

See discussions, stats, and author profiles for this publication at:  
<http://www.researchgate.net/publication/233629663>

# Phylogenetic analysis of larval and adult characters of Adephaga (Coleoptera) using cladistic computer programs

ARTICLE *in* INSECT SYSTEMATICS & EVOLUTION · DECEMBER 1995

Impact Factor: 1.11 · DOI: 10.1163/187631296X00043

---

CITATIONS

23

---

DOWNLOADS

82

---

VIEWS

75

2 AUTHORS, INCLUDING:



Rolf Beutel

Friedrich Schiller University Jena

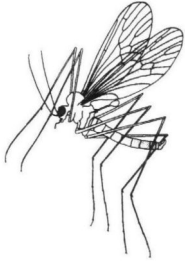
230 PUBLICATIONS 3,088 CITATIONS

SEE PROFILE

# Phylogenetic analysis of larval and adult characters of Adephaga (Coleoptera) using cladistic computer programs

R. G. BEUTEL and A. HAAS

Ent. scand.



Beutel, R. G. & Haas, A.: Phylogenetic analysis of larval and adult characters of Adephaga (Coleoptera) using cladistic computer programs. *Ent. scand.* 27: 197-205. Copenhagen, Denmark. June 1996. ISSN 0013-8711.

Eighty characters of larvae and adults of 35 adephagan genera, 2 polyphagan genera, and 1 cupedid genus were analyzed using the cladistic computer programs PAUP and MacClade. The analysis resulted in 1961 equally parsimonious trees of 131 steps (minimum length cladogram). The monophyly of Adephaga and of all adephagan families is confirmed. A sistergroup relationship between Gyrinidae and the remaining Adephaga, a sistergroup relationship between *Spanglerogyrus* and Gyrininae, the monophyly of Dytiscoidea, a sistergroup relationship between Noteridae and the remaining Dytiscoidea, a sistergroup relationship between Hygrobiidae and Dytiscidae, the monophyly of Caraboidea (Rhysodidae and Carabidae), and the monophyly of Harpalinae sensu Crowson (1955) are in agreement with earlier phylogenetic hypotheses by Beutel & Roughley (1988) and Beutel (1992a, 1993, 1995). The sistergroup relationship between Haliplidae and Dytiscoidea and the monophyly of Geadephaga (Trachypachidae + Caraboidea) are in contrast to Beutel (1992a, 1993, 1995). The high number of equally parsimonious trees is largely due to an inconsistent distribution of character states in basal carabid taxa, i.e. reversals and convergencies. Further evidence is needed for a clarification of these systematic problems.

R. G. Beutel & A. Haas, Institut für spezielle Zoologie und Evolutionsbiologie, Erbertstr. 1, FSU Jena, 07743 Jena, Germany.

## Introduction

The phylogeny and systematics of the coleopteran suborder Adephaga are still discussed controversially despite of substantial interest in the group and numerous relevant publications. Older, typological classifications (e.g. Ganglbauer 1892) are based on diagnostic, distinguishing features. They are not falsifiable due to the subjective choice and interpretation of characters. Since the introduction of Hennigian methods ('Phylogenetische Systematik', Hennig 1950, 1966), a considerable number of hypotheses concerning adephagan phylogeny were published (Burmeister 1976; Bills 1976; Hammond 1979; Ward 1979; Baehr 1979; Roughley 1981; Erwin 1985; Nichols 1985; Kavanaugh 1986; Ruhnau 1986; Beutel & Roughley 1988; Beutel 1992a, 1993, 1995; Arndt 1993). Most of these studies, which are exclusively based on manual character evaluation, are contradictory in essential points. Computer-generated phylogenetic hypotheses have not been presented so far.

The present contribution is a computer analysis

of a broad spectrum of larval and adult characters. The data are based on studies by Arndt (1993), Baehr (1979), Bell (1966, 1967), Beutel (1989a, b, 1990a, 1992a-d, 1993, 1994a, 1994b, 1995), Beutel & Roughley (1988, 1994), Bills (1976), Bousquet (1986), Crowson (1955), De Marzo (1979), Erwin (1985), Folkerts (1979), Hammond (1979), Jeannel (1941-42), Kavanaugh (1986), Lawrence (1982), Seeger (1971), Ruhnau (1986), and Ward (1979).

## Material and methods

A large number of larvae and adults of adephagan and non-adephagan families were studied (see list of taxa examined in Beutel 1992a, 1993, 1994a). 35 genera representing six aquatic and three terrestrial families of Adephaga (Gyrinidae, Haliplidae, Noteridae, Amphizoidae, Hygrobiidae, Dytiscidae, Trachypachidae, Rhysodidae, Carabidae), the polyphagan genera *Ochthebius* Leach (Hydraenidae), *Silpha* L. (Silphidae), and the cupedid genus *Priacma* (LeConte) were included

in the analysis. The non-adephagan taxa were used as outgroup (Farris 1972; Watrous & Wheeler 1981; Nixon & Carpenter 1993) but treated as all other terminals in order to test the monophyly of the ingroup (simultaneous analysis; Nixon & Carpenter 1993).

The use of genera in the analysis is inevitable because most larvae cannot be identified to the species level. In most cases, several representatives of the respective genus were studied. Our own observations and data from the literature (e.g. Jeannel 1941-42; Lindroth 1961-69; Franciscolo 1979) make it plausible to assume that the character states in question belong to the groundplan of each genus.

