemeyer, 1997). The process is absent in adults of Microsporidae and Neuropterida (Hörnschemeyer, 1997) and most adults of Polyphaga (Kukalová-Peck and Lawrence, 1993). However, it is present in adults of most groups of Endopterygota such as Hymenoptera, Lepidoptera, Trichoptera, and Strepsiptera (Snodgrass, 1909; Kinzelbach, 1971; Ivanov, 1995).

83. Fulcrum: (0) underneath 2Ax; (1) underneath 1Ax and 2Ax; (2) underneath 1Ax (Hörnschemeyer, 1997). The fulcrum lies underneath 2Ax in adults of Archostemata. It lies under both axillary sclerites in adults of Megaloptera and Raphidioptera and under 1Ax in adults of Myrmeleontidae, Adephaga, Myxophaga, and Polyphaga (Hörnschemeyer, 1997).

84. 2Ax: (0) without a lateral process; (1) process present (Hörnschemeyer, 1997). A lateral process originates from the ventral side of 2Ax of adults of Adephaga, Myxophaga, and Polyphaga. It extends to the ventral side of 1Ax. The process is absent from adults of Neuropterida and Archostemata (Hörnschemeyer, 1997).

85. Angle between the axis anterior notal process–1Ax and the disto-cranial margin of 1Ax: (0) 50° or more; (1) less than 45° (Hörnschemeyer, 1997). The angle is 50° or more in all adults of Neuropterida, Archostemata, Adephaga, and Myxophaga examined by Hörnschemeyer (1997). It is 45° or less in adults of Polyphaga.

86. M. scutello-postnotalis metathoracis (M. 81; Matsuda, 1970, t 13): (0) present; (1) absent. Absent from adults of *Agulla* (Matsuda, 1956) and Neuroptera (Korn, 1943) and all adults of Coleoptera examined (pers. obs. Beutel; Larsén, 1966; Beutel, 1986, 1988, 1990a, b, 1994b; Belkaceme, 1991; Brodsky, 1994).

87. M. metasterni-primus (M. 82; Matsuda, 1970, s 13; Larsén, 1966, M 62; Baehr, 1975, 52): (0) present; (1) absent. Absent only from adults of *Hydroscapha* and *Microsporus*.

88. M. metasterni-secundus (M. 83; Matsuda, 1970,

s 12; Larsén, 1966, M 63; Baehr, 1975, 53): (0) present; (1) absent. The muscle connecting the metafurca with the spina II is present in adults of *Sialis*, *Corydalus* (Matsuda, 1970), *Priacma* (Baehr, 1975), *Haliplus* (Larsén, 1966), Trachypachidae (Beutel, 1988, 1994b), and most Carabidae (Larsén, 1966). It is absent from adults of Neuroptera (Korn, 1943; Czihak, 1957) and all adults of Myxophaga and Polyphaga examined.

89. Mm. notoepisternales breves III (M. 89; Matsuda, 1970, t-p 3; Baehr, 1975, 56): (0) present; (1) absent. Present in adults of Neuroptera (Matsuda, 1970) and Megaloptera (Matsuda, 1970). Also present but thin in adults of *Priacma* (Baehr, 1975). Absent from adults of all other coleopteran groups examined (Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1991) and probably from *Agulla* (Matsuda, 1956; scored as ?).

90. M. noto-pleuralis a III (M. 91; Matsuda, 1970, t-p 12?; Larsén, 1966, M 68; Baehr, 1975, 58): (0) present in mature adults; (1) absent in mature adults. Absent from adults of Neuroptera (Korn, 1943) and all examined mature adults of Myxophaga, Adepfaga, and Polyphaga (Larsén, 1966; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1991). Probably also absent from adults of *Agulla* (Matsuda, 1956; scored as ?).

91. M. noto-pleuralis b III (M. 92; Matsuda, 1970, t-p 15): (0) present; (1) absent. Absent in all adults of Coleoptera (Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1991). Probably also absent from adults of *Agulla* (Matsuda, 1956; scored as ?).

92. M. pleura-alaris a and b III (Mm. 95, 96; Matsuda, 1970, Mm. t-p 14, t-p 13; Baehr, 1975, 60, 61): (0) separate; (1) with common insertion (Larsén, 1966, M 71). These muscles have a separate area of origin and insertion in adults of Neuroptera (Korn, 1943), Megaloptera (Czihak, 1953; Matsuda, 1970), and *Priacma* (Baehr, 1975). They have a common insertion on a small sclerite proximal to 3Ax in adults of Adepfaga, Myxophaga, and Polyphaga (pers. obs. Beutel; Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1991).

93. Mm. furco-pleurocostales III (M. 99; Matsuda, 1970, p-s 1): present; (1) absent. Absent in all adults of Coleoptera (Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1991).

94. M. noto-trochantinalis III (M. 100; Matsuda, 1970, t-ti(cx) 2; Larsén, 1966, M 74; Baehr, 1975, 69): (0) present; (1) absent. Absent from adults of *Hydroscapha*,

*Microsporus*, Adepfaga, Hydrophilidae, and *Cetonia* (Larsén, 1966; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1991).

95. M. episterno-coxalis III (M. 103; Matsuda, 1970, p-cx 5; Larsén, 1966, M 77; Baehr, 1975, 72): (0) present; (1) absent. Absent from adults of *Selatosomus* and Adepfaga (Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1986, 1991).

96. M. sterno-coxalis III (M. 106; Matsuda 1970, s-cx 5, p-ti(cx) 1?; Larsén, 1966, M 80): (0) present; (1) absent. Absent from all Coleoptera examined (excl. *Ips*; Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1986, 1991).

97. M. episterno-trochantinalis III (M. 110; Matsuda, 1970, p-ti(cx) 3): (0) present; (1) absent. Absent from all adults of Coleoptera examined (Larsén, 1966; Baehr, 1975; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1986, 1991) and from adults of Neuroptera (Korn, 1943).

98. M. trochantero-basalaris (M. 112; Matsuda, 1966, p-tr2; Baehr, 1975, 79): (0) present; (1) absent. Absent from all adults of non-archostematan Coleoptera examined (Larsén, 1966; Beutel, 1986, 1988, 1990a,-b, 1994b; Belkaceme, 1986, 1991).

### Adults, Abdomen

99. Tergum I: (0) without caudally bifid suture; (1) bifid suture present (Achtelig, 1975, 1981; Kristensen, 1991). Adults of Neuropterida are characterized by a caudally bifid suture on the abdominal tergite I.

100. Abdominal sternite I: (0) strongly reduced or absent, not visible externally; (1) present, exposed. The first abdominal sternite is strongly reduced and not exposed in all adults of Coleoptera (Lawrence and Newton, 1982). Abdominal sternites which are reduced in size do also occur in adults of Mecoptera and Neuropterida (New, 1989; Aspöck and Aspöck, 1991); however, the remaining parts are still visible externally (Fig. 4 in Hasken, 1939; Fig. 15 in Acker, 1958).

101. Abdominal sternite II: (0) not divided by hind coxae; (1) completely divided. The abdominal sternite II is completely divided by the metacoxae in all adults of Adepfaga.

102. Abdominal segments IX and X: (0) exposed; (1) retracted into abdominal apex (Lawrence, 1982). The terminal segments of Coleoptera are concealed within the preceding abdominal segments (Fig. 13).

103. Genital appendages IX of females: (0) separate;

(1) fused. The genital appendages IX are fused in females of Neuropterida, thus forming a secondary egg-laying tube (Mickoleit, 1973). Intrinsic musculature is present in these fused third valvulae (gonostylus IX).

104. Number of Malpighian tubules: (0) eight; (1) six; (2) four. Eight Malpighian tubules are present in adults of Myrmeleontidae (New, 1991); six in adults of Raphidioptera (Aspöck and Aspöck, 1991), Myxophaga, Hydrophilidae, Byrrhidae, Tenebrionidae, and Chrysomelidae; and only four in adults of Archostemata, Adephaga, and many groups of Polyphaga.

105. Condition of Malpighian tubules: (0) free; (1) cryptonephric (Lawrence and Newton, 1982). Cryptonephric Malpighian tubules are present in adults of Cucujiformia and Bostrichoidea (excl. Nosodendridae and Derodontidae; Lawrence and Newton, 1982). Cryptonephridism is not described for adults of other groups under consideration.

106. Torsion of aedeagus: (0) absent; (1) torsion during copulation and rest. The aedeagus of adults of Adephaga (excl. Gyrinidae) is rotated through 90° during repose and through 180° during copulation (Beutel and Roughley, 1988).

107. Eggs: (0) laid without cocoon or egg case; (1) enclosed in silk cocoons or egg case. Eggs are enclosed in a silk cocoon or egg case in adults of Hydrophiloidea (sensu Hansen, 1997) and Hydraenidae. A similar condition is not described for other groups of Coleoptera, Mecoptera (Byers, 1991), or Neuropterida (Theischinger, 1991; Aspöck and Aspöck, 1991).

## Adult Characters Not Included in the Analysis

- Klausnitzer (1975): Most transverse veins of alae reduced (putative autapomorphy of Coeloptera excl. Archostemata). Character states are not clearly defined. The nonspecific loss of transverse veins should not be coded as one character state.

- Hansen (1997): Mesothoracic spiracles concealed (0); exposed (1) (28.0 putative autapomorphy of Archostemata + Adephaga). This character state is also found in many adults of Polyphaga. The mesothoracic spiracle seems to be clearly exposed in adults of *Priacma* (Fig. 2 in Baehr, 1975). A clearer definition and

illustration of the respective character states is desirable. The character is misleading according to Hansen (1997).

- Hansen (1997): Ventral face of elytra without “medio-lateral” microspinose binding patch (0); binding patch present (1) (66.0 putative autapomorphy of Coleoptera excl. Polyphaga). The character states are not clearly defined, as the position of these patches differs strongly in different groups of Polyphaga (Hammond, 1979).

- Hansen (1997): sensorial (?) appendage of antenna. Shape, size, and insertion of this structure(s) vary greatly. It is attached to antennomere III in larvae of Cupedidae and Adephaga, to antennomere II in most larvae of Polyphaga and larvae of Micromalthidae, and to antennomere I in larvae of Hydroscaphidae. Varying degrees of reduction occur in closely related taxa (e.g., Trachypachidae, dytiscoid families, Scarabaeoidea, Elateridae, Tenebrionidae). Two appendages are present in larvae of Histeridae, whereas they are completely absent from many larvae (e.g., Gyrininae, Amphizoidae, *Hydrophilus*). The appendage is flattened and forms an incomplete ring around antennomere III in many larvae of Tenebrionidae (Lawrence and Spilman, 1991). It is inserted ventrally in larvae of Micromalthidae, Cupedidae (Lawrence, 1991), and Trachypachidae (not laterally as stated by Hansen, 1997; Arndt and Beutel, 1995). It is attached ventrolaterally (e.g., *Hydroscapha*, *Cantharis* part.), laterally (e.g., Histeroidea, Hydrophilidae part., Elateridae part.; Costa *et al.*, 1988), or dorsolaterally (e.g., *Microsporus*) in other larvae of Coleoptera. The function of this structure in larvae of different groups is not clarified.

- Whiting *et al.* (1997): (0) flight with both wings; (1) flight by posteromotorism (Kristensen, 1981, 1991, 1995). Different degrees of posteromotorism are found not only in adults of Coeloptera and Strepsiptera, but also in adults of Dictyoptera, Dermaptera, and Orthoptera (Brodsky, 1994). Posteromotorism is not treated as a single character here but rather as different, separate changes of musculature and skeleton of the pterothorax. Posteromotorism is obviously not independent of other character transformations (De Pinna, 1991) such as transformation of fore-wings into elytra.

