Zoomorphology (1998) 118:103–116

ORIGINAL ARTICLE

R. G. Beutel · A. Haas

Larval head morphology of *Hydroscapha natans* (Coleoptera, Myxophaga) with reference to miniaturization and the systematic position of Hydroscaphidae

Accepted: 16 December 1997

Abstract The head of third instar larvae of *Hydroscapha natans* was reconstructed three dimensionally on a computer. This technique allowed a detailed examination and presentation of internal features of a representative of the 'suborder' Myxophaga, which is characterized by the very small size of the immature stages and adults. Larval character states of *H. natans* were compared with features found in other representatives of the Coleoptera. The monophyly of the Myxophaga (excluding Lepiceridae) is supported by several autapomorphies of the larval head: a broadened, transverse head, scale-like cuticular surface structures, round and flattened labral sensilla, short antennae with only two antennomeres, a ligula with papillae, and a broadened tentorial bridge. A monophylum comprising the Hydroscaphidae and Microsporidae is characterized by a very unusual semientognathous condition of the mouthparts and an unusual shape and large relative size of the brain. The last common ancestor of the Hydroscaphidae, Torridincolidae, and Microsporidae was probably living in hygropetric habitats. Several apomorphies have evolved in correlation with this peculiar life style. The very dense arrangement of muscles and other internal structures, and the unusual shape and size of the cerebrum have resulted from miniaturization. The overall complexity of the head is not reduced in comparison to larvae of other representatives of Coleoptera. A negative allometric relationship between body size and the size of the brain, and a correlation between brain size and the size of neurons was found in several species of Coleoptera examined.

A. Introduction

The phylogenetic importance of the Myxophaga is emphasized by their position as a separate 'suborder' of the Coleoptera, as proposed by Crowson (1955) and accepted in current classifications (Lawrence and Newton 1995). A sister-group relationship with the Polyphaga was proposed by Klausnitzer (1975) and Beutel (1997), but features of wing venation suggest a sister-group relationship between the Myxophaga and the Adephaga (Kukalová-Peck and Lawrence 1993).

The Myxophaga are represented by four families (Hydroscaphidae LeConte, 1874; Lepiceridae Hinton, 1936; Torridincolidae Steffan, 1964; Microsporidae Crotch, 1873) and comprise approximately 60 species (Lawrence and Newton 1995). There are three genera of Hydroscaphidae: *Scaphydra* Reichardt, 1973 (3 species in Brazil), *Yara* Reichardt and Hinton, 1976 (2 species in Brazil and Panama), and *Hydroscapha* LeConte, 1874 (11 species in North America, Eurasia, North Africa, and Madagascar) (Reichardt 1971, 1973; Reichardt and Hinton 1976; Lawrence and Reichardt 1991; Lawrence and Newton 1995).

All species of Myxophaga are characterized by their very small size. The body length of adults does not exceed 2.6 mm (Reichardt 1973; Reichardt and Hinton 1976; Reichardt and Vanin 1976; Vanin 1991). Adults and larvae of the Hydroscaphidae and Torridincolidae are most commonly collected in hygropetric habitats, whereas adults of the Microsporidae live in moist substrate at the edges of rivers (Britton 1966; Lawrence and Reichardt 1991). Adults of the Lepiceridae were collected along streams in flood debris (Reichardt 1976). Larvae of this family are not yet known.

The present paper is aiming at a clarification of the sister-group relationship of the Hydroscaphidae and the monophyly of Myxophaga, based on a non-numerical phylogenetic evaluation of external and internal character states of the larval head. Morphological features of *Hydroscapha natans*, which are described in detail in the morphological section, are compared with those found in larvae of representatives of the Microsporidae, Torridincolidae, and other groups of the Coleoptera. An attempt is made to clarify which of the presumably derived character states found in larvae of the Hydroscaphidae or Myxophaga is correlated with the unusual hygropetric life style and algae feeding. Another purpose of the present contri-

R. G. Beutel (✉) · A. Haas
Institut für Spezielle Zoologie und Evolutionsbiologie,
Friedrich-Schiller-Universität, Erbertstrasse 1,
D-07743 Jena, Germany
e-mail: b5bero@rz.uni-jena.de, Fax: +03641-949 142

bution is to clarify the effects of miniaturization on the morphology of the larvae of *H. natans*. It is discussed whether shape and size of the brain, the muscle arrangement, and structural changes such as fusion of sclerites are correlated with the very small size of the larvae.

