Koleopterologische Rundschau	64	103 - 131	Wien, Juni 1994
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Phylogenetic analysis of Hydrophiloidea based on characters of the head of adults and larvae (Coleoptera: Staphyliniformia)

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Abstract

Characters of the head of adults and larvae of Hydrophiloidea (sensu CROWSON 1955) are analyzed phylogenetically. The monophyly of the superfamily is strongly suggested by autapomorphies of adults such as palpicorn antenna, antennal groove, postocular emargination, complex hypopharyngeal suspensorium, distal galeomere composed by fimbriate lamellae, large, quadrangular mental plate, and others. First instar larvae of Hydrophiloidea possess cephalic egg bursters as a common derived feature. Hydrophiloidea (excl. Hydraenidae) share two autapomorphies of adults and five larval synapomorphies such as the loss of the clypeolabral and frontoclypeal sutures, and the insertion of the galea on palpomere I. Hydrophiloidea (excl. Hydraenidae and Spercheidae) are characterized by one autapomorphy of adults and 5 larval autapomorphies such as prognathism, strongly reduced intramaxillary moveability, subdivided cardo, partly reduced maxillary fossa, and rudimentary lacinia. The transformation of the broad gula into a median gular suture, contiguous posterior tentorial grooves which are distant from the foramen occipitale, and the presence of a nasal projection and conspicuous triangular adnasalia are significant larval synapomorphies of Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae. Helophoridae are the sistergroup of Georissidae, Epimetopidae, and Hydrophilidae. A separate, cranial submental sclerite is a possible synapomorphy of the latter families. Hydrophilidae are characterized by hyperprognathism, a V-shaped submental suture, complete reduction of the maxillary groove, and dorsal insertion of the antennae. The presence of a pronotal shield which covers parts of the dorsal wall of the head capsule of adults, a strongly deflexed head, cuticular spines along the mesal edges of the larval adnasalia, and an elongated palpomere I with a minute galea are possible synapomorphies of Epimetopidae and Georissidae.

Key words: Hydrophiloidea, head structures, adults, larvae, phylogenetic analysis

Introduction

The concept of the superfamily Hydrophiloidea or Palpicornia was subject to several changes during its taxonomic history. BÖVING & CRAIGHEAD (1931) included Histeridae, but excluded Hydraenidae in their synopsis of the larval forms of Coleoptera. Both families, Hydraenidae and Histeridae, were included in Palpicornia in another larval study by EMDEN (1942). Hydrophiloidea (or Palpicornia) include Hydraenidae, Spercheidae, Hydrochidae, Georissidae, and Hydrophilidae (incl. Helophorinae) in a system proposed by D'ORCHYMONT (1916, 1919) and by CROWSON (1955). Histeroidea are considered as members of Hydrophiloidea, whereas Hydraenidae are transferred to Staphylinoidea, close to Ptiliidae in several recent studies (DYBAS 1976; LAWRENCE 1982; COSTA et al. 1988). Hydrophiloidea include the families Helophoridae, Epimetopidae, Georissidae, Hydrochidae, Spercheidae, and Hydrophilidae in a comprehensive work by HANSEN (1991a). A sistergroup relationship between those groups and Histeroidea is considered as more likely than a sistergroup relationship between Hydrophiloidea (sensu HANSEN 1991a) and Hydraenidae.

The present study of characters of the head of larvae and adults is considered as a contribution towards a clarification of the monophyly or paraphyly of Hydrophiloidea (sensu CROWSON 1955) and of the interrelationships of the hydrophiloid subgroups. Emphasis is placed upon a detailed

discussion of the characters presented. It is well understood that a "final solution" of these questions requires an analyis of a broader set of characters than presented in this paper, even though the head is the most complex structure of an insect body. Detailed study of more structural features (especially internal characters) of adult and larval Staphyliniformia and a phylogenetic evaluation of those data should be the purport of future studies.

Material and methods

Selected larvae and newly hatched adults were imbedded in Histoplast S for microtome sections (5 μ m). The sections were stained with haemalaun. Drawings were made using an ocular grid. Scanning electron microscopy was accomplished after specimens were cleaned with ultra sound, dried (critical point method) and coated with gold-palladium (Cambridge Stereoscan Mk 2).

The determination of the polarity of character states is based on the outgroup and ingroup comparison method described by WATROUS & WHEELER (1981). The outgroup includes Staphylinoidea and other Polyphaga, Adephaga, Myxophaga, and Cupedidae. Character states found in representatives of these groups and subgroups of Hydrophiloidea are considered plesiomorphic. The corresponding character states in other subgroups of Hydrophiloidea as apomorphic. Only synapomorphic i.e. common derived character states are criteria for phylogenetic relationship. Information on several groups discussed in this context, especially larval Staphylinoidea (e.g. Ptiliidae, Leiodidae, Leptinidae) are taken from the literature (e.g. DYBAS 1976; LAWRENCE 1982; STEHR 1991).

Muscular nomenclature and corresponding numbers used in the illustrations are according to KELER (1963).

Plesiomorphic character states = 0; apomorphic character states in a transformation series = 1, 2; alternative apomorphic character states = 1^* ; reversal = 0,5R (partial), 0R (total).

List of species examined:

Hydraenidae: adults: Orchymontia spinipennis BRAUN, Prosthetops WATERHOUSE sp., Gymnochthebius chilenus (J.BALFOUR-BROWNE), Meropathus campbellensis BROOKES, Ochthebius melanescens DALLA TORRE, Hydraena britteni JOY, Limnebius crassipes KUWERT, L. papposus MULSANT

Spercheidae: adults: Spercheus emarginatus (SCHALLER); larvae: Spercheus emarginatus (SCHALLER)

Hydrochidae: adults: Hydrochus angustatus GERMAR

Georissidae: adults: Georissus crenulatus (ROSSI)

Helophorinae: adults: Helophorus aquaticus (L.), Helophorus minutus FABRICIUS; larvae: Helophorus FABRICIUS ssp.

Hydrophilinae: adults: Coelostoma orbiculare (FABRICIUS), Sphaeridium bipustulatum FABRICIUS, Cercyon impressus (STURM), Hydrobius fuscipes (L.), Anacaena globulus (PAYKULL), A. limbata (FABRICIUS), Laccobius minutus (L.), Helochares obscurus (MÜLLER), Enochrus bicolor (FABRICIUS), E. testaceus (FABRICIUS), E. affinis THUNBERG, Hydrochara caraboides (L.), Hydrophilus piceus (L.), H. aterrimus ESCHSCHOLTZ, Berosus signaticollis (CHARPENTIER); larvae: Sphaeridium bipustulatum FABRICIUS, Enochrus THOMSON sp., Hydrobius LEACH sp., Hydrophilus LEACH sp., Sperchopsis tesselata (ZIEGLER), Berosus LEACH sp.

Histeridae: adults: Margarinotus cadaverinus (HOFFMANN); larvae: Saprinus semistriatus (SCRIBA), Paralister BICKHARDT sp., Histeridae ssp.

Silphidae: adults: Oeceoptoma thoracica (L.), Silpha obscura L., Necrophorus vespillo (L.); larvae: Silpha L. sp. Ptiliidae: Acrotrichis MOTSCHULSKY sp.

Leiodidae: adults: Catops PAYKULL sp.; larvae: Catops sp.

Scydmaenidae: Cephennium Müller et KUNZE sp., Neuraphes THOMSON sp.

Staphylinidae: adults: Philonthus decorus (GRAVENHORST), Ocypus olens (MÜLLER); larvae: Philonthus CURTIS sp.

Leptinidae: adults: Platypsyllus castoris RITSEMA

Hydroscaphidae: larvae: Hydroscapha LECONTE sp.