- Kukalová-Peck and Lawrence (1993): Medial bar with distinct abrupt hinge (putative synapomorphy of Archostemata + Myxophaga + Adephaga). The character states are not clearly defined. A more or less

abrupt hinge at the distal end of the medial bar (MP1 + 2) is always present if an oblongum cell is present and if the MP1 + 2 is bent anteriorly. It is this hinge which allows the movement of the oblongum cell during folding (Haas, 1998). The presence of the oblongum cell and the condition of MP1 + 2 have already been coded here (characters 76 and 79) and so this character is not included. The analysis shows that an abrupt hinge is a plesiomorphic character state and not an apomorphy.

- Kukalová-Peck and Lawrence (1993): Anterior anal basivenale (BAA) present, V-shaped (putative synapomorphy of Archostemata + Myxophaga + Adephaga). BAA could not be identified in many taxa (e.g., Figs. 14–34 in Kukalová-Peck and Lawrence, 1993). No character state matrix was presented by Kukalová-Peck and Lawrence (1993).

- Kukalová-Peck and Lawrence (1993): Central field triangular, forming a large pocket (putative synapomorphy of Archostemata + Myxophaga + Adephaga). This is a gradual modification and correlated with other transformations of the hind-wings (pers. obs. Haas).

- Kukalová-Peck and Lawrence (1993): RA3+4 delimiting posterior margin of radial cell only to about the middle of the cell (putative synapomorphy of Myxophaga + Adephaga). The character states in different taxa concerned are unclear.

- Kukalová-Peck and Lawrence (1993): Cubital proxalare (PrCu) fused to tergum (putative synapomorphy of Myxophaga + Adephaga). PrCu is not illustrated in Kukalová-Peck and Lawrence (1993). Therefore character state distribution remains unclear.

- Kukalová-Peck and Lawrence (1993): CuP- completely lost (putative synapomorphy of Archostemata + Myxophaga + Adephaga). CuP- is absent not only in adults of Archostemata, Myxophaga, and Adephaga, but also in adults of many polyphagan groups such as *Coelostoma*, *Sphaerites*, Scarabaeidae (excl. *Phaenognatha*), Clambidae, Elateriformia, Trogossitidae, and others (Figs. 39, 41, 45–52, 66, and 67 in Kukalová-Peck and Lawrence, 1993). A more or less indistinct or very short CuP is present in adults of Hydrophilidae (part.), *Phaenognatha*, Eucinetoida (part.), and Cerambycidae (Kukalová-Peck and Lawrence, 1993). The complete loss in adults of Myxophaga is probably correlated with the strong reduction of the posterior part of the hind-wing.

- Kukalová-Peck and Lawrence (1993): AP3 + 4 unbranched (putative synapomorphy of Myxophaga + Adephaga). Character state distribution within Polyphaga is rather unclear and apparently highly variable (see illustrations in Kukalová-Peck and Lawrence, 1993). AP3 + 4 is absent from adults of Torridincolidae (part.), Microsporidae, and Hydroscaphidae (Kukalová-Peck and Lawrence, 1993).

- Kukalová-Peck and Lawrence (1993): Cross vein r3 absent, r4 shifted proximally (putative synapomorphy of Myxophaga + Adephaga). Character states are not clearly defined. The proximal shift of r4 is a gradual modification (e.g., Hydrophilidae, Histeroidea). The cross vein r3 is apparently present in adults of *Macrogyrus* (Fig. 13 in Kukalová-Peck and Lawrence, 1993) but absent or almost completely reduced in many adults of Polyphaga (e.g., *Coelostoma*, Histeroidea, Scarabaeoidea, Cerambycidae; Figs. 39, 41, 42, 48–53, and 68 in Kukalová-Peck and Lawrence, 1993).

- Kukalová-Peck and Lawrence (1993): RP forming a wide angle with RA, so that radial and central fields are very large (putative synapomorphy of Myxophaga + Adephaga). The different angles between RP and RA are only gradual modifications. Virtually no difference is found between some adephagan adults (*Trachypachus*, *Megacephala*) and adults of Cupedidae. A fairly wide angle is found in some adults of Myxophaga but also in adults of *Micromalthus* (Kukalová-Peck and Lawrence, 1993).

- Kukalová-Peck and Lawrence (1993): Apical field short and broad (putative autapomorphy of the eucinetoid lineage sensu Kukalová-Peck and Lawrence, 1993). The size of the apical field of representatives of the eucinetoid lineage is not distinctly different from that of Dytiscidae, Hydrophiloidea, and Scarabaeidae (Haas, 1998). Consequently, the character is not included in this analysis.

- Ovarioles. Polypitrophic ovarioles are present in females of Hymenoptera, Mecoptera (Byers, 1991), Archostemata, Adephaga (Lawrence, 1982), and *Phaenaeus* (Scarabaeidae; Halfiter and Yrma Lopez, 1970). The homology of telotrophic ovarioles found in most adults of Polyphaga (Lawrence, 1982), in Raphidioptera, and in Sialidae is unclear. A secondary nutritive chamber is absent in the telotrophic ovarioles of the polyphagan taxa but present in raphidiopteran and



sialid females (Achtelig, 1975, "mit zweiter Nährkammer"). Telotrophic ovarioles have evolved independently in Polyphaga and Sialidae according to Büning (1979). Panoistic ovarioles are present in females of Corydalidae (Theischinger, 1991). The condition of myxophagan ovarioles are yet unknown.

- Abdominal ganglia (Reichardt, 1973). Independent abdominal ganglia are present in adults of Adephaga. They are fused in adults of Myxophaga and Polyphaga according to Reichardt (1973). More detailed study of this character is required for a clear definition of character states.

- Male terminal segments. A detailed and comprehensive study of sclerites and muscles of the terminal abdominal segments of males is needed for a proper phylogenetic interpretation. Detailed descriptions are available for only a few species (e.g., Hieke, 1966; Krell, 1996). However, the homology of different structures in males of Coleoptera and other groups of insects remains unclear at present.

- Testes (Reichardt, 1973; Lawrence and Newton, 1982). Tubular testes are present in Adephaga and Myxophaga according to Reichardt (1973). Non-tubular, lobular testes are present in adults of Archostemata (Cooper, pers. comm.). They are follicular but of very heterogeneous shape in the adults of Polyphaga examined (Crowson, 1981). A detailed and comprehensive study of the internal male genital organs is required for a phylogenetic evaluation of this character system.

## Analysis

The analysis of the interrelationships of coleopteran suborders is based upon 107 internal and external characters of immature stages and adults of 4 outgroup and 28 ingroup taxa: 3 genera of Archostemata and Myxophaga (families with known larvae), 9 adephagan genera (8 families), and 13 genera of Polyphaga (13 families). The latter taxa are representatives of major polyphagan subgroups such as Hydrophiloidea, Staphylinioidea, Scarabaeoidea (Staphyliniformia sensu Hansen, 1997), Byrrhoidea, Elateroidea, Cantharoidea (Elateriformia), Derodontoidea, Cucujoidea, Tenebrionoidea, and Chrysomeloidea (Cucujiformia). The outgroup comprises Megaloptera (*Sialis*, *Corydalus*), Raphidioptera (*Agulla*), and Neuroptera (*Myrmeleon*). Neuropterida were chosen as potential sister groups

of Coleoptera (Kristensen, 1991). Strepsiptera are a strongly autapomorphic group (Kristensen, 1991) and were therefore not included in this analysis. A sister-group relationship between this order and Coleoptera as proposed by Kukalová-Peck and Lawrence (1993) was not confirmed by a comprehensive study based on morphological and molecular features (Whiting *et al.*, 1997). The results of these authors strongly suggest a sister-group relationship between Diptera and Strepsiptera (= Halteria). All characters were weighted equally and not ordered. All question marks in the matrix refer to missing data.

Most parsimonious trees were sought using branch and bound search in PAUP (version 3.1; Swofford, 1991). The outgroup taxa were treated as all other groups in the analysis (simultaneous analysis; Nixon and Carpenter, 1993). Analysis of character evolution was conducted in MacClade (version 3; Maddison and Maddison, 1992). Additional analyses were carried out after successive reweighting. Branch support values (Bremer, 1988) were calculated using the "converse approach" (Bremer, 1994). A bootstrap search was not conducted. Bootstrap values should not be used as confidence intervals (e.g., Carpenter, 1996; Meier, pers. comm.).

## RESULTS

The first analysis resulted in 18 trees of a minimal number of 194 steps (CI 0.691; HI 0.309, RC 0.616) (tree 1, Fig. 22; strict consensus tree, Fig. 23). Selected monophyletic groups and apomorphies are listed below (unambiguous characters, Fig. 22).

### *Coleoptera*

20.1 (sclerites firmly connected), 24.1 (11 antennomeres), 31.0 (preepisternal cervical sclerites absent), 32.1 (pronotum with inflected margin), 40.1 (M. cervicale-occipitalis torquatus absent), 44.0 (M. M. pleura-trochanteralis present), 50.1 (mesothoracic meron absent), 51.2 (elytra fully sclerotized), 52.1 (scutellar elytra-locking device), 53.1 (M. scutello-postnotalis absent), 57.1 (M. intraepisternalis II absent), 61.1 (M. pleurocostopraenotalis absent), 67.1 (metascutal fissure