Character analysis was conducted using the

cladistic computer program PAUP (= Phylogenetic Analysis Using Parsimony; by D. L. Swofford; MacIntosh version 3.1). Heuristic tree search was applied on account of the large data set (Table 1) (stepwise addition sequence: random, 10 replicates; branch-swapping algorithm: tree bisection reconnection). The characters supporting the proposed branching patterns were examined in MacClade (by W. P. Maddison & D. R. Maddison).

The results (Figs 1-2) are presented as one of the 1961 equally parsimonious trees (PAUP 1) and as a strict consensus tree (Sokal & Rohlf 1981) in order to summarize the cladistic information. This is a preferable method for representing common components of equally parsimonious trees (Wilkinson 1994).

Table 1. Character state matrix for 2 polyphagan and 1 cupedid genera (outgroup), and 35 adephagan genera.

Table with 13 columns of character state data and 37 rows of genera names (1. Ochthebius to 37. Brachinus). The data consists of binary strings for each character across the different taxa.

**Characters used in the analysis***Larval characters*

1. Cephalic eggbursting absent (0) / present (1) (Arndt 1993)
2. Labrum not fused to clypeus, clypeolabral suture complete (0) / labrum fused to clypeus, clypeolabral suture partly reduced (1) (Lawrence 1982)
3. Frontal suture not sinuate (0) / sinuate (Beutel 1993)
4. Postocular ridges absent (0) / present (1) (Beutel 1993)
5. Cervical ridges absent (0) / present (1) (Beutel 1993)
6. Lateral horizontal keel of head capsule absent (0) / present (1) (Ruhnau 1986)
7. Horizontal row of temporal spines absent (0) / present (1) (Ruhnau 1986)
8. Postocular row of setae absent (0) / present (1) (Ruhnau 1986)
9. Maxillary groove deep (0) / partly reduced (1) / completely reduced (2) (Beutel 1993)
10. Gula absent or short and semimembranous (0) / elongated gula present (1)
11. Caudal tentorial arm absent (0) / short caudal tentorial arm present (1) / caudal tentorial arm strongly elongated, attached to the ventral wall of the head capsule (2) (Beutel 1993)
12. Tentorial bridge not U-shaped (0) / U-shaped, posteriorly directed (1)
13. Nasale not distinctly separated from the clypeofrons, not shovel-like (0) / nasale distinctly separated from the clypeofrons, shovel-like (1)
14. Antenna 4-segmented (0) / 3-segmented (1)
15. Parallel arrangement of antennal muscles (0) / antennal muscles intercrossing (1) (Beutel 1993)
16. Antennomeres II-IV moderately elongated (0) / antennomeres II-IV extremely thin and elongated (1) (Beutel & Roughley 1994)
17. Mandibular tendon simple (0) / longitudinally divided (1) (Ruhnau 1986)
18. Mandibles without penicillum (0) / penicillum present (1)
19. Maxilla and labium not closely connected (0) / maxilla and labium together form maxillolabial complex (1) (Beutel 1992b)
20. Cardo does not articulate with elongated condyle of the head capsule (0) / cardo articulates with elongated condyle (2) (Beutel 1993)
21. Cardo and stipes connected by a hinge (0) / cardo and stipes form a functional unit (1) (Beutel 1993)
22. Cardo as broad as stipes (0) / cardo distinctly narrowed, inserted laterally in the ventral stipital wall (1) (Ruhnau 1986)
23. *M. craniolacinalis* (*M.* 19) inserted on lacinia (0) / *M.* 19 inserted laterobasally on stipes (1) / inserted mediobasally on stipes (2) (Beutel 1993)
24. 2 antagonistic stipitopalpal muscles (0) / *M.* stipitopalpalis internus (*M.* 23) absent (1) (Beutel 1993)
25. Galea inserted on stipes (0) / galea inserted mesally on palpomere I (1)
26. Prementum does not project beyond the clypeolabral margin (0) / prementum distinctly protruding (1) (Beutel 1993)
27. Prementum undivided (0) / completely divided longitudinally, palpiform (1) (Beutel & Roughley 1994)

28. Prehypopharynx without regular row of long hairs (0) / row of hairs sparsely developed (1) / preoral filter apparatus formed by a dense row of hairs (2) (Beutel 1993)
29. Prehypopharynx bulging (0) / partly flattened (1) / completely flattened (2) (Beutel 1993)
30. Prepharynx without lateral diverticula (0) / diverticula present (1) (De Marzo 1979; Beutel 1994b)
31. Prepharynx elongated, moderately broad (0) / prepharynx distinctly shortened, transverse, pharynx narrow (1) (De Marzo 1979; Beutel 1994b)
32. Posthypopharyngeal filter absent (0) / present (1) (Beutel & Roughley 1994)
33. *M. tentoriopharyngalis* (*M.* 52) composed by one bundle (0) / *M.* 52 composed by several bundles (1)
34. Prolegs without clasping apparatus (0) / clasping apparatus present (1) (Seeger 1971; Beutel 1995)
35. Segment X without 2 pairs of hooks (0) / 2 pairs of hooks present (1)
36. Abdominal segments IX and X well developed (0) / reduced (1) (Bell 1966)
37. Abdomen without anal plate (0) / anal plate present (1) (Bousquet 1986)