Cupedidae: adults: Priacma serrata LECONTE

Abbreviations and muscular nomenclature used in Figs. 1 - 36:

7	M. labroepipharyngalis	gu	gula
8	M. frontolabralis	gur	gular ridge
11	M. craniomandibularis internus	gus	gular suture
12	M. craniomandibularis externus	hv	hypopharynx
15	M. craniocardinalis	lbr	labrum
17	M. tentoriocardinalis	lc	lacinia
18	M. tentstipitalis	md	mandible
19	M. craniolacinialis	mo	mola
41	M. frontohypopharyngalis	mst	mediostipes
42	M. tenthypopharyngalis	mt	mentum
43	M. clypeopalatalis	nas	nasale
44	M. clypeobuccalis	pf	palpifer
45	M. frontobucc. anterior	pguscl	pregular sclerite
46	M. frontobucc. posterior	ph	pharynx
	r	r Dl	palpus labialis
adnas	adnasale	pm I	palpomere I
amgupl	anteromedian gular plate	pmt	prementum
ant	antenna	pmtr	premental retractors
antm	antennal muscles	pmx	palpus maxillaris
ata	anterior tentorial arm	poem	postocular emargination
bst	basistipes	ptg	posterior tentorial groove
с	cardo	ret	retinaculum
ce	compound eye	rm	ring muscle
cly	clypeus	sap	sensorial appendage
cscl	cervical sclerite	smt	submentum
dta	dorsal tentorial arm	soes	suboesophageal ganglion
eph	epipharynx	st	stipes
fcls	frontoclypeal suture	ste	stemmata
fm	fossa maxillaris	sus	anterior hypopharyngeal suspensorium
fs	frontal suture	tb	tentorial bridge
ga	galea	y-s	Y-shaped suture
gf	ganglion frontale		

Character analysis (Table I)

I. Autapomorphies of Hydrophiloidea (sensu CROWSON 1955)

Adult features

1. Head protruding (1.0)/ head strongly retracted, transverse posterodorsal ridge present (1.1)

A strongly retracted head capsule as found in adults of Hydraenidae (Fig. 38), Hydrochidae, Helophoridae (Fig. 39), and other Hydrophiloidea is considered as a derived groundplan feature and autapomorphy. The surface structure of the posterior, retracted part of the head capsule is distinctly different from the anterior part (hydrofuge pubescence; Fig. 39). Both areas are separated from each other by a distinct dorsal ridge in adults of Hydraenidae (Figs 1, 38), *Spercheus* KUGELANN (Fig. 4), *Helophorus* FABRICIUS (Fig. 39), *Hydrochus* LEACH, and *Georissus* LATREILLE (Fig. 7). The protruding head of adults of the *Podaena*-group of Hydraenini (HANSEN 1991b) and the absence of the ridge from adults of Hydrophilidae is considered as a secondary feature.

The above described apomorphic condition is not found in the adults of Ptiliidae examined.

Transverse ridge and different surface structures are not found in Histeridae with retracted head capsule. A more or less protruding head capsule as found in adults of Cupedidae, terrestrial Adephaga, and many polyphagan groups such as Syntellidae (JEANNEL 1965), Silphidae (Fig. 17), and Staphylinidae is considered plesiomorphic.

2. Lateral margins of clypeus not distinctly longer than those of frons anterior to eyes (2.0)/ distinctly longer (2.1)

Lateral margins of the clypeus which are more than 1,5 x those of frons are considered as a possible synapomorphy of Hydraenidae and other hydrophiloid groups by HANSEN (1991a). This feature is very unusual within Staphyliniformia according to the same author. The lateral clypeal margin is short in the adults of Ptiliidae examined.

3. Antenna filiform, no breathing function (3.0)/ palpicorn antenna with breathing function (3.1)

Adults of Hydrophiloidea are characterized by a highly specialized antenna: the scapus is strongly elongated and curved at the base, antennomere VI is transformed into a cupule, 3-5 distal antennomeres form a rather elongated pubescent club (Figs. 1-9, 41-43; JEANNEL 1965, fig. 424; PERKINS 1980; HANSEN 1991b). The antenna functions as an accessory breathing organ as described in detail by BEIER (1956) for *Ochthebius* LEACH (Hydraenidae), by HRBACEK (1950) for Hydraenidae, *Spercheus*, *Helophorus*, *Hydrochus*, and Hydrophilidae, and by BROCHER (1911) and BLUNCK & SPEYER (1925) for *Hydrophilus* MULLER. This is considered as a derived groundplan feature and significant autapomorphy of Hydrophiloidea. Similar breathing habits are not known from any other group of Coleoptera.

Secondary modifications of the antenna occur in some hydrophiloid groups, especially in terrestrial taxa. The cupule is reduced in some Hydraenidae (HANSEN 1991b) and in Sphaeridiini (CROWSON 1955).

An 11-segmented filiform antenna as found in adults of Cupedidae, Adephaga, and many polyphagan groups is considered plesiomorphic. This type of antenna (with very slightly dilated antennomeres IX-XI) is also found in the adults of Ptiliidae examined.

An 11-segmented antenna with a 3 segmented club is found in adults of Histeroidea (LAWRENCE 1982). This type of antenna which has of course no breathing function is considered as a result of convergency. Segment VI is never transformed into a cupule and the club is highly compact and not elongated as in most Hydrophiloidea (e.g. *Spercheus, Hydrochus, Helophorus*). Nevertheless, a detailed comparison of histeroid and hydrophiloid antennal structures should be considered as an important future project.

4. Antennal base exposed, furrows and grooves for reception of the antenna absent (4.0)/ antennal base not visible from above, furrows and anterolateral prothoracic pouch present (4.1)

An antennal base which is covered by a lateral clypeal extension, a more or less distinct subocular groove, and a deep, anterolateral prothoracic pouch for reception of the antennal club (Figs 42-43) is considered as a significant derived groundplan feature and autapomorphy of Hydrophiloidea. Variations of this postulated groundplan character state occur. The subocular furrow is indistinct or obsolete in some genera of Hydraenidae according to PERKINS (1980). The prothoracic pouch is secondarily absent from adults of *Spercheus* and Hydrophilidae (hypomeron without antennal grooves; HANSEN 1991a) and from some hydraenids (*Podaena*-group). The typical condition is found in the species of *Hydraena* KUGELANN examined, and in adults of *Hydrochus, Helophorus*, Epimetopidae (HANSEN 1991a), and *Georissus*.

The absence of the specialized structural features described above from the vast majority of Coleoptera clearly indicates that this condition is plesiomorphic. They are absent from adults of Ptiliidae and Histeridae examined, and probably from other histeroids as they are not mentioned in the family diagnoses given by LAWRENCE (1982).

5. Postocular emargination absent (5.0)/ present (5.1)

A characteristic triangular postocular emargination as found in adults of Hydraenidae (Figs 3, 42; PERKINS 1980, fig. 16a), Spercheidae (Fig. 6), Hydrochidae, Helophoridae, and other Hydrophiloidea (Fig. 10) is considered autapomorphic. The absence from adults of *Georissus* (Fig. 9) is probably due to reversal.

A triangular postocular emargination is absent from adults of Silphidae (Figs 17, 18), Staphylinidae, Histeridae, and others. The eye is slightly concave posteriorly in the adults of Ptiliidae examined. However, a distinct emargination is absent.

6. Mentum short and broad (6.0)/ Mentum enlarged and strongly sclerotized (6.1)

A large, square or trapeziform, heavily sclerotized mentum is found in adults of Hydraenidae (Figs 2, 40; PERKINS 1980) and other Hydrophiloidea examined (Figs 5, 8, 11, 41). The prementum is largely or completely covered by the mental plate. This character state is considered autapomorphic.

A similar mental plate is found in adults of Cupedidae. This is almost certainly a result of convergency.

A distinctly smaller, rather narrow mentum, and an exposed prementum as found in adults of Adephaga, Silphidae (Fig. 18), Staphylinidae, Histeridae, Sphaeritidae, Leptinidae, Ptiliidae (WILLIAMS 1938) and others is considered plesiomorphic.

7. Distal galeomere simple, pubescent (7.0)/ distal galeomere composed by several fimbriate lamellae (7.1)

A highly complex distal galeomere, which is composed by several fimbriate lamellae, is found in most adults of Hydraenidae (Fig. 40; PERKINS 1980, figs 153; HANSEN 1991a,b), Hydrochus (Fig. 22), Helophorus, Epimetopidae (HANSEN 1991a), Georissus, Helochares MULSANT (Fig. 13), Hydrobius LEACH, and others. This is a significant derived groundplan feature and autapomorphy of Hydrophiloidea. Some modifications of the groundplan type occur. A gradual simplification of the distal galeomere is found in species of Ochthebius (BEIER 1956; BEIER & POMEISL 1959), and the typical fimbriate condition is not found in adults of Spercheus which are characterized by exceptionally small and retracted maxillae.

A simple, globulous or elongated, pubescent distal galeomere as found in adults of Histeridae, Sphaeritidae, Ptiliidae, and other Staphylinoidea (WILLIAMS 1938) is considered plesiomorphic.