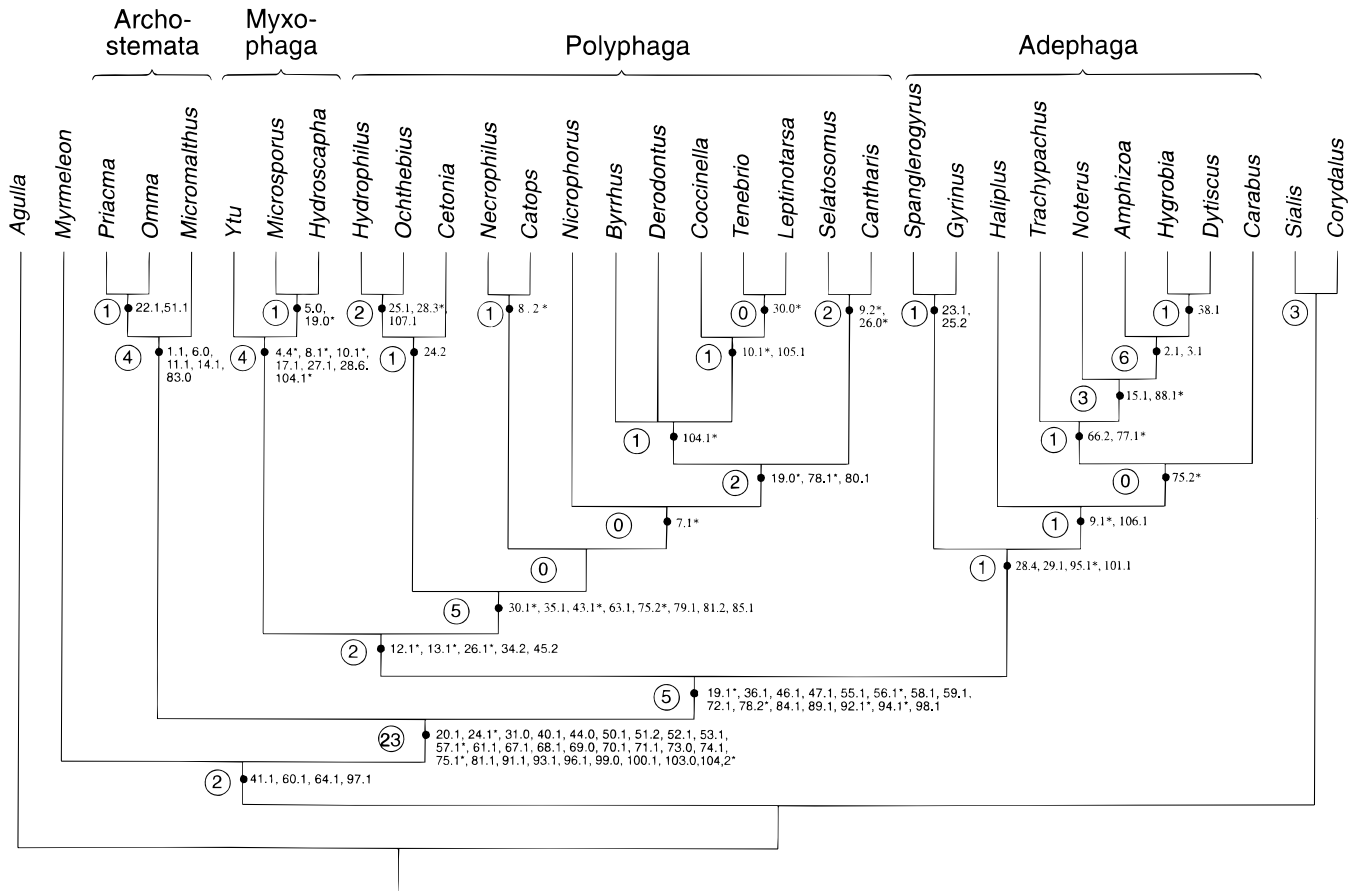


FIG. 22. Tree 1 of 18 cladograms with 194 steps. Unambiguously placed characters mapped on cladogram. \*Homoplasious changes; numbers left of branches are decay indices.

present), 68.1 (alacristae present), 69.0 (metapostnotum undivided), 70.1 (metathoracic meron absent), 71.1 (metacoxae transverse), 73.0 (fewer than five costal cross veins), 74.1 (hind-wings folded under elytra), 75.1 (apical part of hind-wings rolled), 81.1 (triangular fold of alae present, proximal to RA3+4), 91.1 (*M. notopleuralis* b III absent), 93.1 (*M. furco-pleurocostales* III absent), 96.1 (*M. sterno-coxalis* III absent), 99.1 (abdominal tergite I without caudally bifid suture), 100.1 (sternite I strongly reduced), 103.0 (genital appendages VIII of females separate), 104.2 (4 Malpighian tubules).

The monophyly of Coleoptera is only tentatively supported by these character states as not all holometabolan groups were included in this analysis. It cannot be fully excluded that subgroups of Coleoptera may turn out as more closely related to other taxa, if more

groups are taken into consideration. However, this is very unlikely, as most of the supposedly derived features listed here or below do not occur in representatives of other groups of Endopterygota.

### *Coleoptera Excl. Archostemata*

19.1 (urogomphi present), 36.1 (spinasternum I vestigial), 46.1 (mesothoracic katepisternal joint absent), 47.1 (discriminal line of mesoventrite absent), 55.1 (*Mm. notosternales* II absent), 56.1 (*M. noto-pleurocostalis* II longus absent), 58.1 (*M. episterno sternalis* II absent), 59.1 (*M. pleurocosta-alaris* and *M. episterno-alaris* II not separated), 72.1 (metathoracic trochantin not exposed or absent), 78.2 (anterior bending zone of alae present), 84.1 (2-Ax with lateral process), 89.1

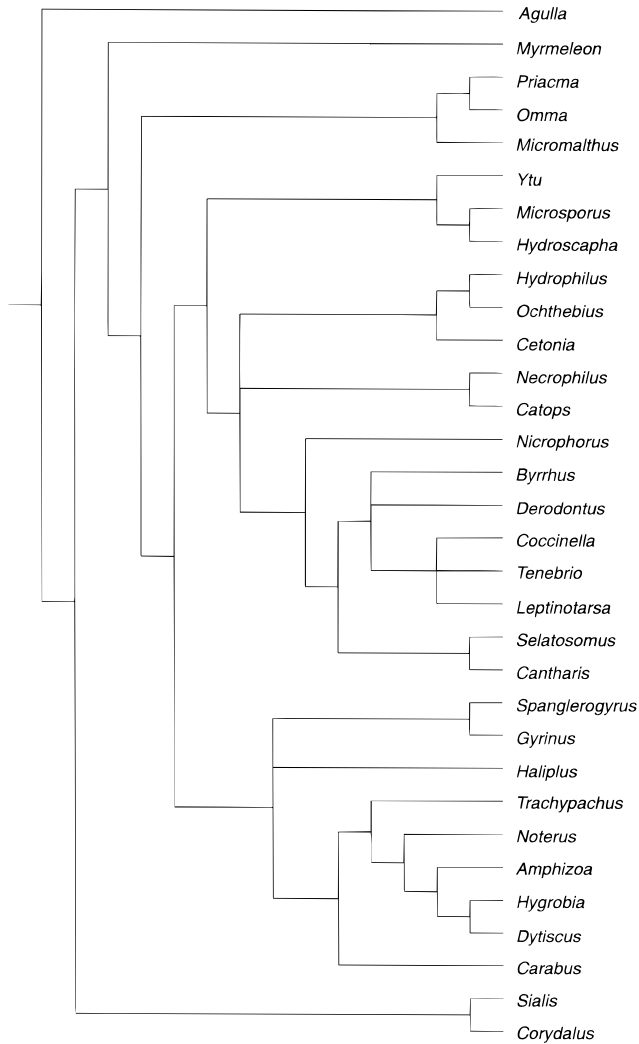


FIG. 23. Strict consensus tree of 18 equally parsimonious cladograms.

(*M. notoepisternalis brevis* III absent), 92.1 (*M. pleura-alaris* a and b III with common insertion), 94.1 (*M. noto-trochantinalis* III absent), 98.1 (*M. trochantero-basalaris* III absent).

### **Myxophaga + Polyphaga**

12.1 (legs five-segmented), 13.1 (larval leg with single claw), 26.1 (mola of adults present), 34.2 (trochantin fused with propleura), 45.2 (meso- and metathoracic ventrites firmly connected)

### **Archostemata**

1.1 (larval endocarina present), 6.0 (larval mandible with three blunt apical teeth), 11.1 (larval ligula sclerotized, wedge-shaped), 14.1 (larval abdomen with transverse ampullae), 83.0 (fulcrum underneath 2-Ax).

### **Polyphaga**

30.1 (presternal cervical sclerites present), 35.1 (propleura internalized), 43.1 (*M. sterno-coxalis* absent), 63.1 (*M. coxa-subalaris* II absent), 75.2 (apical part of hind-wings folded), 79.1 (MP1+2 bent posteriorly), 81.1 (RA3+4 cut twice by triangular fold), 85.1 (angle between the axis anterior notal process/1Ax and distocranial margin of 1Ax less than 45°).

### **Adephaga**

28.4 (galea two-segmented, palp-like), 29.1 (mentum with rounded lateral lobes), 95.1 (*M. episterno-coxalis* III absent), 101.1 (abdominal sternite II divided by metacoxae).

### **Myxophaga**

4.3 (larval antenna two-segmented), 8.1 (rounded larval prostheca), 10.1 (larval galea absent), 17.1 (larval spiracular gills present), 27.1 (left mandible with articulated tooth), 28.6 (galea absent), 104.1 (six Malpighian tubules).

A clade comprising Polyphaga excl. Scarabaeidae, Hydraenidae, and Hydrophilidae (tree 1, Fig. 22) was supported only with accelerated character optimization. Nine trees were obtained when the successive reweighting option was applied. The topologies were congruent with trees of the initial analysis; however, the monophyly of Adephaga excl. Gyrinidae and Halipilidae was confirmed in the strict consensus tree (see Fig. 23). Tree support values (Bremer, 1988) are shown in Fig. 22.

## **DISCUSSION**

The monophyly of Coleoptera, which is widely accepted by systematists, is supported by 28 derived

morphological features of adults in this study (unambiguous characters, Fig. 22). This is in agreement with an analysis of morphological features in Whiting *et al.* (1997), but in contrast to the results of the molecular analyses in the same study. *Priacma* (Archostemata) and *Colpocaccus* (Carabidae) were placed in a monophylum together with *Corydalus* (Megaloptera) and *Agulla* (Raphidioptera) in a tree which was based on 18s DNA, in a combined molecular tree (18s and 28s DNA), and in a total evidence tree (Fig. 17b in Whiting *et al.*, 1997). The 18s sequences in these four taxa (referred to as MRCP) are nearly identical. It was pointed out by Whiting *et al.* (1997) that this may be due to the conservation of a “primitive” Coleoptera–Neuropterida-18s nucleotide sequence in “basal beetles” (Whiting *et al.*, 1997). This interpretation would be in agreement with the results of the present study, i.e., a basal position of Archostemata. The monophyly of Archostemata, Carabidae, Megaloptera, and Raphidioptera is not compatible with the morphological data used in this analysis. An enforced MRCP-clade would require 50 additional steps.

A crucial character transformation in the earliest evolutionary history of Coleoptera was the transformation of the fore-wings into elytra with epipleurae, a meso-scutellar-locking device, and metanotal alacristae (Heberdey, 1938; Lawrence and Newton, 1982; Kukulová-Peck, 1991). The transformation of the fore-wings resulted in posteromotorism, which is also found in Dermaptera and Strepsiptera and to a lesser degree in Dictyoptera (excl. Isoptera) and Orthoptera (Brodsky, 1994).

It was pointed out by Kukulová-Peck (1991) that elytra which distinctly surpass the abdominal apex, and which are not closely adapted to the abdominal segments laterally, belong to the ground plan of Coleoptera s.l. (i.e., including stem lineage; Beutel, 1997). It is plausible to assume that the hind-wings of early Coleoptera such as *Sylvacoleus* were only folded longitudinally (Haas, 1998) and not completely covered by the elytra at rest. Longitudinal wing folding is a derived ground plan feature of Coleoptera s.l. according to Haas (1998).

It was a major transition to evolve a transverse hind-wing folding mechanism subsequently, which allowed the complete storage of the alae under the elytra and a better mechanical fit of elytra and abdominal segments.

Transverse wing folding requires several morphological and functional changes of the alae. The wing membrane is not soft and homogeneous but consists of several more or less stiff plates which are separated by folding lines. This results in characteristic folding patterns (Haas, 1998). A flexible anterior margin of the alae is necessary for transverse folding. However, a distinct bending zone of the costal margin, which is present in Adephaga, Myxophaga, and basal lineages of Polyphaga, is probably not a ground plan feature of extant Coleoptera.

The unfolding mechanism in Coleoptera is completely different from the mechanism in Dermaptera and Blattodea (Haas, 1998). It is achieved in a characteristic manner by the spreading of the veins RA and MP1+2 (approx 15°; Haas, 1998). This is triggered by contraction of *M. pleura alaris* III which is attached to 3Ax and indirectly connected with the base of MP1+2. It was pointed out by Haas (1998) that the same mechanism was probably already involved in the expansion of the longitudinally folded wings of stem-lineage Coleoptera.

Folding and unfolding are two different mechanisms in Coleoptera. Folding cannot be achieved by intrinsic forces of the metathorax (Haas, 1998). Elytra and abdomen play an active role when the alae are stored in the subelytral space.