*Adult characters*

38. No surface-gliding habits (0) / surface-gliding habits (1)
39. Cervical condyle absent (0) present (1) (Bell 1970)
40. Compound eyes undivided (0) / separated by a thin chitinous bar (1) / widely separated (2) (Folkerts 1979)
41. Antenna filiform (0) / antenna strongly modified, scapus and pedicellus enlarged, antennomeres III-XI form a compact club (1) (Beutel 1989a)
42. Scapus not conspicuously shortened, basal part not expanded (0) / scapus short, basal part globulous and enlarged (1) (Beutel & Roughley 1987)
43. Antennomeres I-X not pubescent (0) / antennomeres V-XI densely pubescent (1) (Erwin 1985)
44. Antennomeres V, VII, and IX not extended (0) / extended (Belkaceme 1991)
45. Mentum without rounded lateral lobes (0) / lobes present (1) / lobes strongly enlarged (2) (Beutel 1989a, 1995)
46. Palpiger not fused to prementum (0) / fused to prementum (1) (Beutel 1989a)
47. Prothorax without excavations for the protibiae in repose (0) / excavations present (1) (Beutel 1989b)
48. Prosternal process short and narrow (0) / prosternal process strongly developed, apical part projects beyond the procoxae posteriorly, low grade ventral motility mechanism (Hlavac 1975) (1) / prosternal process strongly developed, apical part truncate, high grade ventral motility mechanism (Hlavac 1975) (2) (Beutel 1992a)
49. Procoxal cavities open (0) / propleural process connected with apical part of the prosternal process (1) / propleural process connected with the basal part of the prosternal process (2) (Beutel 1992a)
50. Procoxae contact anterolateral grooves of the ventral sclerite of the mesothorax (0) / no contact, pro- and mesothorax connected in a globe joint manner (1) (Beutel 1992a)
51. Ventral procoxal articulation absent (0) / present (1) / rudimentary (2) (Baehr 1979)

52. Prothoracic trochantinus short (0) / distinctly elongated, flat and strongly folded (1) (Baehr 1979)
53. Protibia without antenna cleaning organ (0) / cleaning organ present (1) (Kavanaugh 1986)
54. Cleaning organ not extended proximally (0) / proximally extended, isochoetous position of spurs (1) / proximally extended, anisochoetous position of spurs (2)
55. Profurca not shifted caudally (0) / shifted caudally (1) (Baehr 1979)
56. Profurca without caudal process (0) / caudal process short (1) / caudal process elongated (2) (Beutel 1989b)
57. Prothoracic proprioceptive organ absent (0) / present as a row of undifferentiated setae (1) / compact group of spatulate setae (1) (Larsén 1966; Beutel 1989b)
58. Prothoracic glands absent (0) / present (1) (Kavanaugh 1986)
59. Ventral sclerite of mesothorax flat (0) / distinct hexagonal groove and anterolateral grooves present (1) / hexagonal groove reduced, ventral sclerite steeply ascending caudally, round cross section cranially (2) (Beutel 1992a)
60. Mesocoxae triangular, moveability restricted to adduction and abduction or immobile (0) / mesocoxae globular, exclusively rotatory movements (1) (Beutel & Roughley 1988)
61. Mesepimeron broad (0) / narrow, improved mesometapleural articulation (1) (Beutel 1992a)
62. Mesepimeron reaches mesocoxae, mesocoxal cavities disjunct (0) / mesepimeron does not reach mesocoxae, mesocoxal cavities conjunct (1) (Bell 1967)
63. Metepimeron triangular (0) / parallel-sided or lobate, at right angle to body axis (1) (Beutel 1992b)
64. Metepimeron not lobate (0) / lobate (1) (Jeannel 1941-42; Beutel 1992a)
65. Metepimeron externally visible (0) / external lamella concealed by abdominal sternite II (1) (Beutel 1992a)
66. Metacoxae distinctly broader than katepimeron (0) / metacoxae narrowed, as broad as katepisternum or only slightly broader (1) (Kavanaugh 1986; Beutel 1992a)
67. Metacoxae not mesally fused (0) / fused (1) / extensive intercoxal septum (2) (Beutel & Roughley 1988)
68. Metacoxal plates absent (0) / present (1) / metacoxal plates strongly extended, function as accessory breathing-air storage and physical lung (2) (Beutel & Ruhna 1990; Beutel 1994c)
69. *M. furcacoxalis* anterior (M 81) present (0) / absent (1) (Belkaceme 1986; Beutel & Roughley 1988)
70. *M. furcacoxalis* posterior (M 83) present (0) / absent (1) (Belkaceme 1986; Beutel & Roughley 1988)
71. Metafurca arises from katepisternum (0) / metafurca arises from intercoxal septum (1) (Beutel & Roughley 1988)
72. Middle- and hind legs elongated (0) / transformed into short paddles (1) (Folkerts 1979)
73. Anterior and posterior walls of meso- and metatibiae not connected (0) / connected by cuticular columnae (1) (Larsén 1966; Beutel 1990)