8. Maxillary palp short (8.0)/ elongated (8.1)

Elongation of the maxillary palp is characteristic for adults of Hydrophiloidea. However, the degree varies considerably. Extremely elongated maxillary palps are found in adults of *Hydraena* (Fig. 38) and some Hydrophilidae (Fig. 10), whereas comparatively short maxillary palps are found in adults of *Ochthebius* (Fig. 2), *Georissus* (Fig. 8), Sphaeridiini and other Hydrophilidae. As a gradual modification, which is obviously correlated with the highly peculiar shape and breathing function of the antenna, this derived character state should not be overvalued.

Short maxillary palps are found in adults of Silphidae (Fig. 18), Staphylinidae, Leptinidae, Ptiliidae, Sphaeritidae, and Histeridae (WILLIAMS 1938).

9. Large, hypopharyngeal suspensorium absent (9.0)/ present (9.1)

A large, sclerotized, internal apodeme, the suspensorium of the hypopharynx (BEER 1956) is found in adults of *Hydraena* (Fig. 21), *Ochthebius*, *Hydrochus*, *Helophorus*, and the Hydrophilidae examined (Figs 14, 20). The presence of this unusual structure is a significant autapomorphy of Hydrophiloidea.

A similar suspensorium is absent from the adults of Cupedidae, Adephaga, Silphidae (Fig. 19), Ptiliidae, Staphylinidae, and Histeridae examined.

10. Cerebrum approximately at eye level (10.0)/ cerebrum shifted posteriorly (10.1)

The cerebrum of *Hydraena*, *Ochthebius*, *Hydrochus*, *Helophorus*, and the Hydrophilidae examined is shifted to the posterior region of the head capsule (Fig. 14). This condition is considered as an autapomorphy of Hydrophiloidea.

The cerebrum of adults of Silphidae (Fig. 19), Staphylinidae, and Histeridae is situated in the central region of the head capsule, approximately at eye level.

The posterior position of the brain in the adults of Ptiliidae examined is considered as a result of parallelism.

Larval features

11. Cephalic eggbursters absent (11.0)/ present (11.1)

The presence of cephalic eggbursters in Hydraenidae and other Hydrophiloidea (CROWSON 1960; LAWRENCE 1991a) is considered as a possible autapomorphy of Hydrophiloidea. Cephalic eggbursters are absent from first instar larvae of Archostemata (LAWRENCE 1991a), Gyrinidae, Haliplidae, and from most Polyphaga (LAWRENCE 1991a).

Thoraco-abdominal egg-bursters are commonly found in polyphagan larvae (e.g. Histeridae, Staphylinidae) according to LAWRENCE (1991a).

This character should not be overvalued as cephalic egg-bursters have probably evolved independently in several polyphagan groups (e.g. Derodontidae, LAWRENCE 1991c; Cerambycidae, GARDINER 1966). Besides that, the possibility that those structures belong to the groundplan of Polyphaga cannot be ruled out with certainty.

II. Autapomorphies of Hydrophiloidea (excl. Hydraenidae) (= Hydrophiloidea sensu HANSEN 1991a)

Adult features

12. Clypeus moderately long (12.0=2.1)/ clypeus strongly enlarged (12.1)

An exceptionally long and broad clypeus as found in adults of *Spercheus* (Fig. 4), *Hydrochus*, *Helophorus* (Fig. 39), Epimetopidae (HANSEN 1991a), *Georissus* (Fig. 7), and Hydrophilidae (Fig. 10) is considered as a possible autapomorphy of Hydrophiloidea (excl. Hydraenidae). The lateral margins are more than 2,5 those of the frons anterior to eyes.

13. Antennal club 5-segmented (13.0)/ antennal club 3-segmented (13.1)

A 3-segmented antennal club as found in adults of *Spercheus* (Figs 5, 6; cupule and antennomere III pubescent; CROWSON 1955), *Hydrochus* (Fig. 41), *Helophorus* (Fig. 43), Epimetopidae (HANSEN 1991a), *Georissus* (Fig. 8), and Hydrophilidae is considered as an autapomorphy of Hydrophiloidea excl. Hydraenidae.

A 5-segmented pubescent club as found in most adults of Hydraenidae (Figs 2, 3; JEANNEL 1965, fig 424; HANSEN 1991b) is considered as a groundplan feature of Hydrophiloidea. The 3 segmented antennal club of Histeroidea is probably a result of convergent as pointed out above.

Larval features

14. Free labrum, frontoclypeal suture present (14.0)/ labrum fused with clypeus, frontoclypeal suture absent (14.1)

The labrum is fused with the clypeus in larvae of *Spercheus* (Fig. 23), *Hydrochus* (RICHMOND 1920), *Helophorus* (Fig. 25), *Epimetopus trogoides* (SHARP) (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae. The frontoclypeal suture is absent (Figs 27, 31, 33; BERTRAND 1972). This is considered as an autapomorphy of Hydrophiloidea (excl. Hydraenidae).

The labrum is also fused with the clypeus in larvae of Adephaga, Histeroidea, and larvae of other polyphagan groups (STEHR 1991). This is almost certainly a result of convergency.

A free labrum as found in larvae of Archostemata (LAWRENCE 1982), Hydraenidae (Bøving & HENRIKSEN 1938), in most larvae of Staphylinoidea (LAWRENCE 1982), and in other polyphagan groups (STEHR 1991) is considered as a groundplan feature of Hydrophiloidea and Coleoptera.

15. Coronal suture long (15.0)/ coronal suture extremely short or absent (15.1)

The coronal suture is absent or extremely short in larvae of *Spercheus* (Fig. 23), *Hydrochus* (RICHMOND 1920), *Helophorus* (Fig. 25), *Epimetopus* LACORDAIRE (COSTA et al. 1988), *Georissus* (BERTRAND 1972), and Hydrophilidae (Figs 31, 33; BERTRAND 1972). This is a possible autapomorphy of Hydrophiloidea (excl. Hydraenidae).

A long coronal suture is present in larvae of Hydraenidae (BøvING & HENRIKSEN 1938). A moderately long coronal suture is also found in an undeterminded histerid larva examined whereas it is short in others.

16. Galea arises from outer margin of lacinia (16.0)/ galea inserted on the mesal side of palpomere I 1) (16.1)

A 1-segmented, peg-like galea which is inserted on the mesal side of palpomere I is found in larvae of *Spercheus* (Fig. 24), *Helophorus* (Fig. 26), *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae (Figs 31, 32; BERTRAND 1972). This is considered as an autapomorphy of Hydrophiloidea excl. Hydraenidae.

A very similar condition is found in larvae of Trachypachidae + Dytiscoidea (Adephaga) and Histeroidea. This is interpreted as a result of convergency.

The galea is inserted on the lateral edge of the lacinia in larvae of Hydraenidae (BøvING & HENRIKSEN 1938; PAULIAN 1941; BEIER & POMEISL 1959). This is probably a groundplan feature of Hydrophiloidea. The same condition is found in larvae of Archostemata (COSTA et al. 1988), and in larvae of many polyphagan families (STEHR 1991). Galea and lacinia together form a mala which is indistinctly divided at the apex in larvae of Ptiliidae (LAWRENCE 1982).

17. Mola present (17.0)/ absent (17.1)

A mola is completely absent from larvae of *Spercheus*, *Helophorus*, *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae (BERTRAND 1972). This is considered as a possible autapomorphy of Hydrophiloidea (excl. Hydraenidae). The prominent, compressed proximal part of the mandible of larvae of *Hydrochus* is a secondarily developed "pseudomolar area" and not an actual mola according to Bøving & HENRIKSEN (1938). It is not adapted for chewing-purposes.

¹⁾ The stipitopalpal muscle is inserted at the base of this sclerite (DAS 1937; MOULINS 1959). Therefore it should be interpreted as palpomere I and not as palpifer.

The molar area is well developed in larvae of *Hydraena*, *Limnebius* LEACH, *Ochthebius* (BøvING & HENRIKSEN 1938; PAULIAN 1941; BEIER & POMEISL 1959), in larvae of Archostemata and Myxophaga (Costa et al. 1988), and in larvae of several families of Polyphaga. Loss of the mandibular mola has obviously occured several times. The absence of the mola from larvae of Histeroidea (and other polyphagan larvae) is considered as a result of convergency.