It is probably due to the strong degree of miniaturization that internal features of the larvae of Myxophaga have remained undescribed until now. Reliable morphological results are difficult to obtain by dissection; the same is true for a proper understanding of the internal features from serial sections. One purpose of this study is to demonstrate that computer-based three-dimensional reconstruction, which has not yet been applied in the present field, permits a detailed description and innovative presentation of minute and complex internal structures.

B. Materials and methods

The following species were examined (number of specimens in parentheses): **Myxophaga** Hydroscaphidae: *Hydroscapha natans* LeConte, 1874 (20). Microsporidae: *Microsporus* spp. (European and North American species; 3 and 6, respectively). Torridincolidae: *Ytu zeus* Reichardt, 1973 (2), *Iapir britskii* (Reichardt and Costa, 1967) (2), *Delevea namibensis* Endrödy-Younga, 1997 (5), *Torridincola rhodesica* Steffan, 1964 (5), *Satonius kurosawai* (Sato, 1982) (20). **Polyphaga** Hydraenidae: *Davidraena* sp. (8), *Hydraena* sp. (2), *Ochthebius* spp. (30). Leiodidae: *Catops* sp. (30). Agyrtidae: *Necrophilus hydrophiloides* Guérin-Menneville, 1835 (2). Spercheidae: *Spercheus emarginatus* (Schaller, 1783) (5). Helophoridae: *Helophorus* sp. (3). Hydrophilidae: *Berosus* sp. (2), *Hydrochara caraboides* (Linné, 1758) (3), *Hydrophilus piceus* (Linné, 1758) (3). **Adephaga** Haliplidae: *Brychius elevatus* (Panzer, 1794) (6). Trachypachidae: *Trachypachus holmbergi* Mannerheim, 1853 (2). Dytiscidae: *Acilius sulcatus* (Linné, 1758) (2). **Megaloptera** *Sialis* sp. (6).

Specimens of *H. natans*, *Microsporus* sp., *I. britskii*, *D. namibensis*, *Hydraena* sp., *Ochthebius* sp., *N. hydrophiloides*, *Catops* sp., and *A. sulcatus* were embedded in Historesin and cut with a glass knife into 3-µm-thick sections on a microtome (Microm, Walldorf, Germany). The sections were stained with methylene blue and acid fuchsin. Larval skins of *Microsporus* sp. were mounted in glycerin on microscope slides.

All sections (58) of *H. natans* were drawn with the aid of a camera lucida-equipped microscope. Subsequently, the drawings were scanned electronically and digitized interactively. The contour lines obtained were used to reconstruct the larval head anatomy on a Silicon Graphics Indigo^2 Extreme computer (Silicon Graphics, Mountain View, Calif., USA) using Alias Studio 7.01 software (Alias Wavefront, Toronto, Canada). Full-size pictures and video animations of the reconstruction can be requested from the authors.

Scanning electronic microscopy (*H. natans*, *Microsporus* sp., *I. britskii*, *Ytu* sp., *D. namibensis*, *T. rhodesica*, and *S. kurosawai*) was carried out with specimens which had been cleaned with warm water, detergent, and ultrasonic sound, dried (critical-point method), and coated with gold.