→

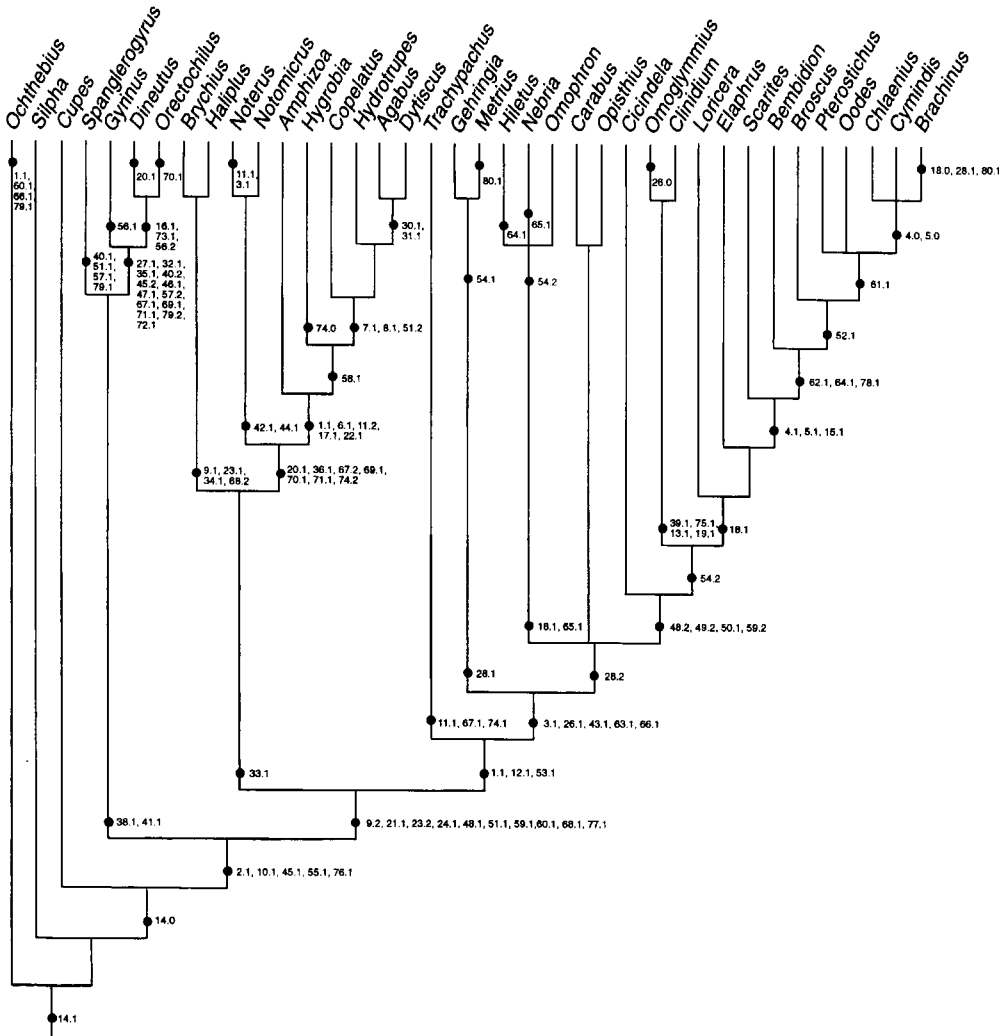
Fig. 1. One of 1961 equally parsimonious trees (131 steps): all characters unweighted and unordered; characters examined in MacClade; apomorphic states (full circles) mapped on the tree. Adephaga + Cupedidae: 14.0 - antenna 4-segmented; Adephaga: 2.1 - labrum fused to clypeus, 10.1 - gula present, 45.1 - mentum with rounded lobes, 55.1 - profurca shifted caudally, 76.1 - abdominal sternite II completely divided; Gyrinidae: 38.1 - surface gliding habits, 41.1 - antenna strongly modified; Gyrininae: 27.1 - prementum completely divided, 32.1 - posthypopharyngeal filter present, 35.1 - 2 pairs of anal hooks present, 40.2 - compound eyes widely separated, 45.2 - lobes of mentum strongly enlarged, 46.1 - palpiger fused to prementum, 47.1 - prothoracic excavations present, 57.2 - proprioceptive organs with spatulate setae, 67.1 - Metacoxae mesally fused, 69.1 - *M. furcacoxalis* anterior absent, 71.1 - metafurca arises from intercoxal septum, 72.1 - middle- and hindlegs transformed into short paddles, 79.2 - gonocoxosterna exposed, medially fused; Adephaga excl. Gyrinidae: 9.2 - maxillary groove completely reduced, 21.1 - intramaxillary moveability reduced, 23.2 - *M. craniolac.* inserted mediobasally on stipes 24.1 - *M. stipitoplalis* interior absent, 48.1 - prosternal process strongly developed, 51.1 - ventral procoxal articulation absent, 59.1 - ventral sclerite of mesothorax narrow, with anterolateral and hexagonal groove, 60.1 - mesocoxae globular, rotatory movements, 68.1 - metacoxal plates present, 77.1 - torsion of aedeagus; Haliplidae + Dytiscoidea: 33.1 - *M. tent.-phar.* composed by several bundles; Dytiscoidea: 20.1 - cardo articulates with elongated condyle, 36.1 - abdominal segments IX and X reduced, 67.2 - extensive intercoxal septum, 69.1 - *M. furcacox.* ant. absent, 70.1 - *M. furcacox.* post. absent, 71.1 - metafurca arises from intercoxal septum, 74.2 - subcuticular setal patch elongated; Dytiscoidea excl. Noteridae: 1.1 - egg-bursters present, 6.1 - lateral horizontal keel present, 11.2 - long caudal tentorial arms, 17.1 - mandibular tendon divided, 22.1 - cardo narrowed; Hygrobiidae + Dytiscidae: 57.1 - prothoracic glands; Trachypachidae + Carabidae: 1.1 - egg-bursters present, 12.1 - tentorial bridge U-shaped, 53.1 - protibial antenna cleaning organ present; Carabidae: 3.1 - frontal suture sinuate, 26.1 - prementum protruding, 43.1 - antennomeres V-XI densely pubescent, 63.1 - metepimeron parallel-sided, 66.1 - metacoxae narrowed; Cicindelinae + Rhysodidae + Loricerini + Elaphrini + Harpalinae (s. Crowson 1955): 48.2 - prosternal process with truncate apex, 49.2 - procoxal cavities closed, propleural process contacts basal part of prosternal process, 50.1 - pro- and mesothorax connected in a globe joint manner, 59.2 - anterolateral and hexagonal groove reduced; Rhysodidae + Loricerini + Elaphrini + Harpalinae: 54.2 - protibial antenna cleaning organ extended proximally; Loricerini + Elaphrini + Harpalinae: 18.1 - mandibular penicillum present; Scaritini + Harpalinae: 4.1 - postocular ridge, 5.1 - cervical ridge, 15.1 - antennal muscles intercrossing; Harpalinae: 62.1 - mesocoxal cavities conjunct, 64.1 - metepimeron lobate, 78.1 - gonocoxa subdivided.