18. Prostheca present (18.0)/ absent (18.1)

The absence of the prostheca from larvae of *Spercheus*, *Hydrochus* (RICHMOND 1920), *Helophorus*, *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae (Figs 31, 33; BERTRAND 1972) is a possible autapomorphy of Hydrophiloidea (excl. Hydraenidae). It appears plausible to assume that a shift from algae-feeding (BEIER & POMEISL 1959) to predacious habits has taken place during the evolution of Hydrophiloidea. This is documented by a considerable number of character state transformations, and by the fact that larvae of *Spercheus* feed not only on small crustaceans but also on algae (WESENBERG-LUND 1943). Therefore, mola and prostheca, which are probably correlated with algae-feeding should be interpreted as groundplan features of Hydrophiloidea.

A prostheca as found in larvae of Hydraenidae (Bøving & HENRIKSEN 1938) is also present in larvae of Ptiliidae and the algae-feeding larvae of Myxophaga (CostA et al. 1988), but is absent from larvae of Archostemata (CostA et al. 1988) and the vast majority of polyphagan larvae.

III. Autapomorphies of Hydrophiloidea (excl. Hydraenidae and Spercheidae)

Adult features

19. Mesal mandibular row of spines or teeth absent (19.0)/ mesal row of spines or teeth present (19.1)

The presence of a mesal row of spines or teeth in adults of *Hydrochus*, *Helophorus*, and Hydrophilidae (Fig. 15) is considered as a possible autapomorphy of Hydrophiloidea excl. Hydraenidae and Spercheidae. A moveable mandibular prostheca is present in adults of Hydraenidae (HANSEN 1991a). Whether a similar, moveable mesal appendage found in adults of *Spercheus* is homologous to the prostheca, which is probably a groundplan feature of Hydrophiloidea, is not clear at present.

Mesal mandibular rows of spines as found in Hydrophiloidea are absent from adults of Archostemata, Myxophaga (LAWRENCE 1982), Adephaga, and from the adults of Polyphaga examined.

Larval features

20. Head subprognathous (20.0)/ head prognathous (20.1)

A horizontal, prognathous head as found in larvae of *Hydrochus* (RICHMOND 1920), *Helophorus* (Fig. 30), *Epimetopus* (COSTA et al. 1988), and *Georissus* (EMDEN 1956) is considered as a derived groundplan character state and synapomorphy of Hydrophiloidea excl. Hydraenidae and Spercheidae.

A subprognathous head as found in larvae of Hydraenidae (BøvING & HENRIKSEN 1938; BEIER & POMEISL 1959) and *Spercheus* (Figs. 23-24) is probably a groundplan feature of Hydrophiloidea. The same condition is found in larvae of Ptiliidae (DYBAS 1976) and many other polyphagan larvae (STEHR 1991).

The prognathous head of histeroid larvae is considered as a result of convergency. Prognathy which is also found in larvae of Adephaga (BEUTEL 1993) and many polyphagan groups is apparently correlated with predacious habits.

21. Cardo and stipes form a hinge (21.0)/ intramaxillary moveability reduced, maxilla palpiform (21.1)

The flexibility between cardo and stipes is largely reduced in larvae of *Hydrochus* (maxilla palpiform; RICHMOND 1920), *Helophorus* (Fig. 26), *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae. The maxilla is extended and flexed as a functional unit. This condition is the result of complex structural transformations and closely correlated with clearly derived, characteristic muscular arrangements observed in larvae of *Helophorus* and larvae of Hydrophilidae (DAS 1937; MOULINS 1959; pers. obs.). The maxilla of Hydrophiloidea (excl. Hydraenidae and Spercheidae) functions as a tactile organ and is used for manipulating the prey during the feeding process (WESENBERG-LUND 1943), but it is not an efficient grasping organ.

Cardo and stipes are flexible on each other by a distinct hinge in larvae of Hydraenidae (BøvING & HENRIKSEN 1938; BEIER & POMEISL 1959) and Spercheidae (Fig. 24). This is almost certainly a groundplan feature of Hydrophiloidea. A similar condition is found in larvae of Archostemata, Myxophaga (COSTA et al. 1988; STEHR 1991; pers. obs.), in larvae of Gyrinidae (BEUTEL 1993), and in many larvae of Polyphaga (STEHR 1991).

22. Cardo undivided (22.0)/ divided into 2 or 3 sclerotized components (22.1)

A voluminous cardo with two or three sclerotized plates is found in larvae of *Helophorus* (Fig. 26), *Georissus* (EMDEN 1956), and most larvae of Hydrophilidae (Figs 32, 34; BøvING & HENRIKSEN 1938; BERTRAND 1972). Considering the shape of the maxillary fossa and the position and size of the stipes, a similar condition is likely to be found in larvae of *Hydrochus*. The advanced type of cardo is considered as a possible groundplan feature and synapomorphy of Hydrochidae (?), Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae. This feature is correlated with the modified function of the cardo and the maxilla as a whole.

The cardo is undivided in larvae of Hydraenidae (BøvING & HENRIKSEN 1938; BEIER & POMEISL 1959) and *Spercheus* (Fig. 24), in larvae of Histeroidea (NIKITSKY 1976; NEWTON 1991) and other polyphagan groups (STEHR 1991), and in larvae of Myxophaga and Archostemata (COSTA et al. 1988).

23. Deep maxillary groove (23.0)/ maxillary groove partly reduced (23.1)

The maxilla is inserted in a moderately deep emargination of the anterior margin of the head capsule in larvae of Hydrochidae (RICHMOND 1920; pl. V, fig. 2), *Helophorus* (Fig. 26), *Epimetopus* (COSTA et al. 1988), and *Georissus* (EMDEN 1956). No externally visible membranous field is present between maxilla and labium. This condition is considered as a derived groundplan feature and significant autapomorphy of Hydrophiloidea excluding Hydraenidae and Spercheidae. It is correlated with the structural and functional transformations of the maxilla outlined above.

A deep maxillary groove, with an extensive membranous field between maxilla and mentum as found in larvae of Hydraenidae (Bøving & HENRIKSEN 1938; BEIER & POMEISL 1959) and *Spercheus* (Fig. 24) is considered plesiomorphic. The same condition is found in larvae of Archostemata and Myxophaga (COSTA et al. 1988; LAWRENCE 1991b).

24. Lacinia well developed (24.0)/ rudimentary (24.1)

A mesal, verruciform swelling on the stipes of larvae of *Hydrochus* has been considered as a rudimentary lacinia by BØVING & HENRIKSEN (1938). If this interpretation is correct, the strongly reduced, vestigial lacinia should be considered as a groundplan feature and synapomorphy of Hydrochidae, Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae.

A strong, hook-like lacinia is found in larvae of Hydraenidae (BØVING & HENRIKSEN 1938; BEIER & POMEISL 1959), Spercheus (Fig. 24), Hydroscaphidae (COSTA et al. 1988), in most larvae of Staphylinoidea (PAULIAN 1941), and in larvae of many other groups of Polyphaga (e.g. Dascillidae, Passalidae; STEHR 1991).

IV. Synapomorphies of Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae

Larval features

25. Prominent nasal and adnasal structures absent (25.0)/ nasale and conspicuous, triangular adnasalia present (25.1)

The presence of a prominent nasale and conspicuous, triangular adnasalia with mesally directed spines or setae as found in larvae of *Helophorus* (Fig. 25), *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and some larvae of Hydrophilidae (BERTRAND 1972) is considered as a derived groundplan feature and synapomorphy of Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae.

Prominent nasal and adnasal structures are completely absent from larvae of Hydraenidae (Bøving & Henriksen 1938), *Spercheus* (Fig. 23), and *Hydrochus* (RICHMOND 1920). This character state is considered as plesiomorphic.

The presence of nasal and adnasal structures in larvae of Histeroidea is considered as a result of convergency. Similar structures are also found in most larvae of Adephaga.

26. Gula broad (26.0)/ Gula reduced to a median suture (26.1)

The gula is reduced to a median suture (confluent gular sutures) in larvae of *Helophorus* (Fig. 26), *Epimetopus* (COSTA et al. 1988), *Georissus* (EMDEN 1956), and Hydrophilidae (Figs 28, 32, 34; BERTRAND 1972). This is considered as a synapomorphy of Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae.

A broad gula as found in larvae of Hydraenidae (BEIER & POMEISL 1959), *Spercheus* (Fig. 24), and *Hydrochus* (RICHMOND 1920) is almost certainly a groundplan feature of Hydrophiloidea. The same condition is found in larvae of Archostemata and Myxophaga (COSTA et al. 1988; STEHR 1991), and in many polyphagan larvae (STEHR 1991).