The close morphological fit of elytra and abdominal segments, which evolved in the early Permian (Beutel, 1997), resulted in an improved sealing from desiccation of the tracheal system (Kukulová-Peck, 1991). The closed subelytral space is also a preadaptation for the change to an aquatic lifestyle (Heberdey, 1938) which was acquired independently in many groups of Coleoptera such as Gyrinidae, Haliplidae, Dytiscoidea, Hydraenidae, Spercheidae, Helophoridae, Hydrophilidae, Elmidae, Dryopidae, and Donaciinae (Beutel, 1997).

Another important feature of adults of Coleoptera is the close mechanical fit of most sclerites and the absence of membranes from the parts which are not covered by the elytra at rest (Lawrence and Newton, 1982). This means at the same time reduced water loss and a distinctly improved mechanical protection (Lawrence and Newton, 1982). The modified condition of the exoskeleton, which involves reduced degrees of freedom, is probably also correlated with muscle reductions in the thorax. Eight losses of thoracic muscles

were interpreted as unambiguous autapomorphies of Coleoptera in this analysis.

Even though the monophyly of Coleoptera is indicated by a considerable number of apomorphies of adults, it is supported by only one derived feature of larvae in this analysis, the presence of urogomphi. Character transformations of immature stages have probably played a minor role in the early evolution of Coleoptera. The presumptive ground plan condition of coleopteran larvae differs probably very little from a common ancestor which Coleoptera may have shared with Neuropterida (Lawrence and Newton, 1982; Kristensen, 1991; Whiting *et al.*, 1997).

The results of this analysis clearly support a sister-group relationship between Archostemata and the remaining Coleoptera (branch support value 5; Fig. 22). This branching pattern is in contrast to the hypothesis presented by Kukalová-Peck and Lawrence (1993) which was based on a non-cladistic evaluation of characters of the hind-wings (see Whiting and Kathirithamby, 1995). A branching pattern with Polyphaga as sister group of Archostemata + (Myxophaga + Adephaga) would require 17 additional steps (tree length 211).

The monophyly of Adephaga + Myxophaga + Polyphaga is based on 15 unambiguous apomorphies (Fig. 22). Important character changes are the transformation of the costal margin of the alae into a bending zone (Haas, 1998), modifications of thoracic sclerites (e.g. close contact of meso- and metathoracic ventrites, absence of the mesothoracic katepisternal joint), and loss of eight pterothoracic muscles. The absence of *M. noto-sternalis* II and *M. noto-pleurocostalis longus* II, which are strongly developed in *Priacma* (Baehr, 1975), may be correlated with a decrease in size of the mesothorax. The maintenance of the locomotor functions of the thoracic segments with a strongly developed exoskeleton, reduced degrees of freedom, and a distinctly reduced set of muscles is an important characteristic of Coleoptera and especially of Coleoptera excl. Archostemata.

The age of clades provides an additional source of evidence with which to test phylogenetic hypotheses (Gauthier *et al.*, 1988; Kluge, 1997). The proposed sister-group relationship between Archostemata and the remaining Coleoptera seems to be in better agreement

with the fossil record than the branching pattern proposed by Kukalová-Peck and Lawrence (1993). Cupedidae are recorded since the Sakmarian (Lower Permian; Labandeira, 1994), probable representatives of Adephaga since the Wordian (Upper Permian, Gyrinidae?; Labandeira, 1994; other groups widespread in the Triassic; Ponomarenko, 1977), whereas the earliest polyphagan fossils are recorded from Upper Triassic formations (Staphylinidae?, Tenebrionidae; Labandeira, 1994). Most subgroups of Polyphaga appear in the fossil record in the Jurassic (e.g., Hydraenidae, Hydrophilidae, Silphidae, Scarabaeidae, Chrysomelidae) or Cretaceous (e.g., Leiodidae, Coccinellidae) (Labandeira, 1994).

A sister-group relationship between Adephaga on one hand and Myxophaga + Polyphaga on the other is also supported by the results of this study. Common derived features of the latter taxa are the fusion of the larval tibia and tarsus, the presence of a single claw, the fusion of the trochantinus and pleura in adults (Hlavac, 1972, 1975), and the firm connection of the meso- and metathoracic ventrites.

The monophyly of all suborders is well supported by autapomorphic features. This is in agreement with Lawrence and Newton (1982), Kukalová-Peck and Lawrence (1993), Beutel (1995a), Beutel *et al.* (1998), and others. Character transformations of immature stages play a highly important role on this systematic level. Archostemata are mainly characterized by larval autapomorphies which are correlated with specialized wood-boring habits (e.g., sclerotized ligula, shortened legs, tergal ampullae; Lawrence, 1982, 1991, 1999). Derived features of myxophagan larvae have probably evolved as adaptations to algae-feeding and life in moist substrate (Lepiceridae, Microsporidae) or hygropetric habitats (Hydrosaphidae, Torridincolidae) (Beutel *et al.*, 1999). Important character transformations of adephagan larvae such as prognathism and fusion of labrum and clypeus are correlated with predacious habits. Larvae of some basal groups of Polyphaga (e.g., Hydraenidae, Leiodidae) are mainly characterized by plesiomorphic features, whereas many larval character transformations occur in subgroups such as Hydrophiloidea, Histeroidea, and Elateriformia (Beutel, 1995, 1999).

Polyphaga is the most highly derived group of Coleoptera in terms of thoracic features of adults (e.g.,

presteral cervical sclerites present, propleura internalized). An important character transformation within this suborder is the secondary loss of the bending zone of the alae. The absence of this structural modification of the hind-wing margin results in a distinctly simplified folding mechanism which involves only the apical field (Haas, 1998). This was interpreted as a “primitive” condition by other authors (e.g., Schneider, 1978), but has clearly turned out as an apomorphy of the eucinetoid-lineage (sensu Hansen, 1997) in this study. Other potential hind-wing autapomorphies of this monophylum were presented by Kukalová-Peck and Lawrence (1993). Another well-founded monophylum within Polyphaga is Cucujiformia (+ Bostrichoidea; Beutel, 1996). The presence of cryptonephric Malpighian tubules (Lawrence and Newton, 1982) results in an improved water reabsorption mechanism and enables representatives of this large lineage to live in drier habitats (e.g., Tenebrionidae) or to spend more time on exposed parts of plants. This may be considered a prerequisite for the strong diversification of the very species-rich groups of phytophagous beetles. The cucujiform families Cerambycidae, Chrysomelidae, and Curculionidae comprise more than 110,000 species.

Characters presented in this study were focused on a clarification of the interrelationships of coleopteran suborders. Therefore relationships between non-coleopteran groups and families of Archostemata, Adephaga, Myxophaga, and Polyphaga will not be discussed here. An inclusion of all other endopterygotan groups is necessary for a clarification of the position of Neuropterida and other groups, especially Strepsiptera (see Whiting *et al.*, 1997). A reliable clarification of the interrelationships of higher groups of Polyphaga would require the inclusion of many more characters and taxa.

## CONCLUSIONS

This analysis strongly supports the monophyly of Coleoptera, Coleoptera excl. Archostemata, and Myxophaga + Polyphaga. The transformation of the forewings into elytra, specific hind-wing folding mechanisms, the strong coadaptation and simplification of sclerites, and a highly efficient use of a distinctly reduced muscular apparatus play an important role in the evolution of adults of Coleoptera. Character transformations of adults characterize a Permian evolutionary stage of this unusually species-rich group of insects, whereas many larval apomorphies, which characterize subgroups such as Archostemata, Adephaga, Myxophaga, Scarabaeidae, and Elateriformia, may have contributed to the strong radiation in the earlier Mesozoic (see also Beutel, 1997).

The present study is based to a considerable extent on older morphological studies of Coleoptera and other groups of insects. It emphasizes the importance of detailed study of external and internal structures. The current tendency to restrict phylogenetic investigations to exoskeletal features may be appropriate and efficient on a lower taxonomic level. However, for a resolution of interrelationships of higher ranking taxa, the improvement of the morphological knowledge—especially of internal features—is of great importance.

## APPENDIX I: CHARACTER STATE MATRIX

A question mark refers to unknown character states.

characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36					
Agulla	0	0	0	2	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0				
Myrmeleon	0	0	0	0	1	1	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Sialis	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Corydalus	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Priacma	1	0	?	2	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0				
Omnia	1	0	?	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	?	0	0	0	0	0	0	0					
Micromalthus	1	0	?	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	?	?	5	0	0	0	1	0	3	0	?				
Ytu	0	0	0	4	1	1	0	1	0	1	0	1	1	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	6	0	0	0	1	0	2	0	1				
Microspor	0	0	0	4	0	1	0	?	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	6	0	0	0	0	0	1	0	2	0	1			
Hydroscapha	0	0	0	4	0	1	0	?	0	1	0	1	1	0	0	0	0	1	0	0	1	0	0	2	0	1	1	6	0	0	0	1	0	2	0	1	1				
Spanglerogyrus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	2	0	0	4	1	0	0	1	0	1	0	1	1			
Gyrinus	0	0	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	2	0	0	4	1	0	0	1	0	1	0	1	1			
Halipus	0	0	0	2	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	4	1	0	0	0	0	1	0	1	0	1	1		
Trachypachus	0	0	0	2	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	4	1	0	0	0	0	0	1	0	1	0	1		
Noterus	0	0	0	2	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	4	1	0	0	0	0	0	1	0	1	0	1		
Amphizoa	0	1	2	1	1	1	1	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	4	1	0	0	0	0	0	0	1	0	1	0	1	
Hygrobia	0	1	1	2	1	1	1	0	1	0	0	0	0	0	0	0	1	2	0	0	1	0	1	2	0	0	0	4	1	0	0	0	0	0	0	1	0	1	0	1	
Dytiscus	0	1	1	2	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	4	1	0	0	0	0	0	0	0	1	0	1	0	1
Carabus	0	0	0	2	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	4	1	0	0	0	0	0	0	0	1	0	1	0	1
Hydrophilus	0	0	0	3	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	4	1	0	0	0	0	0	0	0	1	0	1	0	1
Ochthebius	0	0	0	3	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	1	1	0	3	0	1	0	0	1	0	2	1	0	2	1	1	
Necrophilus	0	0	0	3	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	2	1	1	1	1	
Catops	0	0	0	3	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	2	1	1	1		
Nicrophorus	0	0	0	3	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	2	1	1	1	1	
Cetonia	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	1	0	0	0	0	0	2	1	1	1	
Byrrhus	0	0	0	3	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	2	1	1	1	
Selatosomus	0	0	0	3	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	2	1	1	1	
Cantharis	0	0	0	3	1	1	1	0	2	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	2	1	1	
Derodontus	0	0	0	3	1	1	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	2	1	1	
Coccinella	0	0	0	3	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	2	1	1	
Tenebrio	0	0	0	3	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	2	1	1	
Leptinotarsa	0	0	0	3	1	2	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1