- 74. Subcubital setal binding patch absent (0) / present, round (1) / elongated (2) (Hammond 1979; Ward 1979; Kavanaugh 1986; Beutel & Roughley 1988)
- 75. Large, separate sclerite (sternite II) between metacoxae absent (0) / present (1) (Crowson 1955)
- 76. Abdominal sternite II not divided by metacoxae (0) / completely divided by metacoxae (1) (Crowson 1955)
- 77. No torsion of male genital appendages (0) / aedeagus rotated through 90° during repose and through 180° during copulation (1) (Beutel & Roughley 1988)
- 78. Gonocoxa not completely subdivided (0) / completely subdivided into a cranial and caudal portion by a membranous zone (1) (Bils 1976)
- 79. Gonocoxosterna covered by sternite VII (0) / gonocoxosterna exposed, sternit VII truncate (1) / gonocoxosterna exposed, medially fused (2)

- 80. Pygidial glands without explosive mechanism (0) / pygidial glands with explosive mechanism (1) (Erwin 1985)

**Discussion**

The phylogenetic hypotheses proposed by Beutel (1992a, 1993, 1994b, 1995) are largely confirmed by the analysis: sistergroup relationship between Gyrinidae and the remaining adephagan families, sistergroup relationship between Spanglerogyrinae and Gyrininae, monophyly of Dytiscoidea, monophyly of Dytiscoidea excluding Noteridae, sistergroup relationship between Hygrobiidae and Dytiscidae, monophyly of Dytiscidae excl. *Hydro-*



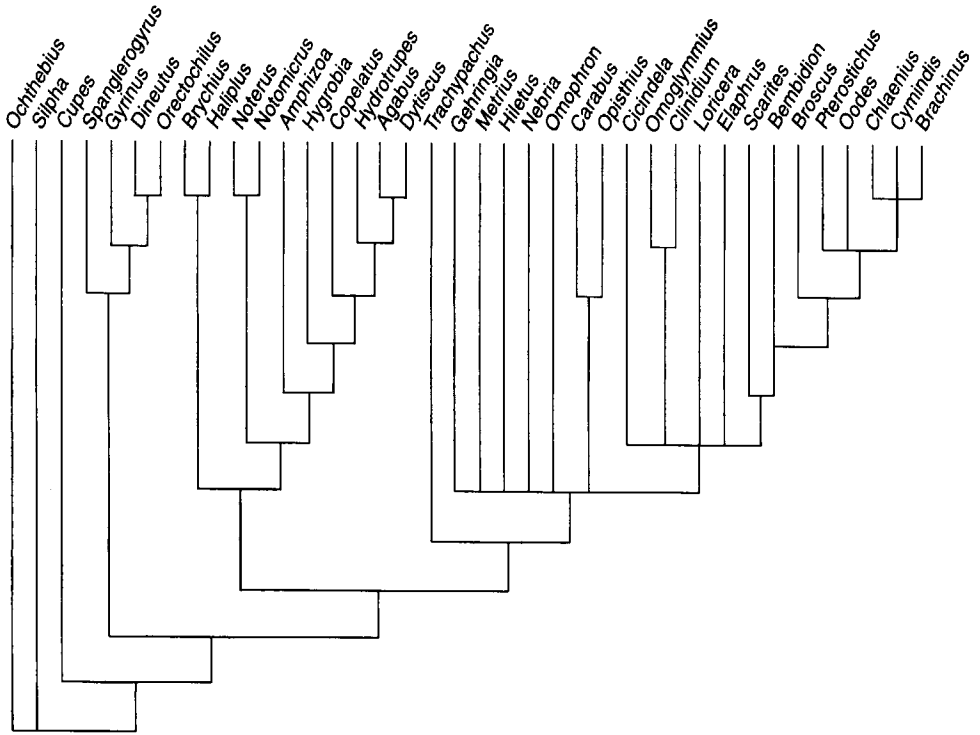


Fig. 2. Strict consensus tree computed from 1961 equally parsimonious trees.