The confluent gular sutures found in larvae of Synteliidae and Histeridae (LAWRENCE 1982) are considered as a result of convergency. The gular sutures are approximate but separated in larvae of Sphaeritidae (LAWRENCE 1982).

27. Posterior tentorial grooves close to the foramen occipitale (27.0)/ shifted cranially (27.1)

The posterior tentorial grooves are shifted to the craniomesal region of the head capsule in larvae of *Helophorus* (Fig. 26), *Georissus* (EMDEN 1956), *Epimetopus* (COSTA et al. 1988), and in larvae of Hydrophiliodae (MOULINS 1959; BØVING & HENRIKSEN 1938). This is considered as a synapomorphy of Helophoridae, Georissidae, Epimetopidae, and Hydrophilidae.

The posterior tentorial arms originate close to the foramen occipitale in larvae of *Ochthebius* and *Spercheus*, and probably also in larvae of *Hydrochus* (RICHMOND 1920; pl. V, fig. 2). This is considered as a groundplan feature of Hydrophiloidea.

28. Lacinia rudimentary (28.0=24.1)/ absent (28.1)

The complete loss of the lacinia (Figs 26, 28, 32, 34) is a possible synapomorphy of Helophoridae, Georissidae, Epimetopidae, and Hydrophilidae.

The absence of the lacinia from larvae and Histeroidea is considered as a result of parallel evolution. The lacinia is also absent from many larvae of Adephaga (BEUTEL 1993) and others.

29. Mandible without strong, bidentate retinculum (29.0)/ with strong, bidentate retinaculum (29.1.)

A strong, bidentate retinaculum is found in larvae of *Helophorus*, *Georissus* (EMDEN 1956), *Epimetopus* (with additional tooth; COSTA et al. 1988), and many Hydrophilidae (BøvING & HEN-RIKSEN 1938; BERTRAND 1972). This feature is considered as a derived groundplan character state of a monophylum which comprises Helophoridae, Epimetopidae, Georissidae, and Hydrophilidae. Several variations occur within Hydrophilidae. Left and right mandible are frequently differently shaped.

A small retinaculum as found in larvae of Hydraenidae and Spercheidae (BØVING & HENRIKSEN 1938) is probably a groundplan feature of Hydrophiloidea. A membranous mandibular apex with a strong seta, a slender, elongated, bifid tooth, a rather short and pointed proximal tooth (retinaculum?), and a pseudomolar area are found in larvae of *Hydrochus* (RICHMOND 1920; pl. V, figs 1, 3). This is almost certainly an autapomorophic condition.

V. Synapomorphies of Georissidae, Epimetopidae and Hydrophilidae

Larval features

30. Submentum completely fused with ventral wall of head capsule (30.0)/ distinct cranial submental sclerite present (30.1)

A distinct suture separating a cranial submental sclerite (subgular sclerite; BØVING & HENRIKSEN 1938) from the posterior submental area, which is firmly fused with the ventral wall of the head capsule, is present in larvae of Hydrophilidae (Figs 28, 32, 34; BØVING & HENRIKSEN 1938; QUENNEDEY 1965; BERTRAND 1972), in larvae of *Epimetopus* (COSTA et al. 1988; fig. 4), and in larvae of *Georissus* (EMDEN 1956; fig. 3). This character state is considered synapomorphic. The pregular sclerite is absent from larvae of Hydraenidae (BØVING & HENRIKSEN 1938), *Spercheus* (Fig. 24), *Hydrochus* (RICHMOND 1920), and *Helophorus* (Fig. 26).

VI. Autapomorphies of Hydrophilidae

Larval features

31. Head prognathous (31.0=20.1)/ hyperprognathous (31.1)

The ventral wall of the head capsule is convex and distinctly longer than the dorsal wall in larvae of Hydrophilidae (Figs 28, 29, 31 - 34; Bøving & HENRIKSEN 1938). The foramen occipitale is oblique and the mouthparts are distinctly directed upwards (Fig. 29). This character state is probably autapmorphic. It is almost certainly correlated to specialized feeding habits as described by MEGUSAR (1909) and WESENBERG-LUND (1943).

32. Maxillary groove partly reduced (32.0=23.1)/ absent (32.1)

The maxilla is inserted at the same level as the mandibular articulation in larvae of Hydrophilidae (Figs 28, 32, 34). The maxillary groove is completely reduced. This is considered as an autapomorphic feature.

33. Antennae inserted laterally (33.0)/ inserted dorsally (33.1)

The antennae are inserted dorsally, closer to the median line of the head than the condyles of the mandibles in larvae of Hydrophilidae (Figs 27, 31, 33; BØVING & HENRIKSEN 1938). This derived condition is probably correlated with specialized feeding habits: hydrophilid larvae hold their prey between mouthparts and antennae when feeding outside the water WESENBERG-LUND (1943).

A lateral insertion of the antennae as found in larvae of Hydraenidae (Bøving & HENRIKSEN 1938), Spercheus (Fig. 23), Hydrochus (RICHMOND 1920), Helophorus (Fig. 25), Epimetopus (CostA et al. 1988), and Georissus (EMDEN 1956) is certainly plesiomorphic. The same condition is found in the vast majority of coleopteran larvae.

34. Transverse submental suture straight (34.0=29.1)/V-shaped (34.1)

The cranial submental sclerite is separated from the posterior submental area by a V-shaped suture in larvae of Hydrophilidae (e.g. *Sperchopsis* LeCONTE; BERTRAND 1972; fig. 28; BøVING & HENRIKSEN 1938). Labial retractor muscles arise from a ridge or apodeme at the posterior edge of the sclerite (MOULINS 1959). The presence of a straight, transverse submental suture as found in larvae of Epimetopidae (COSTA et al. 1988) and Georissidae (EMDEN 1956) is considered as a groundplan feature of a monophylum which comprises the latter two families and Hydrophilidae.

VII. Synapomorphies of Georissidae and Epimetopidae

Adult features

35. Posterodorsal part of head capsule exposed (35.0)/ covered by a pronotal shield (35.1)

The posterodorsal area of the head capsule is concealed by a shelf-like projection of the pronotum in adults of Epimetopidae and Georissidae (HANSEN 1991a). This unusual feature is considered as a synapomorphic character state of both families. Less distinct pronotal projections as found in other Hydrophiloidea (e.g. Spercheidae) are considered as the result of parallel evolution.

36. Head not strongly deflexed (36.0)/ head strongly deflexed, vertical (36.1)

A strongly deflexed head as found in adults of Epimetopidae and Georissidae (HANSEN 1991a) is considered as a possible synapomorphy of both families.

The plesiomorphic character state is found in the remaining taxa of Hydrophiloidea with the exception of Berosini and Chaetarthriini (HANSEN 1991a). The condition in the latter two taxa is almost certainly the result of parallel evolution.

37. Lateral margin of clypeus not excised anterior to eyes (37.0)/ abruptly excised anterior to eyes (37.1)

The presence of a clypeal notch in front of the eyes in adults of *Georissus* (Fig. 7) and *Epimetopus* (HANSEN 1991a) is considered as a possible derived groundplan character state of Epimetopidae and Georissidae. However, the clypeal margin is hardly excised in adults of *Eumetops* BALFOUR-BROWNE (HANSEN 1991a). Parallel evolution cannot be excluded in this case. A similar condition is also found in adults of Omicrini and Megasternini (HANSEN 1991a).

Larval features

38. Mesal margin of adnasalia with setae (38.0=25.1)/ mesal margin of adnasalia with cuticular spines (38.1)

The mesal margin of the adnasalia is armoured with solid, cuticular spines in larvae of

Epimetopus (COSTA et al. 1988; pl. 23, fig. 7) and *Georissus* (EMDEN 1956). This is considered as a possible synapomorphy of Epimetopidae and Georissidae.

An adnasal margin with setae as found in larvae of *Helophorus* and many Hydrophilidae is considered as a groundplan feature of Hydrophiloidea excluding Hydraenidae, Spercheidae, and Hydrochidae.

39. Palpomere I short, galea moderately sized (39.0=16.1)/ palpomere I distinctly elongated, galea minute (39.1)

A palpomere I which is almost as long or longer than the stipes bears a minute galea in larvae of *Epimetopus* (COSTA et al. 1988) and *Georissus* (EMDEN 1956). This feature is considered as a possible synapomorphy of Epimetopidae and Georissidae.