characters	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73			
Agulla	0	0	1	?	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	?	?	0	0	0	0	0	0	1	0	0	0	0	1			
Myrmeleon	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1			
Sialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
Corydalis	0	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
Priacma	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0		
Omma	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Micromalthus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Ytu	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Microsporus	0	0	1	1	1	1	0	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0		
Hydroscapha	0	0	1	1	1	1	0	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	
Spanglerogyrus	1	0	1	1	1	1	0	0	1	1	1	1	0	1	2	1	1	?	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	1	1	1	1	0	
Gyrinus	0	0	1	1	1	1	1	0	1	1	1	0	1	0	2	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	
Haliphus	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	2	1	?	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	1	0	
Trachypachus	1	0	1	1	1	1	?	0	1	1	1	1	1	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Noterus	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	0	0	1	0	2	1	1	0	1	1	1	1	0	
Amphizoa	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	2	1	?	1	1	1	1	1	1	1	1	1	0	1	0	2	1	1	0	1	0	1	1	0	
Hygrobia	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	0	2	1	1	0	1	1	1	1	0	
Dytiscus	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	1	0	2	1	1	0	1	0	1	1	1	0
Carabus	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	0
Hydrophilus	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Ochthebius	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Necrophilus	0	0	?	?	?	?	?	?	2	1	1	1	1	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Catops	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Microphorus	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	1	0
Cetonia	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Byrrhus	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Selatosomus	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Cantharis	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Derodontus	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coccinella	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Tenebrio	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0
Leptinotarsa	0	0	1	1	1	1	1	0	2	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0



characters	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107					
Agalla	0	0	1	0	0	0	0	0	0	1	0	0	1	?	0	?	?	?	?	0	0	?	?	?	0	0	1	0	0	1	1	0	0	0					
Myrmeleon	0	0	1	0	0	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0				
Sialis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	0	0	0	0				
Corydalis	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	0	0	0	0			
Priacma	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	1	0	2	0	0	0	0			
Omnia	1	1	0	0	1	0	0	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	2	0	0	0	0			
Micromalthus	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	?	?	0	0	0			
Ytu	1	1	0	0	2	0	0	1	?	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	?	?	0	0	0			
Microsporus	1	1	0	0	2	0	0	1	0	2	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0			
Hydroscapa	1	1	1	0	2	0	0	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	?	0	1	0	1	0	1	0	0	0	0			
Spanglerogyrus	1	1	0	0	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	?	0	0	0	0	0			
Gyrinus	1	2	0	0	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	2	0	0	0	0	0			
Haliphus	1	1	0	0	2	0	0	1	1	2	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	2	0	1	0	1	0	0		
Trachypachus	1	2	0	1	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	2	0	1	0	1	0	0		
Noterus	1	2	0	1	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	2	0	1	0	1	0	0		
Amphizoa	1	2	0	1	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	?	0	1	0	1	0	0		
Hygrobia	1	2	0	0	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	?	0	1	0	1	0	0		
Dytiscus	1	2	0	1	2	0	0	1	1	2	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	?	0	1	0	1	0	0		
Carabus	1	2	0	0	2	0	0	1	1	2	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	2	0	1	0	1	0	1	0	
Hydrophilus	1	2	1	0	2	1	0	2	0	2	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	0	1	0	1	0	0	1	0	
Ochthebius	1	2	1	0	2	1	0	2	0	2	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	?	0	1	0	1	0	?	0	0	1	0	1	0	
Necrophilus	1	2	1	?	2	1	0	2	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	2	0	0	0	0	0	0	
Catops	1	2	1	0	2	1	0	2	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	2	0	0	0	0	0	0	
Nicrophorus	1	2	1	0	2	1	0	2	0	2	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	
Cetonia	1	2	1	0	3	1	0	2	0	2	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	
Byrrhus	1	2	1	0	1	1	1	2	1	2	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	?	0	1	0	1	0	1	0	1	0	0	0	0	0
Selatosomus	1	2	1	0	1	1	1	2	0	2	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	
Cantharis	1	2	1	0	1	1	1	2	0	2	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	2	0	0	0	0	0	0	
Derodontus	1	2	1	?	1	1	1	2	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	0	2	0	0	0	0	0	0	
Coccinella	1	2	1	0	1	1	1	2	0	2	1	1	1	1	0	1	1	1	1	1	1	0	?	?	?	?	0	1	0	1	0	?	1	0	0	0	0	0	
Tenebrio	1	2	1	0	1	1	1	2	0	2	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	
Leptinotarsa	1	2	1	0	1	1	1	2	0	2	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	0	1	0	1	0	1	0	0	

## APPENDIX II

## List of Species Examined for Skeletal and Muscular Features

Specimens were fixed in 70% ethanol unless otherwise noted. A, adult; L, larva; diss, dissection; FAE, fixed in formol-ethanol-acetic acid; micr sect, microtome section; SEM, scanning electron microscope.

Archostemata, Cupedidae: *Priacma serrata* LeConte, 1861 (A, diss, SEM); *Cupes capitatus* Fabricius, 1801 (A, dried). *Prolixocupes latreillei* (Solier, 1849) (A, dried).

Ommatidae: *Omma stanleyi* Newman, 1839 (A, diss); *Tetraphalerus* sp. (A, dried).

Myxophaga, Lepiceridae: *Lepicerus horni* (Sharp, 1882) (A, dried).

Hydroscaphidae: *Hydroscapha natans* LeConte, 1874 (L, FAE, micr, SEM; A, FAE, micr sect, SEM).

Microsporidae: *Microsporus* spp. (undetermined species from Arizona and Europe) (L, A, FAE, micr sect, SEM).

Torridincolidae: *Delevea namibensis* Endrödy-Younga, 1997 (L, micr sect, SEM); *Iapir britskii* (Reichardt and Costa, 1967) (L, SEM; A, diss); *Incoltorrida madegassica* Steffan, 1973 (A, dried), *Satonius kurosawai* (Sato, 1982) (L, micr sect, SEM; A, diss); *Torridincola rhodesica* Stefan, 1964 (L, A, micr sect, SEM); *Ytu zeus* Reichardt, 1973 (L, micr sect, SEM; A, micr sect).

Polyphaga, Hydraenidae: *Davidraena* sp. (L, SEM; A, diss); *Hydraena* sp. (L, FAE, micr sect); *Hydraena gracilis* Germar, 1824 (A, FAE, diss); *Ochthebius* spp. (L, A, FAE, micr sect, SEM).

Leiodidae: *Catops* sp. (L, micr sect; A, diss).

Agyrtidae: *Necrophilus hydrophiloides* Guérin-Menneville, 1835 (L, micr sect).

Spercheidae: *Spercheus emarginatus* (Schaller, 1783) (L, FAE, micr sect; A, FAE, diss).

Hydrophilidae: *Berosus signaticollis* (Charpentier, 1825) (L, FAE, micr sect; A, FAE, diss); *Enochrus* sp. (L, A, FAE, diss); *Hydrobius fuscipes* L., 1758 (L, A, FAE, diss); *Hydrochara caraboides* L., 1758 (L, FAE, micr sect; A, diss); *Hydrophilus* sp. (L, FAE, diss); *Hydrophilus aterimus* Eschscholtz, 1822 (A, dried); *H. piceus* (L., 1758) (A, FAE, diss).

Scarabaeidae: *Cetonia aurata* L., 1758 (L, A, FAE, diss); *Liocola* sp. (L, FAE, diss); //sp. (A, FAE, diss).

Byrrhidae: *Byrrhus* sp. (A, diss); *Cytilus alternatus* Say, 1825 (L, diss).

Elateridae: *Denticollis linearis* L., 1758 (L, FAE, diss); *Melanotus* sp. (L, FAE, micr sect); *Melanotus villosus* Geoffroy, 1785 (A, dried); *Selatosomus aeneus* (L., 1758) (A, dried) (thoracic muscular treated in Larsén, 1966).

Cantharidae: *Cantharis* spp. (L, FAE, diss); *Cantharis fusca* (L., 1758) (A, FAE, diss).

Coccinellidae: *Coccinella* sp. (L, A, FAE, diss).

Tenebrionidae: *Tenebrio molitor* L., 1758 (L, A, FAE, diss).

Chrysomelidae: *Chrysomela* spp. (A, FAE, 70% ethanol); *Donacia* sp. (A, FAE, diss); *Galeruca tanacetii* (L., 1758) (A, FAE, diss); *Lema melanopus* (L., 1758) (A); *Leptinotarsa decemlineata* (Say, 1824) (L, A, FAE, 70% ethanol, diss); several undetermined species (L, FAE, diss).

Adephaga: Gyrinidae: *Spanglerogyrus albiventris* Folkerts, 1979 (A, FAE, micr sect); *Gyrinus substriatus* Stephens, 1828 (L, A, Bouin, micr sect).

Halipilidae: *Brychius elevatus* (Panzer, 1794) (L, FAE, micr sect, SEM; A, FAE, diss, SEM); *Halipilus lineatocollis* Marsham, 1802 (L, Dubosq-Brasil, FAE, micr sect; A, Dubosq-Brazil, diss, SEM).

Trachypachidae: *Trachypachus holmbergi* Mannerheim, 1853 (L, micr sect, SEM; A, FAE, diss, SEM); *Systolosoma breve* Solier (L, A, diss).

Carabidae: *Carabus* spp. (L, FAE, micr sect); *Carabus coriaceus* (A, diss); *C. granulatus* L., 1758 (A, FAE, diss); *C. nemoralis* Müller, 1764 (A, FAE, diss); *Metrius contractus* Eschscholtz, 1829 (L, micr sect; A, diss); *Omus californicus* Eschscholtz, 1829 (A, FAE, diss); *Nebria brevicollis* (F., 1792) (A, FAE, diss); *Pterostichus niger* (Schaller, 1783) (A, FAE, diss).

Noteridae: *Noterus crassicornis* Müller, 1776 (L, FAE, micr sect; A, FAE, diss).

Dytiscidae: *Dytiscus marginalis* L., 1758 (L, FAE; A, FAE).

Hygrobiidae: *Hygrobia tarda* (Herbst, 1804) (L, Bouin; A, Bouin, micr sect, diss).

Amphizoidae: *Amphizoia lecontei* Matthews, 1872 (L, ethanol, micr sect; A, FAE, diss).

Mecoptera, Panorpidae: *Panorpa communis* Linnaeus, 1758 (L, A, diss).

Megaloptera, Sialidae: *Sialis* sp. (L, A, FAE, diss).

Raphidioptera, Raphidiidae: *Raphidia* sp. (L, A).

Neuroptera, Hemerobiidae: undet. species (L, FAE); Chysopidae: *Chysopa* sp. (A, FAE, diss).

Myrmeleontidae. *Myrmeleon* sp. (L, A, FAE).  
Strepsiptera, Halictophagidae: *Halictophagus* sp.  
(male) (A, dried).

### APPENDIX III: LIST OF THORACIC MUSCLES

The muscle names are adopted from Larsén (1966). Muscles not described in that study are designated according to origin and insertion in *Sialis* (Czihak, 1953).

#### Prothorax

##### Dorsal Muscles

M. 1: M. pronoti primus (Matsuda, 1970, op-t 2; Larsén, 1966, M 1; Baehr, 1975, 2).

M. 2: M. M. pronoti secundus (Matsuda, 1970, cv(d)-t 1; Larsén, 1966, M 2; Baehr, 1975, 1).

M. 3: M. pronoti tertius (Matsuda, 1970, op-t 3; Larsén, 1966, M 3; Baehr, 1975, 3).

M. 4: M. mesonoto-occipitalis lateralis (Matsuda, 1970, t 11; Coleoptera: -).

M. 5: Mm. pronoto-occipitales tenues (Matsuda, 1970, t-s(cv) 1; Coleoptera: -).

M. 6: M. pronoti quartus (Matsuda, 1970, t-12; Larsén, 1966, M 4; Baehr, 1975, 4).

M. 7: M. pleuro-occipitalis (Matsuda, 1970, op-p 2; Coleoptera: -).

M. 8: M. cervicale-occipitalis torquatus (Matsuda, 1970, op-cv 1, 2; Coleoptera: -).

##### Ventral Muscles

M. 9: M. prosterni primus (Matsuda, 1970, s 1, 2; Larsén, 1966, M 5; Baehr, 1975, 5).

M. 10: M. prosterni secundus (Matsuda, 1970, p-s(cv) 7; Larsén, 1966, M 6; Baehr, 1975, 8).

##### Dorsoventral Muscles

M. 11: M. furco-cervicalis (Matsuda, 1970, cv-s 3; Larsén, 1966, —; Bauer, 1910, M. rotator capitis inferior?; Baehr, 1975, 10).