*trupes* and Copelatini, monophyly of Geadephaga excluding Trachypachidae, monophyly of Caraboidea Limbata (Jeannel 1941-42), and monophyly of Harpalinae sensu Crowson (1955). However, sistergroup relationships between Haliplidae and Dytiscoidea, and the monophyly of Geadephaga (Trachypachidae + Carabidae incl. Rhysodidae) are in contrast to the interpretations in Beutel (1993, 1995).

The proposed sistergroup relationship between Haliplidae and Dytiscoidea is based on one synapomorphic character state: *M. tentoriopharyngalis* composed by several bundles (larvae) (CI 1.000). However, the increase of muscle bundles in *M. tentoriopharyngalis* has a different functional significance in Haliplidae and Noteridae on one hand, and in Dytiscoidea excluding Noteridae on the other. The muscle is the antagonist of *M. frontobuccalis* in the former taxa, but the antagonist of an unusually strongly developed *M. verticopharyngalis* in larvae of Amphizoidae, Hygrobiidae, and Dytiscidae. The increase in size is correlated

with the enlargement of *M. verticopharyngalis* and with the elongation of the caudal tentorial arm in larvae of these families, but not in Haliplidae and Noteridae. Therefore, parallel evolution appears plausible.

The sistergroup relationship between Haliplidae and Dytiscoidea implies the secondary presence of a maxillary groove (reversal from 9.2 to 9.1) and the secondary attachment of *M. craniolacinalis* (*M.* 19) to the lateral stipital wall (reversal from 23.2 to 23.1). These interpretations appear quite unlikely. There is absolutely no reason to assume that completely reduced maxillary grooves with mesal attachment of *M.* 19 is a groundplan feature of Adephega excluding Gyrinidae.

The monophyly of Geadephaga is based on the presence of eggbursters (independently in Dytiscoidea excl. Noteridae), a U-shaped tentorial bridge, and the presence of a protibial antenna cleaning organ. The latter character states are indeed sound arguments, whereas the first apo-

morphic state is probably misplaced at this node. The presence of eggbursting as a groundplan feature of Adepshaga excl. Gyrinidae and Haliplidae as proposed by Arndt (1993) appears more plausible than independent acquisition of these structures in larvae of Dytiscoidea excluding Noteridae and Geadephaga. Whether the U-shaped tentorial bridge is a synapomorphy of Trachypachidae + Caraboidea as proposed in this study, or a groundplan feature of Adepshaga excluding Gyrinidae and Haliplidae is not quite clear at present. It cannot be excluded that the caudal tentorial arms of dytiscoid larvae are fused with the caudally directed parts of a U-shaped tentorial bridge. This would result in an H-shaped structure which is actually found in larvae of Dytiscoidea excl. Noteridae (Beutel 1993). The aberrant tentorial bridge of larvae of *Noterus* Sharp (Beutel 1993) is almost certainly correlated with the apomorphic, caudal position of the posterior tentorial grooves.

A sistergroup relationship between Trachypachidae and Caraboidea as already proposed by Erwin (1985) and Kavanaugh (1986) implies parallel acquisition of several apomorphic character states in Trachypachidae and Dytiscoidea: caudal tentorial arms, absence of the lacinia, insertion of the galea on palpomere I, partial reduction of the meta'sternal' transverse ridge, fusion of mesal metacoxal walls, expansion of metacoxae, and presence of a subcubital binding patch (Beutel & Roughley 1988, Beutel 1992a, Beutel 1993). Further evidence should be introduced to resolve these conflicting hypotheses.

The systematic placement of Rhysodidae or Rhysodini is complicated by numerous autapomorphic features of larvae and adults (Beutel 1990b, 1992b), which are obviously correlated with highly specialized, wood-associated habits. The position proposed in the present study is based on the assumption that apomorphic pro- and mesothoracic character states (chars. 48.2, 49.2., 59.2.) did not develop independently in rhysodids and 'higher' carabids. This interpretation is conform with Beutel (1990b, 1992a) but in contrast to a proposed sistergroup relationship between Rhysodidae and Carabidae based on larval features (Beutel 1992b). It is apparent that new characters (e.g. molecular data) are needed for a reliable placement of rhysodids.

The carabid characters available at present are controversial and obviously not sufficient for a sound hypothesis of the phylogeny of the family,

even though some monophyletic groups seem to be well founded (e.g. Caraboidea Limbata, Harpalinae). A proposed position of Brachininae within Harpalinae (Beutel 1992a) is confirmed. This implies independent acquisition of the pygidial explosive mechanism in Metriini-Paussini and Brachininae, which is in agreement with many structural differences (Forsyth 1972) as pointed out in Beutel (1992a).

The proposed sistergroup relationship between Cupedidae and Adepshaga (Fig. 1) is in agreement with Bachr (1979). However, the interpretation of 4 antennomeres as a synapomorphy of both taxa is probably incorrect, as the same character state is also found in larvae of Sialidae (Megaloptera) and some larvae of Polyphaga. It is obvious that the characters presented in the present contribution are not sufficient for a clarification of the interrelationships of the suborders of Coleoptera.