C. Results

I. Head capsule

1. General appearance (Figs. 1, 2)

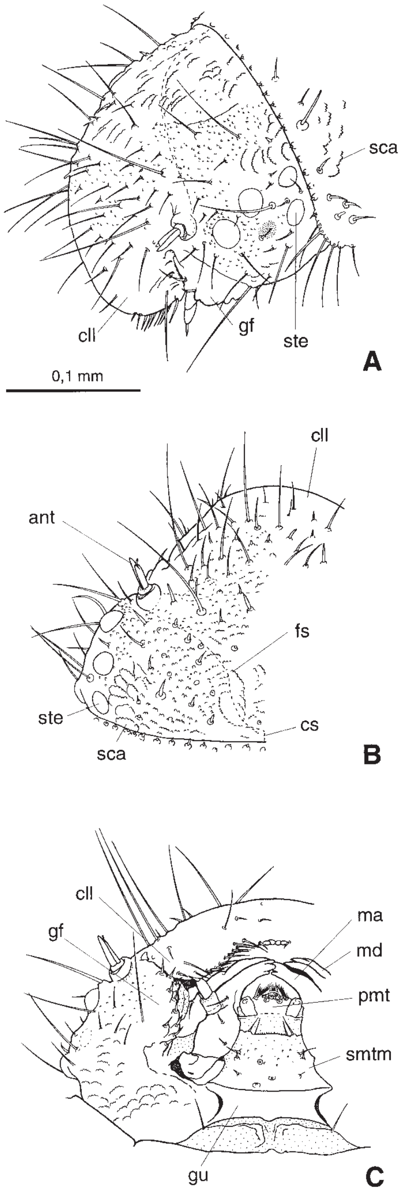

Fig. 1A–C *Hydroscapha natans*, head. **A** Anterolateral view, external structures. **B** Dorsal view. **C** Ventral view. *ant* Antenna, *cll* clypeolabrum, *cs* coronal suture, *fs* frontal suture, *gf* genal fold, *gu* gula, *ma* mala, *md* mandible, *pmt* prementum, *sca* scale, *smtm* submentomentum, *ste* stemma

The head of *H. natans* is subprognathous, distinctly broadened, and large in relation to the body size (head length: 0.2 mm, head width: 0.3 mm, total length: 1.1 mm). It is only slightly compressed dorsoventrally, rounded laterally, and the posterior part is retracted into the prothorax. Distinct paramedian impressions are present on the posterodorsal part of the head capsule (Fig. 2D). The labrum is completely fused with the clypeus. The clypeolabrum extends strongly anteroventrally, almost completely covering the mandibles, and is connected laterally with the anterior margin of a conspicuous triangular genal fold. A clypeofrontal suture is absent, but the frontal suture is fairly distinct and lyriform. The frons is strongly extended posteriorly and the coronal suture is very short. Five stemmata are present, arranged in two