M. 12: M. dorsoventralis primus (Matsuda, 1970, t-cv 2; Larsén, 1966, M 7; Baehr, 1975, 6).

M. 13: M. dorsoventralis secundus (Matsuda, 1970, t-s(cv) 9; Larsén, 1966, M 8; Baehr, 1975, -).

M. 14: M. dorsoventralis tertius (Matsuda, 1970, t-cv 1; Larsén, 1966, M 9; Baehr, 1975, 7).

M. 15: M. dorsoventralis quartus (Matsuda, 1970, op-s 1, op-cv 3?; Larsén, 1966, M 10; Baehr, 1975, 9).

M. 16: M. dorsoventralis quintus (Matsuda, 1970, t-s 1; Larsén, 1966, M 11; Baehr, 1975, 13).

##### Lateral Muscles

M. 17: M. notopleuralis (Matsuda, 1970, t-p?; Larsén, 1966, M 12; Baehr, 1975, 11).

M. 18: M. pronoto-mesepisternalis (Matsuda, 1970, t-p 1; Larsén, 1966, M 13; Baehr, 1975, 12).

M. 19: M. mesonoto-postpleuralis (Matsuda, 1970, t-p 17; Coleoptera: -).

M. 20: M. mesepisterno-spinalis (Matsuda, 1970, ?; Coleoptera: -).

M. 21: M. pleurofurco-spinalis (Matsuda, 1970, p-s 2; Coleoptera: -).

##### Leg Muscles

M. 22: M. noto-trochantinalis (Matsuda, 1970, t-cx 6; Larsén, 1966, M 14; Baehr, 1975, 15).

M. 23: M. noto-coxalis (Matsuda, 1970, t-cx 6; Larsén, 1966, M 15; Baehr, 1975, 15).

M. 24: M. episterno coxalis (Matsuda, 1970, p-ti(cx) 2, p-cx 4?; Larsén, 1966, M 16; Baehr, 1975, 16).

M. 25: M. epimero-coxalis (Matsuda, 1970, t-cx 8; Larsén, 1966, M 17; Baehr, 1975, 17).

M. 26: M. cervicale-coxalis (-trochantinalis) (Matsuda, 1970, cv-cx 3; Coleoptera: -).

M. 27: M. sterno-coxalis (Matsuda, 1970, s-cx 5; Larsén, 1966, M 18; Baehr, 1975, 18).

M. 28: M. spino-coxalis (Matsuda, 1970, s-cx 4; Coleoptera: -).

M. 29: M. postpleuro-coxalis transversus (Matsuda, 1970, p-cx 7 (x); Coleoptera: -).

M. 30: Mm. furca-coxales (Matsuda, 1970, s-cx 3; Larsén, 1966, M 19; Baehr, 1975, 19).

M. 31: M. pleura-trochanteralis (Matsuda, 1970, p-tr 3; Larsén, 1966, M 20; Baehr, 1975, 20).

M. 32–38: intrinsic leg muscles, present in all adult insects

## Mesothorax

### Dorsal Muscles

M. 39: *M. mesonoti primus* (Matsuda, 1970, t 14; Larsén, 1966, M 28; Baehr, 1975, 23).

M. 40: *M. mesonoti secundus* (Matsuda, 1970, t 12; Larsén, 1966, M 29; Baehr, 1975, 24).

M. 41: *M. scutello-postnotalis* (Matsuda, 1970, t-13; Coleoptera: –)

### Ventral Muscles

M. 42: *M. mesosterni primus* (Matsuda, 1970, s-13; Larsén, 1966, M 30; Baehr, 1975, 25).

M. 43: *M. mesosterni secundus* (Matsuda, 1970, s-12; Larsén, 1966, M 31; Baehr, 1975, 26).

### Dorsoventral Muscles

M. 44: *Mm. noto-sternales* (Matsuda, 1970, t-p 5; Larsén, 1966, —; Baehr, 1975, 27).

M. 45: *M. dorsoventralis* (Matsuda, 1970, t-s 1; Larsén, 1966, M. 32; Baehr, 1975, 32).

### Lateral Muscles

M. 46: *M. noto-pleurocostalis longus* (Matsuda, 1970, t-p 12; Larsén, 1966, —; Baehr, 1975, 28).

M. 47: *M. noto-pleuralis* (Matsuda, 1970, t-p 3; Larsén, 1966, M 33; Baehr, 1975, 29).

M. 48: *M. notoepisternalis longus* (Matsuda, 1970, t-p 8; Coleoptera: –).

M. 49: *M. noto-pleurocostalis brevis* (Matsuda, 1970, ?; Coleoptera – ?).

M. 50: *M. episterno-sternalis* (Matsuda, 1970, p 3; Larsén, 1966, —; Baehr, 1975, 33).

M. 51: *M. episterno-spinalis* (Matsuda, 1970, p-s 2; Larsén, 1966, —; Baehr, 1975, 35).

M. 52: *M. epimero-subalaris* (Matsuda, 1970, t-p 16; Larsén, 1966, M 34, 35; Baehr, 1975, —).

M. 53: *M. pleura-alaris a* (Matsuda, 1970, t-p 14; Larsén, 1966, M 36a; Baehr, 1975, 31).

M. 54: *M. pleura-alaris b* (Matsuda, 1970, t-p 13; Larsén, 1966, M 36b; Baehr, 1975, 30).

M. 55: *M. furca-pleuralis* (Matsuda, 1970, p-s 1; Larsén, 1966, M 37; Baehr, 1975, 34).

M. 56: *M. intraepisternalis* (Matsuda, 1970, p 1; Coleoptera: –).

M. 57: *M. pleurocosto-praenotalis* (Matsuda, 1970, t-p 4; Larsén, 1966, —; Baehr, 1975, —).

### Leg Muscles

M. 58: *M. profurca-mesepisternalis* (Matsuda, 1970, p-s 3; Larsén, 1966, M 38; Baehr, 1975, —).

M. 59: *M. noto-trochaninalis* (Matsuda, 1970, t-ti(cx) 2; Larsén, 1966, M 39; Baehr, 1975, 36).

M. 60: *Mm. noto-coxalis* (Matsuda, 1970, t-cx 6; Larsén, 1966, M 40; Baehr, 1975, 37).

M. 61: *M. episterno-coxalis* (Matsuda, 1970, p-cx 5; Larsén, 1966, M 41; Baehr, 1975, 38).

M. 62: *M. coxa-basalaris* (Matsuda, 1970, p-ti(cx) 2, p-cx 47; Larsén, 1966, M 42; Baehr, 1975, 39).

M. 63: *M. sterno-trochantinalis* (Matsuda, 1970, ?; Coleoptera: –).

M. 64: *M. coxa-subalaris* (Matsuda, 1970, t-cx 8; Larsén, 1966, 43; Baehr, 1975, 40).

M. 65: *M. furca-coxalis anterior* (Matsuda, 1970, s-cx 5; Larsén, 1966, M 44; Baehr, 1975, 41).

M. 66: *M. furca-coxalis lateralis* (Matsuda, 1970, s-cx 2; Larsén, 1966, M 45; Baehr, 1975, 42).

M. 67: *M. furca-coxalis posterior* (Matsuda, 1970, s-cx 3; Larsén, 1966, M 46; Baehr, 1975, 43).

M. 68: *M. episterno-trochantinalis* (Matsuda, 1970, p-ti(cx) 3; Coleoptera: –).

M. 69: *M. noto-trochanteralis* (Matsuda, 1970, t-tr 1; Larsén, 1966, M 47; Baehr, 1975, 44).

M. 70: *M. episterno-trochanteralis* (Matsuda, 1970, p-tr 2 (Larsén, 1966, M 48; Baehr, 1975, 45).

M. 71: *M. trochantero-basalaris* (Matsuda, 1970, p-tr 2; Larsén, 1966, M 50; Baehr, 1975, 46).

M. 72: *M. episterno-trochanteralis* (Matsuda, 1970, s-tr 1; Larsén, 1966, M 52; Baehr, 1975, 47).

M. 73–78: intrinsic leg muscles, present in all adult insects.

## Metathorax

### Dorsal Muscles

M. 79: *M. metanoti primus* (Matsuda, 1970, t 14; Larsén, 1966, M 60; Baehr, 1975, 50).

M. 80: *M. metanoti secundus* (Matsuda, 1970, t 12; Larsén, 1966, M 61; Baehr, 1975, 51).

M. 81: *M. scutello-postnotalis* (Matsuda, 1970, t 13; Coleoptera: –).

### ***Ventral Muscles***

M. 82: *M. metasterni primus* (Matsuda, 1970, s 13; Larsén, 1966, M 62; Baehr, 1975, 52).

M. 83: *M. metasterni secundus* (Matsuda, 1970, s 12; Larsén, 1966, M 63; Baehr, 1975, 53).

### ***Dorsoventral Muscles***

M. 84: *M. dorsoventralis primus* (Matsuda, 1970, t-p 5; Larsén, 1966, M 64; Baehr, 1975, 55).

M. 85: *M. dorsoventralis secundus* (Matsuda, 1970, t-s 1; Larsén, 1966, M 65; Baehr, 1975, 62).

M. 86: *M. dorsoventralis tertius* (Matsuda, 1970, t-s 1?; Larsén, 1966, M 66; Baehr, 1975, 63).

### ***Lateral Muscles***

M. 87: *M. episterno-spinalis* (Matsuda, 1970, p-s 2; Larsén, 1966, —; Baehr, 1975, 67).

M. 88: *M. mesofurca-basalaris* (Matsuda, 1970, p-s 3?; Larsén, 1966, —; Baehr, 1975, 68).

M. 89: *Mm. noto-episternales breves* (Matsuda, 1970, t-p 3; Larsén, 1966, —; Baehr, 1975, 56).

M. 90: *M. pleura-praealaris* (Matsuda, 1970, t-p 4; Larsén, 1966, 67; Baehr, 1975, 58).

M. 91: *M. noto-pleuralis* (Matsuda, 1970, t-p 12?; Larsén, 1966, 68; Baehr, 1975, 59).

M. 92: *M. noto-pleuralis* (Matsuda, 1970, t-p 15?; Larsén, 1966, 68; Baehr, 1975, 57).

M. 93: *M. noto-basalaris* (Matsuda, 1970, t-p 8; Larsén, 1966, 69; Baehr, 1975, 57).

M. 94: *M. epimero-subalaris* (Matsuda, 1970, t-p 16; Larsén, 1966, M 70; Baehr, 1975, 66.).

M. 95: *M. pleura-alaris a* (Matsuda, 1970, t-p 14; Larsén, 1966, M 71a; Baehr, 1975, 60).

M. 96: *M. pleura-alaris b* (Matsuda, 1970, t-p 13; Larsén, 1966, M 71b; Baehr, 1975, 61).

M. 97: *M. sterno-episternalis* (Matsuda, 1970, p 1; Larsén, 1966, 72; Baehr, 1975, 64).

M. 98: *M. sterno-basalaris* (Matsuda, 1970, p 3; Larsén, 1966, M 73, sterno-basalaris; Baehr, 1975, 65).

M. 99: *Mm. furco-pleurocostales* (Matsuda, 1970, p-s 1; Coleoptera: –).

### ***Leg Muscles***

M. 100: *M. noto-trochaninalis* (Matsuda, 1970, t-ti(cx) 2; Larsén, 1966, M 74; Baehr, 1975, 69).

M. 101: *M. noto-coxalis anterior* (Matsuda, 1970, t-cx 6?; Larsén, 1966, M 75; Baehr, 1975, 70).

M. 102: *M. noto-coxalis posterior* (Matsuda, 1970, t-cx 7?; Larsén, 1966, M 76; Baehr, 1975, 71).

M. 103: *M. episterno-coxalis* (Matsuda, 1970, p-cx 5; Larsén, 1966, M 77; Baehr, 1975, 72).

M. 104: *M. coxa-basalaris* (Matsuda, 1970, p-cx 4; Larsén, 1966, M 78; Baehr, 1975, 73).

M. 105: *M. coxa-subalaris* (Matsuda, 1970, t-cx 8; Larsén, 1966, 79, *M. coxa-subalaris*; Baehr, 1975, 74).

M. 106: *M. sterno-coxalis* (Matsuda, 1970, s-cx 5, p-ti(cx) 1?; Larsén, 1966, M 80; Baehr, 1975, —).