Cladistic computer analysis is a highly useful and important technique when a larger number of taxa and characters are involved. In addition to pragmatic advantages, certain weak points of manual character analyses may be compensated by complementary use of computer programs. Alternative branching patterns and relationships not taken into consideration in manual analyses (e.g. sistergroup relationship between Trachypachidae and Carabidae in Beutel 1993, 1995) may be revealed by a computer conducted analysis. Weak points in a phylogenetic hypothesis (such as 'basal' carabids in the present study) are clearly demonstrated (unresolved polytomies in consensus trees). The comparatively large number of equally parsimonious trees (1961 in this contribution) is not a methodological weakness, but reflects inherent ambiguities (convergence, reversal) of phylogenetic reconstructions. The presentation of only one cladogram in most traditional phylogenetic studies is the subjective choice of one possible hypothesis.

Computer-generated character analyses as such are free from subjectivity and preconception which are probably involved in all manual analyses to a higher or lesser degree. However, the choice and coding of characters are subject to bias and subjectivity to the same degree as in a manual phylogenetic reconstruction. The degree of congruence of a computed cladogram with the actual (historical) phylogeny of a group depends on the adequacy of the choice and subsequent coding of characters. Careful treatment and transparent



presentation of characters, and a profound knowledge of the group in question are necessary prerequisites for any computer conducted or manual cladistic analysis.

### Acknowledgements

We wish to thank Dr R. E. Roughley. Study of selected valuable specimens was made possible by Natural Sciences and Engineering Research Council of Canada, operating grant No. A0428 held by R. E. R. (Dept. of Entomology, University of Manitoba). The helpful comments and criticisms of the reviewer (Dr J. Muona) are gratefully acknowledged.

### References

- Arndt, E. 1993. Phylogenetische Untersuchungen larvalmorphologischer Merkmale der Carabidae (Insecta: Coleoptera). *Stuttgarter Beiträge zur Naturkunde (A)* 488: 1-56.
- Baehr, M. 1979. Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax der Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). *Zoologica* 44 (130): 1-76.
- Belkaceme, T. 1986. Skelet und Muskulatur der Hinterhüfte von *Haliplus lineatocollis* Mrsh. (Halipilidae, Coleoptera). *Stuttgarter Beiträge für Naturkunde (A)* 393: 1-12.
- 1991. Skelet und Muskulatur des Kopfes und Thorax von *Noterus laevis* Sturm. Ein Beitrag zur Morphologie und Phylogenie der Noteridae (Coleoptera: Adephaga). *Ibidem (A)* 462: 1-94.
- Bell, R. T. 1966. Trachypachus and the origin of the Hydradephaga (Coleoptera). *Coleopterist's Bulletin* 20: 107-112.
- 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). *Annals of the Entomological Society of America* 60: 101-107.
- 1970. The Rhyssodini of North America, Central America, and the West Indies (Coleoptera: Carabidae). *Miscellaneous Publications of the Entomological Society of America* 6: 289-324.
- Beutel, R. G. 1989a. The head of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga. *Zoologische Jahrbücher für Anatomie* 118: 431-461.
- 1989b. The prothorax of *Spanglerogyrus albiventris* Folkerts, 1979 (Coleoptera, Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae. *Entomologica basiliensia* 13: 151-173.
- 1990a. Phylogenetic analysis of the family Gyrinidae (Coleoptera) based on meso and metathoracic characters. *Quaestiones entomologicae* 26: 163-191.
- 1990b. Metathoracic features of *Omoglymmius hamatus* and their significance for classification of Rhyssodini (Coleoptera: Adephaga). *Entomologica generalis* 15: 185-201.
- 1992a. Phylogenetic analysis of thoracic structures of Carabidae (Coleoptera). *Zeitschrift für zoologische Systematik und Evolutionsforschung* 30: 53-74.
- 1992b. On the morphology of the head of the larva of *Omoglymmius hamatus* (LeConte) and the systematic position of Rhyssodidae (Coleoptera, Adephaga). *Entomologica scandinavica* 23: 169-184.
- 1992c. Study on the systematic position of Metriini (Coleoptera, Carabidae) based on characters of the larval head. *Systematic Entomology* 17: 207-218.
- 1992d. Larval head structures of *Licinus silphoides* Rossi (Coleoptera: Carabidae) and their phylogenetic implications. *Entomologica basiliensia* 15: 169-194.
- 1993. Phylogenetic analysis of Adephaga (Coleoptera) based on characters of the larval head. *Systematic Entomology* 18: 127-147.
- 1994a. Phylogenetic analysis of Hydrophiloida based on characters of the head of adults and larvae (Coleoptera: Staphyliniformia). *Koleopterologische Rundschau* 64: 103-131.
- 1994b. On the systematic position of *Hydrotrupes palpalis* Sharp (Coleoptera: Dytiscidae). *Aquatic Insects* 16: 157-164.
- 1995. The Adephaga (Coleoptera): phylogeny and evolutionary history. Pp. 173-217 in Pakaluk & Sliński (Eds.): *Biology, phylogeny, and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson*. 1092 pp. Warszawa.
- Beutel, R. G. & Roughley, R. E. 1987. On the systematic position of the genus *Notomicrus* Sharp (Hydradephaga, Coleoptera). *Canadian Journal of Zoology* 65: 1898-1905.
- 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). *Zeitschrift für zoologische Systematik und Evolutionsforschung* 26: 380-400.
- 1994. Phylogenetic analysis of Gyrinidae based on characters of the larval head (Coleoptera: Adephaga). *Entomologica scandinavica* 24: 459-468.
- Beutel, R. G. & S. Ruhnau 1990. Phylogenetic analysis of the genera of Halipilidae (Coleoptera) based on characters of adults. *Aquatic Insects* 12: 1-17.
- Bils, W. 1976. Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung für die Phylogenie. *Zoomorphology* 84: 113-193.
- Bousquet, Y. 1986. Description of first instar larvae of *Metrius contractus* Eschscholtz (Coleoptera: Carabidae) with remarks about phylogenetic relationships and ranking of the genus *Metrius* Eschscholtz. *Canadian Entomologist* 118: 373-388.
- Burmeister, E. G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. *Zoomorphology* 85: 165-257.
- Crowson, R. A. 1955. The natural classification of the families of Coleoptera. 187 pp. London.
- De Marzo, L. 1979. Studi sulle larve dei Coleotteri Dytiscidi. X. Anatomia e funzionamento dell'apparato succhiante cibario-faringeo in alcune forme larvali delle subff. Dytiscinae, Colymbetinae, Laccophilinae e Hydroporinae. *Entomologica (Bari)* 15: 5-72.
- Erwin, T. L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Pp. 437-472 in Ball (Ed.): *Taxonomy, phylogeny and zoogeography of beetles and ants*. 514 pp. The Hague.
- Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. *American Naturalist* 106: 645-668.