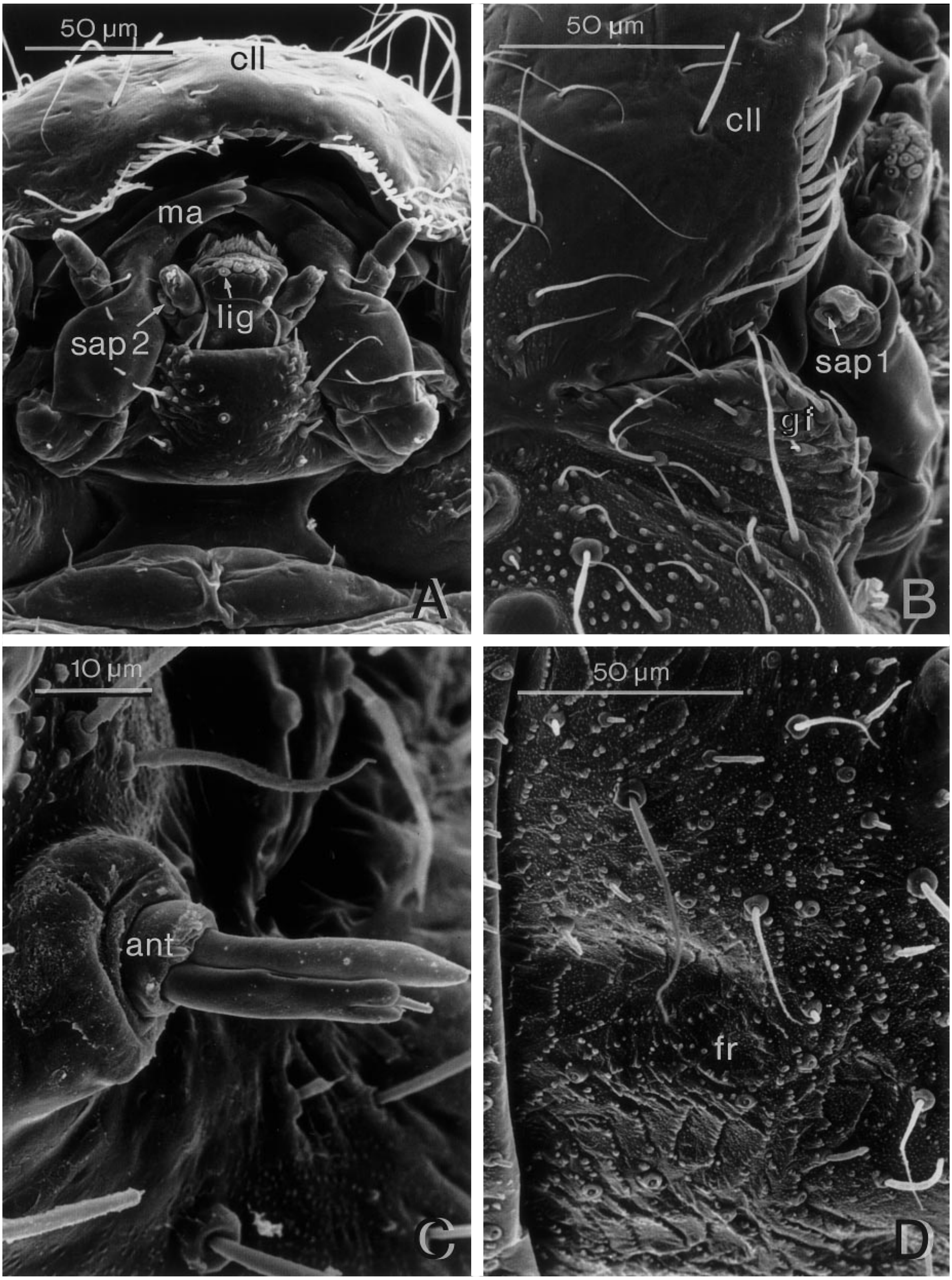

Fig. 2A–D *H. natans*, head, SEM micrographs. **A** Mouthparts, ventral view. **B** Labrum and triangular genal fold. **C** Antenna, posterolateral view. **D** Posterodorsal surface of head capsule. *ant* antenna, *cll* clypeolabrum, *fr* frons, *gf* genal fold, *lig* ligula, *ma* mala, *sap1* sensorial appendage of maxillary palp, *sap2* sensorial appendage of labial palp

horizontal rows of three and two. Stemma 5 is located below the second stemma of the upper row and is only visible as an internal pigmented spot, not as a cuticular elevation (Figs. 1A, 3). The ventral part of the head capsule is much shorter than the dorsal part and the ventral mouthparts are retracted. The maxillary articulatory area (fossa