M. 107: (Matsuda, 1970, s-cx 5; Larsén, 1966, M 81; Baehr, 1975, 75).

M. 108: *M. furca-coxalis lateralis* (Matsuda, 1970, s-cx 2; Larsén, 1966, M 82; Baehr, 1975, 76).

M. 109: *M. furca-coxalis posterior* (Matsuda, 1970, s-cx 3; Larsén, 1966, M 83; Baehr, 1975, 77).

M. 110: *M. episterno-trochantinalis* (Matsuda, 1970, p-ti(cx) 3; Coleoptera: –).

M. 111: *M. noto-trochanteralis* (Matsuda, 1970, t-tr 1; Larsén, 1966, M 84; Baehr, 1975, 78).

M. 112: *M. trochantero-basalaris* (Matsuda, 1970, p-tr 2; Larsén, 1966, —; Baehr, 1975, 79).

M. 113: *M. furca-trochanteralis* (Matsuda, 1970, s-tr 1; Larsén, 1966, M 85; Baehr, 1975, 80).

M. 114–122: intrinsic leg muscles, present in all adult insects.

## APPENDIX IV: LIST OF THORACIC MUSCLES

An x means present, o means absent. The numbers of muscles for Strepsiptera refer to Kinzelbach (1971).

taxa/muscles	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<b>Larsén</b>	1	2	3			4			5	6		7	8	9	10	11	12	13
<i>Perla</i>	x	x	x	o	x	o	o	x	x	o	o	x	o	o	x	x	x	?
<i>Panorpa</i>	o	x	o	o	x	x	o	x	x	o	o	x	x?	o	x	x	x	x?
<i>Strepsiptera</i>	51	39	40	41a	?	41	53	o	46	?	?	51	42	49	o	44	o	?
<i>Myrmeleon</i>	x	x	x	o	o	o	o	x	x	o	o	x	x	x	o	o	x	o
<i>Sialis</i>	x	x	x	x	x	x	x	x	x	x	o	x	x	x	o	o	x	x
<i>Corydalus</i>	x	x	x	x	o	x	x	x	x	x	x	x	x	x	o	x	x	x
<i>Chauliodes</i>	x	x	o	o	o	x	o	x	x	o	o	x	o	x	o	x	x	x
<i>Priacma</i>	x	x	x	o	o	x	o	o	x	x	x	x	x	x	x	x	x	x
<i>Hydroscapha</i>	x	x	x	o	o	x	o	o	x	x	o	x	x	o	x	x	x	o?
<i>Microsporus</i>	x	x	x	o	o	x	o	o	x	x	o	x	x	o	x	x	x	o?
<i>Satoniüs</i>	?	?	?	o	o	?	o	o	?	?	o	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	x	x	x	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Gyrinus</i>	o	x	x	o	o	o	o	o	x	x	o	x	o	o	x	x	o	x
<i>Haliphus</i>	x	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	o	o
<i>Trachypachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	x	?	x	?
<i>Noterus</i>	x	x	o	o	o	o	o	o	x	x	o	x	x	o	x	x	x	x
<i>Amphizoa</i>	?	?	?	o	o	?	o	o	?	?	o	?	?	?	x	?	x	?
<i>Hygrobia</i>	o	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Dytiscus</i>	x	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Carabus</i>	x	x	x	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Elaphrus</i>	x	x	x	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Pterostichus</i>	x	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Ochthebius</i>	o?	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Sphaeridium</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Hydrophilus</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Nicrophorus</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Creophilus</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Aphodius</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Cetonia</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Selatosomus</i>	x	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Cantharis</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	x	x	x	x	x
<i>Lytta</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	x	x	x	x	x
<i>Meloe</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	x	x	x	x	x
<i>Coccinella</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	x	x	x	x	x
<i>Tenebrio</i>	x	x	o	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x
<i>Cassida</i>	x	x	o	o	o	x	o	o	x	x	o	x	o	o	x	x	x	x
<i>Donacia</i>	x	x	x	o	o	x	o	o	x	x	o	x	x	o	x	x	x	x

taxa/muscles	19	20	21	22	23	24	25	26	27	28	29	30	31	39	40	41	42	43
<b>Larsén</b>				14	15	16	17		18			19	20	28	29		30	31
<i>Perla</i>	x	?	o	x	x	o	x	o	x	o	o	x	o	x	o	x	x	x
<i>Panorpa</i>	o	?	o	o	o	o	x	o?	x	o	o	x	o	x	x	x	x	o
<i>Strepsiptera</i>	o	o	o	o	54	57	?	o	58	o	o	o	59	68	70	69	95	?
<i>Myrmeleon</i>	o	?	o	x	x	x	o	o	o	o	o	x	o	x	x	x	x	o
<i>Sialis</i>	x	x	x	x	x	x	x	x	x	x	x	x	o	x	x	x	x	x
<i>Corydalus</i>	x	o	o	x	x	x	o	x	x	o	o	x	o	x	x	x	x	x
<i>Chauliodes</i>	o	o	o	x	x	x	o	x	x	o	o	x	o	x	x	x	x	o
<i>Priacma</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	x	o	x	x
<i>Hydroscapha</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	o	o	x	o
<i>Microsporus</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	o	o	x	o
<i>Satonius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	o	o	o	x	x	x	o	o	o	o	o	x	x	x	?	o	?	?
<i>Gyrinus</i>	o	o	o	x	x	x	x	o	o	o	o	x	x	x	o	o	x	x
<i>Haliplus</i>	o	o	o	x	x	x	o	o	x	o	o	x	x	x	x	o	x	o
<i>Trachypachus</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	?	o	x	?
<i>Noterus</i>	o	o	o	x	x	x	o	o	x	o	o	x	x	x	x	o	x	o
<i>Amphizoa</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	?	o	x	?
<i>Hygrobia</i>	o	o	o	x	x	x	o	o	x	o	o	x	x	x	o	o	x	o
<i>Dytiscus</i>	o	o	o	x	x	x	o	o	x	o	o	x	x	x	o	o	x	x
<i>Carabus</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	o	o	x	x
<i>Elaphrus</i>	o	o	o	x	x	x	o	o	x	o	o	x	x	x	x	o	x	x
<i>Pterostichus</i>	o	o	o	x	x	x	x	o	x	o	o	x	x	x	o	o	x	x
<i>Ochthebius</i>	o	o	o	x	x	?	?	o	o	o	o	x?	x	x	x	?	x	o
<i>Sphaeridium</i>	o	o	o	x	x	o	o	o	o	o	o	o	x	x	x	o	x	o
<i>Hydrophilus</i>	o	o	o	x	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Nicrophorus</i>	o	o	o	x	x	x	x	o	o	o	o	x	x	x	x	o	x	o
<i>Creophilus</i>	o	o	o	x	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Aphodius</i>	o	o	o	o	x	x	x	o	o	o	o	o	x	x	x	o	x	o
<i>Cetonia</i>	o	o	o	o	x	x	x	o	o	o	o	o	x	x	x	o	x	o
<i>Selatosomus</i>	o	o	o	o	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Cantharis</i>	o	o	o	o	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Lytta</i>	o	o	o	x	x	x	x	o	o	o	o	o	x	x	x	o	x	x
<i>Meloe</i>	o	o	o	x	x	x	x	o	o	o	o	o	x	x	x	o	x	x
<i>Coccinella</i>	o	o	o	o	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Tenebrio</i>	o	o	o	x	x	x	o	o	o	o	o	o	x	x	x	o	x	o
<i>Cassida</i>	o	o	o	x	x	x	o	o	o	o	o	x	x	x	x	o	x	o
<i>Donacia</i>	o	o	o	x	x	x	o	o	o	o	o	o	x	x	x	o	x	o

taxa/muscles	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
<b>Larsén</b>		32		33					34-	36	36	37			38	39	40	41
<i>Perla</i>	x	x	o	x	?	?	x	o	x	o	x	x	x	x	o	x	x	x
<i>Panorpa</i>	x	x	x	x	x	?	x	o	x	o	x	x	x	o	o	x	o	x
<i>Strepsiptera</i>	o	67	o	89	o	o	o	o	o	o	o	o	o	o	o	o	96	97
<i>Myrmeleon</i>	x	x	o	x	x	?	x	o	x	x	x	o	o	x	x	x	x	x
<i>Sialis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	o	x	x	x
<i>Corydalus</i>	x	x	x	x	x	o	x	o	x	x	x	x	x	x	o	x	x	x
<i>Chauliodes</i>	x	x	x	x	x	o	x	o	x	x	x	x	x	x	o	x	x	x
<i>Priacma</i>	x	x	x	x	o	o	x	x	o	x	x	x	o	o	o	x	x	x
<i>Hydroscapha</i>	o	x	o	o	o	o	o	o	x	a	b	x	o	o	x	o	x	x
<i>Microsporus</i>	o	o	o	?	o	o	o	o	?	?	?	x	o	o	x	o	x	x
<i>Satoniüs</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	o	?	?	?	o	o	o	o	?	?	?	?	o	o	?	?	x	?
<i>Gyrinus</i>	o	o	o	x	o	o	o	o	o	a	b	o	o	o	x	o	x	x
<i>Haliplus</i>	o	o	o	x	o	o	o	o	o	a	b	o	o	o	o	x	x	x
<i>Trachypachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Noterus</i>	o	o	o	x	o	o	o	o	o	a	b	o	o	o	o	x	x	x
<i>Amphizoa</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hygrobia</i>	o	x	o	x	o	o	o	o	o	a	b	o	o	o	o	x	x	x
<i>Dytiscus</i>	o	x	o	x	o	o	o	o	o	a	b	x	o	o	o	x	x	x
<i>Carabus</i>	o	o	o	o	o	o	o	o	o	a	b	x	o	o	x	x	x	x
<i>Elaphrus</i>	o	o	o	x	o	o	o	o	o	a	b	o	o	o	x	x	x	x
<i>Pterostichus</i>	o	o	o	x	o	o	o	o	o	a	b	o	o	o	x	x	x	x
<i>Ochthebius</i>	o	o	?	x	o	o	o	o	?	?	?	o	o	o	o	o	?	x
<i>Sphaeridium</i>	o	o	o	x	o	o	o	o	x	a	b	o	o	o	o	o	x	x
<i>Hydrophilus</i>	o	x	o	x	o	o	o	o	x	a	b	o	o	o	o	o	x	x
<i>Nicrophorus</i>	o	o	o	x	o	o	o	o	o	a	b	x	o	o	o	o	x	x
<i>Creophilus</i>	o	x	o	x	o	o	o	o	x	a	b	o	o	o	o	o	x	x
<i>Aphodius</i>	o	x	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Cetonia</i>	o	x	o	x	o	o	o	o	x	a	b	o	o	o	o	o	x	x
<i>Selatosomus</i>	o	x	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Cantharis</i>	o	x	o	x	o	o	o	o	x	a	b	o	o	o	o	o	x	x
<i>Lytta</i>	o	o	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Meloe</i>	o	o	o	x	o	o	o	o	o	a	o	o	o	o	o	o	x	x
<i>Coccinella</i>	o	o	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Tenebrio</i>	o	o	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Cassida</i>	o	o	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x
<i>Donacia</i>	o	o	o	x	o	o	o	o	x	a	b	x	o	o	o	o	x	x