A rather short palpomere I and a distinct galea as found in most larvae of Hydrophilidae (Figs 28, 32; Bøving & HENRIKSEN 1938; BERTRAND 1972) is considered as a groundplan feature of the monophylum which comprises Epimetopidae, Georissidae, and Hydrophilidae.

Discussion of systematic concepts published by previous authors

A systematic transfer of Hydraenidae from Hydrophiloidea to Staphylinoidea has been proposed by DYBAS (1976), and Histeroidea are considered as a part of Hydrophiloidea in several recent publications (NIKITSKY 1976; LAWRENCE & NEWTON 1982; COSTA et al. 1988). This systematic concept which was already proposed by BÖVING & CRAIGHEAD (1931) will be discussed in the following.

Unfortunately, DYBAS (1976) does not propose a precise systematic placement of Hydraenidae within Staphylinoidea (sistergroup), and a clear presentation of character states found in the taxa involved (character state matrix, cladogram) is wanting. Nevertheless, he regards Hydraenidae as "clearly belonging to the Staphylinoidea". This determined statement is based on the presence of a fimbriate galea in larvae of the "leptinid association" of Staphylinoidea and in Hydraenidae, and on the presence of a pair of anal hooks in larvae of Ptiliidae and Hydraenidae.

The fimbriate type of galea as found in most larvae of Ptiliidae, Leiodidae, Leptinidae, and Limulodidae is indeed a remarkable character. However, this characteristic galea differs considerably from what is found in an undetermined larva of Hydraena (DYBAS 1976; fig. 31). The "leptinid-type" of galea is broad and set with one or two well developed, laterally directed fringes of hairs, whereas only a few mesally directed hairs are present on the slender galea of the Hydraena-larva examined by DYBAS (1976). Only three setae are present in larvae of Hydraena pennsylvanica KIESENWETTER (BØVING & HENRIKSEN 1938), the apex of the galea is covered with papillae in larvae of Limnebius truncatellus THUNBERG (D'ORCHYMONT 1913), and a setal fringe of the galea is completely absent from larvae of Ochthebius (BEIER & POMEISL 1959) and Meropathus Enderlein (Paulian 1941). Therefore it is doubtful whether a "fimbriate galea" is a groundplan feature of Hydraenidae. Galeae with dense fringes of hairs do also occur in many larvae of Anobiidae (BÖVING 1954), in larvae of Silphidae, Helodidae (LESAGE 1991), Elmidae (BROWN 1991), Nosodendridae (BÖVING 1929), and others. The "staphylinoid-like" fringe on the galea in the larva of Saphophagus SHARP (Dermestoidea) has been emphasized by CROWSON (1959). Considering these facts, parallel evolution of different forms of fringed galeae in larvae of staphylinoid subgroups and some larvae of Hydraenidae appears likely. In any case, this character is not a sound basis for far-reaching systematic changes. The typical fimbriate galea (DYBAS 1976; fig. 30a-d) however, may turn out as a significant common derived feature of the "Leptinid association" (excl. Hydraenidae).

A pair of anal hooks as found in larvae of Hydraenidae (not in *Meropathus*) and Ptiliidae (not in Leiodidae, Limulodidae, and Leptinidae) is not a unique feature as stated by DYBAS (1976). One

pair is also present in larvae of *Hydroscapha natans* LECONTE (BÖVING 1914). Three pairs of anal hooks are present in larvae of *Sphaerius ovensensis* (OKE) (BRITTON 1966), and two pairs of anal hooks are present in larvae of Gyrinidae (COSTA et al. 1988). The polarity of this character is not sufficiently clarified, and parallel evolution in larvae of Ptiliidae and Hydraenidae appears possible. Besides that, it is not clear whether anal hooks are a groundplan feature of Hydraenidae. The correlation between the special running water habitat of larvae of *Ochthebius* and the presence of anal hooks has been emphasized by BEIER & POMEISL (1959).

The general resemblance between larvae of Ptiliidae and Hydraenidae (DYBAS 1976) is irrelevant for systematic conclusions as the affinities between both larval types is due to symplesiomorphy. "The close resemblance in numerous features of the dorsum of the abdomen" of the adults of Hydraenidae and the ptiliid *Nossidium* ERICHSON (cited as unpublished data in DYBAS 1976) cannot be evaluated here, as the data are not available.

The similarity between the hind wings of Staphylinoidea and Hydraenidae (PERKINS 1980) is probably due to parallel reduction in both groups (see also HANSEN 1991a).

No autapomorphic features of Staphylinoidea (incl. or excl. Hydraenidae) are presented by COSTA et al. (1988). Most of the features given as general characteristics of Staphylinoidea are plesiomorphic. Other features are not found in Hydraenidae (e.g. fronto-clypeal suture absent in most cases, gula generally more or less reduced).

Four presumptive synapomorphies of Staphylinoidea are presented by LAWRENCE & NEWTON (1982): wing folding (primitively) with simple convex and concave folds and without a hinge, medio-cubital loop of wing poorly developed or absent, phallobase small and strap-like or absent, only four Malpighian tubules. All these derived character states are reductions, which may be related to ancestral size reduction according to LAWRENCE & NEWTON (1982), and parallelism or convergency in Hydraenidae (and other polyphagan groups) cannot be excluded.

Several synapomorphies of Hydraenidae and Ptiliidae are listed by LAWRENCE & NEWTON (1982): apical maxillary palpomere with characteristic, complex sensory appendage, anal lobes with 2 hooks (larvae), functional spiracles on abdominal segment I only (pupae), mandibles concealed, with weak apices, genital segments permanently everted and well sclerotized, ovipositor with connate or fused gonocoxites (adults).

The sensory appendage of the maxillary palp is only shown for one species of *Hydraena* in DYBAS (1976) and is not described in detail. It is absent from larvae of *Ochthebius* (BEER & POMEISL 1959) and it is not clear whether this structure is a groundplan feature of Hydraenidae. It is also unclear whether this structure is a unique feature of Ptiliidae and Hydraenidae (partim) or whether it is also present in other groups. Anal hooks are not an exclusive feature of Hydraenidae (partim) and Ptiliidae as pointed out above. Pupal characters should be treated cautiously as only very few pupae are known at present. Concealed mandibles with weak apices are also found in other groups such as Elmidae (BEIER 1948).

It is well understood that the characters presented by LAWRENCE & NEWTON (1982) are weighty arguments in favour of the proposed relationship of Hydraenidae and Ptiliidae. However a more detailed presentation of data would be worth while and necessary for a more detailed discussion of conflicting evidences.

To include Hydraenidae in Staphylinoidea would imply the assumption that all autapomorphic features of adult Hydrophiloidea proposed in this study, cephalic egg-bursters of larvae, aquatic existence of adults with highly specialized breathing habits (HRBACEK 1949), a peculiar type of plastron respiration (micro- and macroplastron; THORPE 1950), and a stridulatory file on the basal abdominal pleuron (HAMMOND 1979) have evolved independently in Hydraenidae. It appears more plausible to assume that some isolated characters have evolved independently in Hydraenidae and some representatives of staphylinoid groups, especially Ptiliidae. Finally the different egg-laying habits are a strong argument against a close relationship between

Hydraenidae and staphylinoid families. The eggs of all Hydrophiloidea are covered by silken material (Hydraenidae, some Sphaeridiini; RICHMOND 1920) or enclosed in egg-cases (all other Hydrophiloidea; RICHMOND 1920). Eggs which are enclosed in silken cocoons have not been described for any group of Staphylinoidea.

LAWRENCE & NEWTON (1982) include Histeroidea in Hydrophiloidea (excl. Hydraenidae) on the basis of "numerous derived larval features". A discussion of this systematic approach is considerably complicated by the fact that the authors do not specify whether they consider Histeroidea (or a subgroup) as the sistergroup of Hydrophiloidea (sensu HANSEN 1991a) or whether they assume a closer relationship between Histeroidea (or a subgroup) and a hydrophiloid subgoup. A clear presentation of the character states found in different taxa is wanting (see above). Some inconsistencies will be pointed out below.