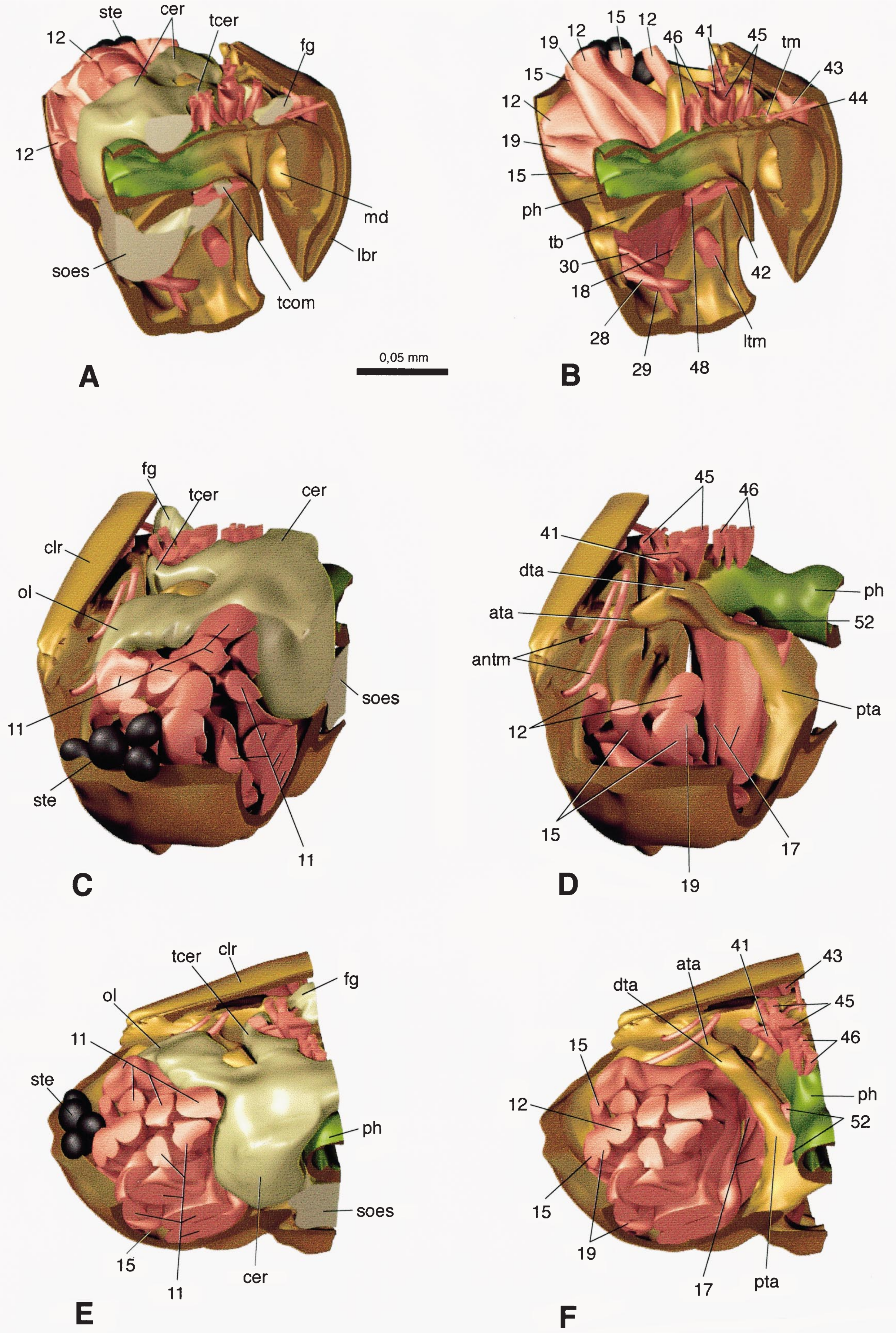
ste
cer
12
tcer
fg
12
md
lbr
soes
tcom
0,05 mm
A
15
12
19
12
46
41
45
tm
15
43
12
44
19
15
ph
tb
30
42
18
28
ltm
29
48
B
fg
tcer
cer
clr
ol
soes
11
ste
11
C
45
46
41
dta
ph
ata
52
antm
pta
12
15
17
19
D
clr
tcer
fg
ol
11
ste
ph
soes
15
cer
11
E
41
43
ata
dta
45
15
46
12
ph
52
15
19
17
pta
F

Fig. 3A–F

maxillaris) is deep, with a well-developed articulating membrane, laterally adjacent with the genal fold. The edge of the fold is very distinct and set with conspicuous, setiferous tubercles (Figs. 1C, 2A,B). The gula is broad and short, sclerotized, inserted between the fissure-like posterior tentorial grooves, and distinctly separated from the submentomentum (Figs. 1C, 2A).

2. Setation and microsculpture (Figs. 1, 2)

The distribution of setae is fairly irregular (Fig. 1B). Most parts of the cuticula are covered with minute tubercles and spines. The interspaces are covered with extremely small cuticular micropapillae (Fig. 2). There are dorsomedian, dorsolateral, and ventrolateral areas with unusual scale-like surface structures with serrate anterior edges. Sensilla campaniformia are present between the cuticular scales (Fig. 2D). The anterior clypeolabral area is smooth.

3. Tentorium (Fig. 3B,D,F)

Strong posterior tentorial arms arise close to the foramen occipitale and are continuous with the postoccipital ridge posterolaterally. The tentorial bridge is unusually broad (Fig. 3A). The anterior arms are strong and round in cross-section (Fig. 3F) whereas the dorsal arms are short, very broad (Fig. 3D), and attached to the dorsal wall of the head capsule by means of fibrillar structures.