taxa/muscles	62	63	64	65	66	67	68	69	70	71	72	79	80	81	82	83	84	85
<b>Larsén</b>	42		43	44	45	46		47	48	50	52	60	61		62	63	64	65
<i>Perla</i>	o	?	x	x	x	x	x	x	x	x	x	o	o	x	x	x	x	x
<i>Panorpa</i>	o?	?	x	x	x	x	x	x	x	x	x	x	x	o	x	o	x?	o
Strepsiptera	o	o	o	75?	o	o	o	o	79	o	o	90	91	o	95	94	112	o
<i>Myrmeleon</i>	x	?	x	x	x	x	o	x	x	x	x	x	x	o	o	o	x	x
<i>Sialis</i>	x	x	x	x	o	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Corydalus</i>	x	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Chauliodes</i>	x	o	x	x	x	x	x	x	x	x	x	x	x	x	x	o	x	x
<i>Priacma</i>	x	o	x	x	x	x	o	x	x	x	x	x	x	o	x	x	x	x
<i>Hydroscapha</i>	o	o	x	x	x	x	o	x	x	o	x	x	x	o	o	o	x	x
<i>Microsporus</i>	o	o	x	x	o	x	o	o	x	o	x	x	x	o	o	o	x	x
<i>Satonius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	?	o	x	x	o	x	o	x	x	?	x	?	?	o	x	?	?	?
<i>Gyrinus</i>	o	o	x	o	o	x	o	x	x	o	x	o	o	o	x	o	o	o
<i>Haliplus</i>	x	o	x	x	o	x	o	x	x	o	x	x	x	o	x	x	x	o
<i>Trachypachus</i>	?	?	?	?	?	?	?	?	?	?	?	d	d	o	x	x	d	?
<i>Noterus</i>	o	o	x	x	x	x	o	x	x	o	x	x	x	o	x	o	x	x
<i>Amphizoia</i>	?	?	?	?	?	?	?	?	?	?	?	d	d	o	x	o	d	o
<i>Hygrobia</i>	o	o	x	x	x	x	o	x	x	o	x	x	x	o	x	o	x	x
<i>Dytiscus</i>	o	o	x	x	x	x	o	x	x	o	x	x	x	o	x	o	x	x
<i>Carabus</i>	o	o	x	x	o	x	o	x	x	o	x	o	o	o	x	x	o	o
<i>Elaphrus</i>	o	o	x	x	o	x	o	x	x	o	x	x	x	o	x	x	x	x
<i>Pterostichus</i>	o	o	x	x	o	x	o	x	x	o	x	x	x	o	x	x	x	x
<i>Ochthebius</i>	o	o	o	?	o	x	o	o	x	o	o	x	x	o	x?	o?	x	x
<i>Sphaeridium</i>	x	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Hydrophilus</i>	x	o	o	x	o	x	o	o	o	o	x	x	x	o	x	o	x	x
<i>Nicrophorus</i>	o	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Creophilus</i>	x	o	o	x	o	x	o	o	x	o	o	x	x	o	x	o	x	x
<i>Aphodius</i>	x	o	o	x	o	x	o	o	o	x	x	x	x	o	x	o	x	x
<i>Cetonia</i>	x	o	o	x	o	x	o	o	o	o	o	x	x	o	x	o	x	x
<i>Selatosomus</i>	x	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Cantharis</i>	o	o	o	x	x	x	o	o	x	o	x	x	x	o	o	o	x	x
<i>Lytta</i>	x	o	o	x	x	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Meloe</i>	o	o	o	x	x	x	o	o	o	o	x	o	o	o	x	o	o	x
<i>Coccinella</i>	x	o	o	o	x	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Tenebrio</i>	x	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Cassida</i>	x	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x
<i>Donacia</i>	x	o	o	x	o	x	o	o	x	o	x	x	x	o	x	o	x	x

taxa/muscles	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103
<b>Larsén</b>	66				67	68	68	69	70	71	71	72	73		74	75	76	77
<i>Perla</i>	x	o	o	x	x	o	x	o	x	o	x	x	x	x	x	x	x	x
<i>Panorpa</i>	o	o	o	x	x	x	o	x	x	o	x	x	x	x	x	o	x	x
Strepsiptera	o	o	o	o	o	114	?	109	111	60	117	115	108	o	o	96	o	97
<i>Myrmeleon</i>	x	o	x	x	x	o	x	x	x	x	x	o	x	x	x	x	x	x
<i>Sialis</i>	o	o	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Corydalus</i>	o	o	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Chauliodes</i>	o	o	o	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Priacma</i>	x	x	x	o	x	x	x	x	x	x	x	x	x	o	x	x	x	x
<i>Hydroscapha</i>	x	o	o	o	x	o	o	x	o	a	b	x	x	o	o	x	o	x
<i>Microsporus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	o	o	o	x
<i>Satonius</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	?	o	o	o	?	?	?	?	?	a	b	x	?	o	o	?	x	o
<i>Gyrinus</i>	o	o	o	o	x	o	o	x	x	a	b	o	o	o	o	o	x	o
<i>Haliplus</i>	o	o	o	o	x	o	o	x	x	a	b	x	x	o	o	x	x	o
<i>Trachypachus</i>	o	o	o	o	x	o	o	x	x	a	b	o	d	o	o	d	x	o
<i>Noterus</i>	o	o	o	o	x	o	o	x	o	a	b	x	x	o	o	x	x	o
Amphizoa	o	o	o	o	x	o	o	x	x	a	b	x	d	o	o	d	x	o
<i>Hygrobia</i>	o	o	o	o	x	o	o	x	x	a	b	o	x	o	o	x	x	o
<i>Dytiscus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	o	x	x	o
<i>Carabus</i>	o	o	o	o	x	o	o	x	x	a	b	o	o	o	o	o	x	o
<i>Elaphrus</i>	o	o	o	o	x	o	o	x	x	a	b	o	x	o	o	x	x	o
<i>Pterostichus</i>	o	o	o	o	x	o	o	x	x	a	b	o	x	o	o	x	x	o
<i>Ochthebius</i>	x	o	o	o	x	o	o	x	x?	a	b	x	x	o	o	x	x	x
<i>Sphaeridium</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	o	x	x	x
<i>Hydrophilus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	o	x	x	x
<i>Nicrophorus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	x	x	x
<i>Creophilus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	x	x	x
<i>Aphodius</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	x	x	x
<i>Cetonia</i>	x	o	o	o	x	o	o	x	x	a	b	o	x	o	o	x	x	x
<i>Selatosomus</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	x	x	o
<i>Cantharis</i>	o	o	o	o	x	o	o	x	o	a	b	x	x	o	x	x	x	x
<i>Lytta</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	x	x	x
<i>Meloe</i>	o	o	o	o	o	o	o	o	o	a	b	x	o	o	o	o	x	x
<i>Coccinella</i>	x	o	o	o	x	o	o	x	x	a	b	x	x	o	x	o	x	x
<i>Tenebrio</i>	x	o	o	o	x	o	o	x	x	a	b	o	x	o	x	x	x	x
<i>Cassida</i>	x	o	o	o	x	o	o	x	x	a	b	o	x	o	x	o	x	x
<i>Donacia</i>	x	o	o	o	x	o	o	x	x	a	b	o	x	o	x	o	x	x

taxa/muscles	104	105	106	107	108	109	110	111	112	113
<b>Larsén</b>	78	79	80	81	82	83		84		85
<i>Perla</i>	o	x	?	x	x	x	o	x	x	x
<i>Panorpa</i>	o	x	x	x	x	x	x	x	x	x
Strepsiptera	107	110	o	o	o	o	o	o	o?	99
<i>Myrmeleon</i>	x	x	x	x	x	x	o	x	x	x
<i>Sialis</i>	x	x	x	o	o	x	x	x	x	x
<i>Corydalus</i>	x	x	x	x	x	x	x	x	x	x
<i>Chauliodes</i>	x	x	x	o	x	x	x	x	x	x
<i>Priacma</i>	x	x	o	x	x	x	o	x	o	x
<i>Hydroscapha</i>	x	x	o	?	o	x	o	o	o	x
<i>Microsporus</i>	x	x	o	?	o	x	o	o	o	x
<i>Satanius</i>	?	?	?	?	?	?	?	?	?	?
<i>Spanglerogyrus</i>	?	?	o	x	x	x	o	o	o	x
<i>Gyrinus</i>	x	o	o	o	o	x	o	x	o	x
<i>Haliphus</i>	o	x	o	x	x	x	o	o	o	x
<i>Trachypachus</i>	d	d	o	x	x	x	o	o	o	x
<i>Noterus</i>	o	x	o	o	o	o	o	o	o	x
<i>Amphizoa</i>	d	d	o	o	x	o	o	o	o	x
<i>Hygrobia</i>	o	x	o	o	x	o	o	o	o	x
<i>Dytiscus</i>	x	x	o	o	x	o	o	o	o	x
<i>Carabus</i>	o	o	o	x	x	x	o	o	o	x
<i>Elaphrus</i>	x	x	o	x	x	x	o	o	o	x
<i>Pterostichus</i>	x	x	o	x	x	x	o	o	o	x
<i>Ochthebius</i>	?	x	o	x	x	x	o	x	o	x
<i>Sphaeridium</i>	x	x	o	x	x	x	o	x	o	x
<i>Hydrophilus</i>	o	x	o	x	x	x	o	o	o	x
<i>Nicrophorus</i>	x	x	o	x	x	x	o	o	o	x
<i>Creophilus</i>	o	x	o	x	x	x	o	o	o	x
<i>Aphodius</i>	x	x	o	x	x	x	o	o	o	x
<i>Cetonia</i>	o	x	o	x	x	x	o	o	o	x
<i>Selatosomus</i>	x	x	o	x	x	x	o	o	o	x
<i>Cantharis</i>	x	x	o	x	x	x	o	o	o	x
<i>Lytta</i>	x	x	o	x	x	x	o	o	o	x
<i>Meloe</i>	o	o	o	x	x	x	o	o	o	x
<i>Coccinella</i>	o	o	o	x	x	x	o	o	o	x
<i>Tenebrio</i>	x	o	o	x	x	x	o	o	o	x
<i>Cassida</i>	x	o	o	x	x	x	o	o	o	x
<i>Donacia</i>	o	x	o	x	x	x	o	o	o	x

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