Several characters presented, such as the fused labrum, loss of the mandibular mola, loss of the lacinia (present in *Spercheus*), and the largely membranous abdomen with small scattered sclerites (not present in *Spercheus* and *Hydrochus*) are rather commonly found in coleopterous larvae. A galea which is inserted on the basal segment of the palp is also found in some larvae of Adephaga (Trachypachidae and Dytiscoidea). Ecdysial lines which are reported as absent from final instars of hydrophiloid larvae are present in larvae of *Helophorus* sp. examined. The tentorial character presented by LAWRENCE & NEWTON (1982) is rather puzzling. Tentorial structures of different hydrophilid larvae described in detail by MOULINS (1959) seem different from the character state outlined in LAWRENCE & NEWTON (1982). The tentorium of larvae of *Spercheus* is very similar to that of larvae of *Ochthebius*, but distinctly different from that of the histerid larvae examined. The presence of a 3-segmented, pubescent antennal club is probably not a sound argument for a close relationship between Hydrophiloidea (sensu HANSEN 1991a) and Histeroidea if morphological and functional differences are taken into consideration. Besides that, antennal clubs (without breathing function) occur in many groups of Coleoptera.

A considerable number of arguments indicate that Histeroidea should not be included in Hydrophiloidea. None of the proposed autapomorphies of adult and larval Hydrophiloidea is found in adults of Histeroidea (see above). Parallel evolution of 10 derived character states in several hydrophiloid lineages or secondary loss of all these features in Histeroidea appears quite unlikely.

Histeroidea are primarily terrestrial as larvae and adults according to CROWSON (1955), whereas Hydrophiloidea are almost certainly primarily aquatic. Adults of Hydrophiloidea are characterized by highly specialized breathing habits and the suitable structural features such as the palpicorn antenna (6-9-segmented in Hydrophiloidea excl. Hydraenidae). Adults of Hydrophiloidea are phytophagous. They possess a large mandibular mola (Fig. 15), an unusually voluminous cibarium, and poorly developed cibarial dilator muscles (Figs 12, 14). Adults of Histeroidea are probably primarily carnivorous. Their mandibles are strongly projecting (JEANNEL 1965; LAWRENCE 1982), the cibarium is narrow, and the cibarial dilators are strongly developed. The absence of the Y-shaped suture on the head and of spiracles on abdominal segment VIII from adults of Histeridae are further features opposed to an inclusion of that family in Hydrophiloidea according to CROWSON (1974).

Various larval features are likewise not compatible with a close relationship between histeroid and hydrophiloid groups, or with a sistergroup relationship between both superfamilies. Thoracoabdominal eggbursters are characteristic for histerid larvae, whereas cephalic eggbursters are found in larvae of Hydrophiloidea (CROWSON 1960; 1974). A secondary shift of the eggbursters from the head to the abdomen appears quite unlikely. A horizontal or elevated head, absence of the lacinia, and presence of epistomal lobes (HANSEN 1991a) cannot be regarded as arguments for a sistergroup relationship between Histeroidea and Hydrophiloidea (excl. Hydraenidae) because these features are probably not groundplan character states of the latter group (Spercheus, Hydrochus). A long coronal suture is found in some larvae of Histeridae (undetermined species from Transcaucasus). An extremely short or absent coronal suture is found in larvae of Hydrophiloidea (excl. Hydraenidae). A broad gula is found in larvae of Spercheus and Hydrochus, the gular sutures are very slightly separated in larvae of Sphaeritidae (NIKITSKY 1976), whereas a fused median gular suture is found in Synteliidae, Histeridae (STEHR 1991), Helophoridae, Georissidae, Epimetopidae, and Hydrophilidae. A voluminous, subdivided cardo is characteristic for Hydrophiloidea (excl. Hydraenidae and Spercheidae) (Hydrochidae?). The cardo is vestigial and largely or completely fused with the stipes in larvae of Histeroidea (LAWRENCE 1982). The extrinsic maxillary musculature is clearly different in the larvae of Hydrophilidae (MOULINS 1959) and histerid larvae examined. A well developed preoral filter, which includes a mandibular penicillum, is present in larvae of Histeroidea (Fig. 36), but well developed and sclerotized in larvae of Hydrophiloidea (Figs 24, 26, 28, 32, 34).

As in Staphylinoidea, naked eggs are deposited by Histeridae. This is clearly in contrast to the specialized egg-laying habits of Hydrophiloidea (see above).

A systematic combination of Histeroidea and Hydrophiloidea is impossible according to PAULIAN (1941) if characters of pupae are taken into consideration. Specific reasons are not given by that author.

There is no doubt that the systematic concept presented by LAWRENCE & NEWTON (1982) and LAWRENCE (1982) is an interesting and important contribution to the phylogeny of Staphyliniformia. However, a more detailed presentation including polarity rationale, character state matrix, and cladogram would faciliate the discussion of conflicting hypotheses considerably as pointed out above.

A subdivision of Hydrophiloidea into six families - Helophoridae, Epimetopidae, Georissidae, Hydrochidae, Spercheidae, and Hydrophiloidae has been proposed in a comprehensive study by HANSEN (1991a). A sistergroup relationship between Hydrophiloidea sensu HANSEN and Histeroidea (see above) appears more likely to the author than a sistergroup relationship between Hydrophiloidea (sensu HANSEN) and Hydraenidae, even though more characters linking the latter two groups are presented in that study.

HANSEN (1991a) has evaluated 176 characters of 118 genera (Hydraenidae, Agyrtidae, Sphaeritidae, Hydrophiloidea sensu HANSEN). Emphasis is placed upon external (integumental) features of adults. Larval features used in the phylogenetic analysis are almost exclusively based on descriptions in the literature. Three genera, i.e. *Ochthebius, Necrophilus* LATREILLE (Agyrtidae), and *Sphaerites* DUFTSCHMIDT (Sphaeritidae) were used as outgroup. Computer programs (PAUP, Hennig86) were used for a phylogenetic analysis of initially 232 characters, which were not weighted when running the analysis. 65 characters were deleted subsequently. The first analysis resulted in 20 equally parsimonious phylogenetic trees, with a quite low consistency index, resulting from many weak characters included in the analysis according to HANSEN (1991a). Subsequent steps provided nine trees of length 534, which were rejected in favor of 535 step cladograms. Finally, a few steps are added and a 538 step cladogram forms the basis for the discussion of the phylogeny of Hydrophiloidea (HANSEN 1991a; fig. 2).

It would be beyond the scope of the present paper to discuss the results and procedures applied by HANSEN (1991a) in detail. However some problematic points of the highly interesting study should be pointed out in the following. It has been mentioned above that immature stages have not been examined by HANSEN (1991a) in detail, and some presumptive character misinterpretations may have resulted from lack of larval material. The polarity determination of some of the characters, which are generally treated very briefly, appears questionable. The interpretation of a fused labrum as character state 0 (plesiomorphic?) is very hard to understand, if the larvae of Archostemata, Myxophaga, Hydraenidae, and Agyrtidae (outgroup !) are taken into consideration. The absence of epistomal lobes from larvae of *Spercheus* (character 146; HANSEN 1991a) is almost certainly a plesiomorphic feature as demonstrated by the absence from

larvae of Archostemata, Myxophaga, Hydraenidae, and Agyrtidae, Besides that, epistomal lobes are also completely absent from larvae of Hydrochus (RICHMOND 1920). The inclined (subprognathous) head of larvae of Hydraenidae and Agyrtidae (and Spercheus!) (character 150; HANSEN 1991a) should be considered as plesiomorphic, and not as derived (character state 1) as suggested by HANSEN (1991a). This results from the condition found in larvae of Archostemata, Myxophaga, Ptiliidae and others. The presence of a lacinia (well developed in Spercheus) is probably plesiomorphic and not derived as proposed by HANSEN (1991a). Well developed, hooklike laciniae are almost certainly a groundplan feature of Polyphaga and Coleoptera as pointed out above. Some of these problematic interpretations may have resulted from the fact, that the outgroup comprises only 3 genera. It appears as if several character states found in larvae of Sphaerites have been considered as plesiomorphic, even though it is quite evident that this taxon shows many derived features (compared to those found in larvae of Achostemata, Myxophaga, Staphylinoidea, and Hydraenidae) which are correlated with predacious habits. Other important larval features, especially the plesiomorphic, maxilla (intramaxillary articulation), maxillary groove, and tentorium of Spercheus have not been taken into consideration. The rejection of the 534 step cladograms in favour of the 535 step cladogram is based on the presence of an abdominal stigmatic atrium and a tergal shield VIII (character 153; HANSEN 1991a) in larvae of Spercheus. This is indeed a sound argument and strong emphasis on this character appears appropriate. In any case, the phylogenetic hypothesis presented in this study requires the assumption that the stigmatic atrium has evolved several times independently (HANSEN 1991a assumes that the stigmatic atrium of Hydrochus is non-homologous with the one found in other hydrophiloids), or is secondarily absent from the terrestrial larvae of Helophorus, Georissus, and Epimetopidae.