II. Appendages and their musculature

1. Labrum (Figs. 1, 2A,B, 3A,B)

The labrum is fused with the clypeus and is strongly extended. The anterior margin is lined with setae and four scale-like, round sensilla are present medially (Figs. 1C, 2A). *Musculature (Table 1).* M. labroepipharyngalis (M. 7) is probably present, but is not clearly identified on microtome sections. M. frontoepipharyngalis (M. 9) is absent.

◀ **Fig. 3A–F** *H. natans*, head, three-dimensional reconstruction. **A** Similar view as in Fig. 1A, sagittal section, dorsal wall of head capsule removed. **B** Head, same view, dorsal wall of head capsule and brain removed. **C** Dorsolateral view, dorsal wall of head capsule removed. **D** Same view, dorsal wall of head capsule, brain, and M. craniomandibularis internus removed. **E** Posterodorsal view, dorsal wall of head capsule removed. **F** Same view, dorsal wall of head capsule and brain removed. *antm* antennal muscles, *ata* anterior tentorial arm, *cer* cerebrum, *clr* clypeal region, *dta* dorsal tentorial arm, *fg* frontal ganglion, *lbr* labrum, *ltm* labial transverse muscle, *md* mandible, *ol* optical lobes, *ph* pharynx, *pta* posterior tentorial arm, *soes* subesophageal ganglion, *ste* stemma, *tb* tentorial bridge, *tcer* tritocerebrum, *tcom* tritocerebral commissure, *tm* transverse muscle, *11* M. craniomandibularis internus, *12* M. craniomandibularis externus, *15* M. craniocardinalis externus, *17* M. tentoriocardinalis, *18* M. tentoriostipitalis, *19* M. craniolacinialis, *28* M. submentopraementalis, *29* M. tentoriopraementalis inferior, *30* M. tentoriopraementalis superior, *41* M. frontohypopharyngalis, *42* M. tentoriohypopharyngalis, *43* M. clypeopalatalis, *44* M. clypeobuccalis, *45* M. frontobuccalis anterior, *46* M. frontobuccalis posterior, *48* M. tentoriobuccalis anterior, *52* M. tentoriopharyngalis (muscular nomenclature: von Kéler 1963). Full-sized pictures and video animations of the reconstruction can be requested from the authors

2. Antenna (Figs. 1, 2C)

The antennae are very short, composed of two antennomeres, and inserted on a distinct cuticular elevation. Antennomere 1 is moderately broad and short whereas antennomere 2 is very slender, with a minute distal sensilla. A sensorial appendage is present. It is slightly longer than antennomere 2. *Musculature (Fig. 3C–F, Table 1).* M. tentorioscapalis anterior (M. 1) is a very thin muscle originating on the dorsal wall of the head capsule, on a small internal cuticular elevation. It inserts anteriorly on the scapal base. M. tentorioscapalis posterior or medialis (M. 2 or 4) is also very thin and originates on the dorsal wall of the head capsule, on an internal cuticular elevation, but inserts posteriorly on the scapal base. The strongly shortened antenna may be slightly turned forward and backward by these thin muscles.

3. Mandible (Figs. 3A, 4C)

The mandible is fairly short, with a moderately flattened, broad basal part. A well-developed, sclerotized mola is covered with rows of minute spines and a small mesal tooth is present immediately anterior to the molar region. There is a narrow distal part with several apical and subapical teeth. A fairly large subapical pseudomola is present which is semimembranous and set with posteriorly directed spines. The outer margin of the mandible forms a distinct angle and two setae are inserted in a shallow excavation of the lateral edge. The anterior seta is modified, with a varying number of minute spine-like protuberances or with a frayed apex in other specimens. *Musculature (Fig. 3A,C,E, Table 1).* M. craniomandibularis internus (M. 11) is the strongest muscle of the head and is composed of ten subcomponents. It arises from extensive parts of the dorsolateral, lateral, and ventrolateral areas of the head capsule and inserts on the adductor tendon. M. craniomandibularis externus (M. 12) is divided into three subcomponents which originate on the dorsolateral and lateral wall of the head capsule and insert on the abductor tendon. These muscles act as adductor or abductor of the mandible respectively.