- Folkerts, G. W. 1979. *Spanglerogyrus albiventris*, a primitive new genus and species of Gyrinidae (Coleoptera) from Alabama. *Coleopterist's Bulletin* 33: 1-8.
- Forsyth, D. J. 1972. The structure of the pygidial defence glands of Carabidae (Coleoptera). *Transactions of the Zoological Society of London* 32: 249-309.
- Franciscolo, M. E. 1979. Fauna d'Italia XIV. Coleoptera. Haliplidae, Hygrobiidae, Gydrinidae, Dytiscidae. 804 pp. Bologna.
- Ganglbauer, L. 1892. Die Käfer von Mitteleuropa. I. Familienreihe Caraboidea. 577 pp. Wien.
- Hammond, P. M. 1979. Wing folding mechanisms of beetles, with special reference to Adepagan phylogeny. Pp. 113-180 in: Erwin et al. (Eds.): Carabid beetles: Their evolution, natural history and classification. 635 pp. The Hague.
- Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. 370 pp. Berlin.
- 1966. Phylogenetic systematics. 263 pp. Urbana.
- Hlavac, T. F. 1975. The prothorax of Coleoptera (except Bostrichiformia - Cucujiformia). *Bulletin of the Museum of Comparative Zoology* 147: 137-183.
- Jeannel, R. 1941-42. Coléoptères Carabiques. Parts 1-2. *Faune de France* 39-40. 1173 pp. Paris.
- Kavanaugh, D. H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adepaga. *Proceedings of the Californian Academy of Science* 44: 67-109.
- Larsén, O. 1966. On the morphology and function of locomotor organs of the Gyrinidae and other Coleoptera. *Opuscula entomologica*, Suppl. 30: 1-241.
- Lawrence, J. F. 1982. Coleoptera. Pp. 482-533 in Parker (Ed.): *Synopsis and classification of Living Organisms*. 1232 pp. New York.
- Lindroth, C. H. 1961-69. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 1-6. *Opuscula entomologica*. 1961, Part 2, Suppl. 20: 1-20; 1963, Part 3, Suppl. 24: 201-408; 1966, Part 4, Suppl. 29: 409-648; 1968, Part 5, Suppl. 33: 649-944; 1969 Part 6, Suppl. 34: 945-1192; 1969 Part 1, Suppl. 35: I-XLVIII.
- Nichols, S. W. 1985. *Omophron* and the origin of Hydradephaga (Insecta: Coleoptera: Adepaga). *Proceedings of the Academy of Sciences of Philadelphia* 137: 182-201.
- Nixon, K. C. & Carpenter, J. M. 1993. On outgroups. *Cladistics* 9: 413-426.
- Roughley, R. E. 1981. Trachypachidae and Hydradephaga (Coleoptera): a monophyletic unit? *Pan-Pacific Entomologist* 57: 273-285.
- Ruhnau, S. 1986. Phylogenetic relations within the Hydradephaga (Coleoptera) using larval and pupal characters. *Entomologica basiliensia* 11: 231-271.
- Seeger, W. 1971. Morphologie, Bionomie und Ethologie von Halipliden, unter besonderer Berücksichtigung funktionsmorphologischer Gesichtspunkte (Haliplidae; Coleoptera). *Archiv für Hydrobiologie* 68: 400-435.
- Sokal, R. R. & Rohlf, F. J. 1981. Taxonomic congruence in the Leptodomorpha re-examined. *Systematic Zoology* 30: 309-325.
- Ward, R. D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adepaga (Coleoptera). Pp. 181-192 in: Erwin et al. (Eds.): Carabid beetles: Their evolution, natural history and classification. 635 pp. The Hague.
- Watrous, L. E. & Wheeler, Q. D. 1981. The outgroup comparison method of character analysis. *Systematic Zoology* 30: 1-11.
- Wilkinson, M. 1994. Common cladistic information and its consensus representation: reduced adams and reduced consensus trees and profiles. *Systematic Biology* 43: 343-368.