It is quite obvious that a reevaluation of some of the characters used by HANSEN (1991a) is necessary. The phylogenetic results may differ if other characters, especially internal features are taken into consideration.

Conclusions (Cladogram, Fig. 37)

The monophyly of Hydrophiloidea (sensu CROWSON 1955) is suggested by a considerable number of autapomorphic features of the head of adults. These common derived characteristics comprise features which are correlated with extremely specialized breathing habits (antenna, antennal groove), features of mouthparts (mentum, galea, maxillary palp), and internal features (hypopharyngeal suspensorium, cerebrum). It appears very unlikely that such a complex set of different characters has evolved independently in different groups (e.g. Hydraenidae and remaining Hydrophiloidea). The presence of cephalic eggbursters is a possible autapomorphy of larvae. A further argument for the monophyly of Hydrophiloidea is the fact that the eggs are either covered by silken material or enclosed in egg cases as pointed out above. Independent evolution of these specialized egg-laying habits in Hydraenidae and Hydrophiloidea sensu HANSEN (1991a) appears quite unlikely, but cannot be fully excluded.

Whereas head structures of adult hydrophiloids remain largely unchanged during the evolutionary history of the group, there is a large morphological gap between the algae-feeding larvae of Hydraenidae and those of the highly evolved predacious Hydrophilidae. Hydraenid larvae share many plesiomorphic features with larvae of other supposedly basal lineages of Polyphaga. However, if larvae of all hydrophiloid families are taken into consideration, comparatively small evolutionary steps lead from Hydraenidae to the most highly evolved forms. A continuous transformation series of characters of the head capsule and mouthparts is fully consistent with the proposed monophyly of Hydrophiloidea.

Larval autapomorphies indicate the monophyly of Hydrophiloidea (excl. Hydraenidae), of Hydrophiloidea (excl. Hydraenidae and Spercheidae), and of Helophoridae + Epimetopidae + Georissidae + Hydrophilidae. The monophyly of Epimetopidae + Georissidae + Hydrophilidae, and the monophyly of Epimetopidae + Georissidae are proposed as working hypotheses. The monophyly of Hydrophilidae is suggested by several autapomorphic features.

It should be reemphasized that this study is a hypothesis which is based on a complex but still limited character set. For a "final solution" of phylogenetic questions concerning Hydrophiloidea, Histeroidea, and Staphylinoidea more detailed studies are required, especially of internal structures and functional aspects.

Acknowledgements

I am greatly indebted to Dr. E. Arndt (Leipzig) for loan and gift of valuable material and to Dr. M. Jäch (Naturhistorisches Museum Wien) for his generous support. I also wish to thank Dr. R.E. Roughley for proof-reading the manuscript. Collecting of North American species of Adephaga (outgroup) was made possible by Natural Sciences and Engineering Research Council of Canada, operating grant No. A0428 held by Dr. Roughley (Dept. of Entomology, Univ. of Manitoba). The use of SEM facilities at the Institut für Biologie III, Universität Tübingen, was made possible by Prof. Dr. W. Maier, and is gratefully acknowledged.

Zusammenfassung

Merkmale des Kopfes von Imagines und Larven der Hydrophiloidea (sensu CROWSON 1955) wurden phylogenetisch analysiert. Die Monophylie der Überfamilie wird durch eine Anzahl von Autapomorphien der Imagines nahegelegt: Antennen mit behaarter Keule, Antennengrube, postokularer Vorsprung, komplexes hypopharyngeales Suspensorium, distales Glied der Galea aus gefiederten Lamellen zusammengesetzt, ausgedehntes, stark sklerotisiertes Mentum, e.t.c. Das Vorhandensein von cephalen Eizähnen beim ersten Larvenstadium ist ein weiteres gemeinsames abgeleitetes Merkmal. Die Hydrophiloidea (ohne Hydraenidae) sind durch zwei imaginale und fünf larvale Synapomorphien charakterisiert. Besonders bedeutsam sind der Verlust der Clypeolabral- und Frontoclypealnaht, sowie die Insertion der Galea auf dem Palpomer I bei den Larven. Die Hydrophiloidea (ohne Hydraenidae und Spercheidae) lassen sich durch eine imaginale und die fünf folgenden larvalen Synapomorphien als monophyletisch begründen: Prognathie, stark eingeschränkte intramaxilläre Beweglichkeit, Cardo unterteilt, Maxillengrube teilweise reduziert. Lacinia rudimentär. Die Umwandlung der breiten Gula in eine schmale Gularsutur, nahe beieinanderliegende hintere Tentorialgruben die weit vom Hinterhauptsloch entfernt sind, sowie das Vorhandensein eines vorspringenden Nasale und auffallender dreieckiger Adnasalia sind gewichtige larvale Synapomorphien der Helophoridae, Epimetopidae, Georissidae, und Hydrophilidae. Die Helophoridae sind die Schwestergruppe der Epimetopidae, Georissidae und Hydrophilidae. Ein abgegrenztes submentales Sklerit stellt eine mögliche larvale Synapomorphie der letztgenannten drei Familien dar. Die Larven der Hydrophilidae zeichnen sich durch Hyperprognathie, eine V-förmige submentale Sutur, völlige Reduktion der Maxillengrube, und dorsale Insertion der Antennen aus. Das Vorhandensein eines pronotalen Schildes das den hinteren Teil des stark nach unten geneigten Kopfes der Imagines überwölbt, cutikuläre Dornen am Innenrand der larvalen Adnasalia, sowie ein verlängertes Palpomer I mit einer winzigen Galea sind mögliche Synapomorphien der Epimetopidae und Georissidae.

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Figs. 1 - 3: Ochthebius sp., head of adult; 1) dorsal view; 2) ventral view; 3) lateral view. Figs. 4 - 6: Spercheus emarginatus, head of adult; 4) dorsal view; 5) ventral view; 6) lateral view. Figs. 7 - 9: Georissus crenulatus, head of adult; 7) dorsal view; 8) ventral view; 9) lateral view.



Figs. 10 - 13: *Helochares obscurus*, head of adult; 10) dorsal view; 11) ventral view; 12) labrum, epipharynx, pharynx; 13) horizontal section, ventral part.



Figs. 14 - 16: *Helochares obscurus*, head of adult; 14) sagittal section; 15) horizontal section, dorsal part; 16) horizontal section, dorsal part, mandible and pharynx removed.



Figs. 17 - 19: Necrophorus vespillo, head of adult; 17) dorsal view; 18) ventral view; 19) sagittal section.



Figs. 20 - 22: 20) *Hydrophilus piceus*, prementum, mentum and hypopharyngeal suspensorium, ventral view; 21) *Hydraena* sp., prementum, mentum and hypopharyngeal suspensorium, ventral view; 22) *Hydrochus angustatus*, maxilla, ventral view.

Figs. 23 - 25: Larval heads; 23) Spercheus emarginatus, L3, dorsal view; 24) same, ventral view; 25) Helophorus sp., dorsal view.



Figs. 26 - 33: Larval heads; 26) *Helophorus* sp., ventral view; 27) *Sphaeridium* sp., dorsal view; 28) same, ventral view; 29) same, lateral view; 30) *Helophorus* sp., lateral view; 31) *Enochrus* sp. (L 3?), dorsal view; 32) same, ventral view; 33) *Hydrophilus* sp. (L 2?), dorsal view.



Figs. 34 - 36: Larval heads; 34) Hydrophilus sp. (L 2?), ventral view; 35) undetermined histerid larva, dorsal view; 36) same, ventral view.



Fig. 37: Phylogenetic interrelationships of the families of Hydrophiloidea, distribution of character states; apomorphic character states of adults: full squares; apomorphic character states of larvae: full circles.



Figs. 38 - 43: SEM micrographs; 38) *Hydraena britteni*, dorsal view; 39) *Helphorus minutus*, dorsal view; 40) *Hydraena britteni*, anterior part of head, ventral view; 41) *Hydrochus angustatus*, ventral view; 42) *H. britteni*, antennal pouch; 43) *Helophorus minutus*, antennal pouch.

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Zeitschrift/Journal: Koleopterologische Rundschau

Jahr/Year: 1994

Band/Volume: 64_1994

Autor(en)/Author(s): Beutel Rolf Georg

Artikel/Article: <u>Phylogenetic analysis of Hydrophiloidea based on characters</u> of the head of adults and larvae (Staphyliniformia). 103-131