4. Maxilla (Figs. 1C, 2A)

The maxillary articulatory area and articulatory membrane are well developed and are bordered laterally by a triangular genal fold. The cardo is moderately sized, transverse, laterally rounded and divided into an external and an internal portion by a distinct cuticular furrow. The stipes is moderately elongated. The galea and lacinia are completely fused, thus forming a sclerotized, hook-like mala. The apical part of the mala bears three distinct teeth and the

Table 1 Muscles of the larval head (numbers: von Kéler 1963): *ata* anterior tentorial arms, *dta* dorsal tentorial arms, *hc* head capsule, *l* lateralis, *la* longitudinal arrangement, *m* medialis, *su* subunit, *v* strictly vertical arrangement, + present, ++ unusually strong, * unclear homology, *8* M. frontolabralis, *21* M. stipitogalealis, *33* M. praementopalpalis internus, *19b* M. craniolacinialis with insertion shifted to stipital base. The following larvae were examined by other authors: *Sialis* (Röber 1942), *Corydalus* (Kelsey 1954), *Pterostichus* (Tröster 1987), *Hydrochara* (Moulins 1959), *Helodes* (Beier 1949), *Oryctes* (Crome 1957), *Limnius* (Delachambre 1965), *Cantharis* (Lagoutte 1966). For more detailed information on larval musculature, see Beutel (1993, 1995, 1996)

Muscle	1	2	4	7	8	9	11	12	15	17	18	19a	19b	20	21	22	23
Megaloptera																	
Corydalus	hc	hc	hc	+	+	+	+	+	+	+	+	+	–	+	–	+	+
Sialis	hc	–	hc	+	+	+	+	+	+	+	+	+	–	+	–	+	+
Myxophaga																	
Hydroscapha	hc	hc*	hc*	+?	–	–	+	+	+	+	+	+	–	+	–	+	+
Microsporus	ata	ata	ata	?	–	++	+	+	+	+	+	+	–	?	–	+	+
Adephaga																	
Dineutus	dta	dta	dta	–	–	–	+	+	+	la	la	+	–	–	–	+	+
Trachypachus	dta	dta	dta	–	–	–	+	+	+	la	la	–	+	–	–	+*	–
Pterostichus	dta	dta	dta	–	–	–	+	+	+	la	la	–	+	–	–	–	+*
Staphyliniformia																	
Catops	ata	ata	ata	+	–	+	+	+	+	+	+	+	–	+	–	+	+
Silpha	ata	ata	ata	–	–	+	+	+	+	+	+	+	–	+	–	+	+
Tachinus	dta	dta	dta	–	–	+	+	+	+	+	+	+	–	+	–	+	+
Staphylinus	dta	dta	dta	–	–	–	+	+	+	la	la	–	+	–	–	–	+
Hydraena	ata	ata	ata	?	–	+	+	+	+	+	+	+	–	+	–	+	+
Hydrochara	dta	dta	dta	–	–	–	+	+	+	la	la	–	+	–	–	+	–
Eucinetoidea																	
Elodes	dta	–	dta	–?	–?	–?	+	+	+	+	+	+	–	+	–	+*	–?
Scarabaeoidea																	
Oryctes	hc	hc	hc	+	–	+	+	+	+	+	+	+	–	+	–	+	+
Dryopoidea																	
Lanternarius	hc	–	hc	+	–	–	+	+	+	ve	ve	+	–	–	+	+	–
Elmis	hc	–	hc	+	–	–	+	+	+	ve	ve	+	–	–	–	+	+
Elateroidea																	
Eurypogon	hc	?	hc	–	–	–	+	+	+	ve	ve	+	–	?	?	?	?
Melanotus	hc	hc	hc	–	–	–	+	+	+	ve	ve	+	–	–?	+	+	+
Cantharoidea																	
Cantharis	hc	–	hc	–	–	–	+	+	+	ve	ve	+	–	–?	+	+	+
Derodontoidea																	
Nosodendron	dta	dta	dta	–	–	–	+	+	+	+	+	+	–	+	–	+	+

mesal margin is set with a row of spines. A palpifer is absent. Two palpomeres are present. The proximal one is partly subdivided by a fairly indistinct ventral furrow and the distal palpomere is moderately elongated and laterally adjacent to a fairly large appendage with two openings bearing short cone-shaped sensilla (Fig. 2A). A small, unsclerotized and pointed apical sensillum is flanked by two small, tooth-like structures at its base (Fig. 2A). *Musculature* (Fig. 3A,B,D,E, Table 1). M. craniocardinalis (M. 15), the extensor of the maxilla, has two separate areas of origin, posterodorsally from the head capsule below the origin of M. 19 and laterally from the head capsule between the attachment areas of the lateral portions of M. 12. The insertion is the lateral condyle of the cardinal base. M. tentoriocardinalis (M. 17) is divided into a stronger lateral component and a thinner mesal component. The origin is laterally from the tentorial bridge and the insertion is on the lateral parts of the inner surface and the semimembranous mesal margin of the cardo. This muscle acts as a flexor and levator of the cardo. M. tentoriostipitalis (M. 18) is a strong muscle which originates mesally from the tentorial bridge and laterally from the upper part of the posterior tentorial arm. It inserts onto the mesal edge of the stipes and acts as a flexor and levator of the stipes and mala.

M. craniolacinialis (M. 19) originates posterolaterally from the head capsule, between the attachment areas of the dorsal portions of M. 15 and M. 12 and inserts on the base of the mala by means of a short tendon. It is a flexor and levator of the mala. M. stipitolacinialis (M. 20), which originates laterally on the stipes and probably inserts on the proximomesal margin of the mala (not identified on microtome sections), has an unknown function.

M. stipitopalpalis (M. 22, 23) originates ventrally and laterally from the stipes, but the point of insertion could not be identified on available microtome sections. It probably functions as an extensor and flexor of the palp.

5. Labium (Figs. 1C, 2A)

The mentum and submentum are fused, thus forming a trapeziform submentomentum. This is laterally bordered by the maxillary groove, is sclerotized posteriorly, and

Table 1 (continued)

Muscle	28a	28b	29	30	33	41	42m	42l	43	44	45	46	48	51	52
Megaloptera															
Corydalus	–	+	+	+	+	+	+	+?	2su	?	+	?	?	+	+
Sialis	–?	+	+	+	+	+	+	–	3su	+	+	+	+	+	+
Myxophaga															
Hydroscapha	+	+	+*	+*	+	+	+	–	4su	+	+	+	+	–	+
Microsporus	+	–	+	–	?	+	+	–	++	–	+	+	+	–	+
Adephaga															
Dineutus	+	–	+	+	+	+	–	+	3su	–	+	+	–	+	+
Trachypachus	+	–	+	+	+	+	+	+	3su	–	+	+	–	+	+
Pterostichus	–	–	+	+	+	+	–	+	5su	–	+	–	–	–	–
Staphyliniformia															
Catops	+	+	+	+	+	+	+	–	2su	–	+	7su	+	–	+
Silpha	–	+	+	+	+	+	+	–	+	?	+	2su	?	–	+
Tachinus	+	+	+	+	+	+	+	–	3su	–	+	2su	+	–	–?
Staphylinus	+	–	+	+	–	+	+	–	5su	–	+	+	–	+	+
Hydraena	+	+	+	+	+	+	+	–	2su	–	+	4su	++	–	+
Hydrochara	+*	+	+*	+	–?	+	+	–	3su	–	+	+	+	–?	–
Eucinetoidea															
Elodes	–	–	–	+	–	+	+	+?	+	–	+	2su	–	–	–
Scarabaeoidea															
Oryctes	–	–	+	+	+	+	–	–	3su	+	+	+	+	+	+
Dryopoidea															
Lanternarius	–	–	+	+	–	3su	+	–	5su	–	+	3su	–	–	+
Elmis	–	–	+	+	–	3su	–	–	5su	+	+	8su	+*	–	+*
Elateroidea															
Eurypogon	–	–	+	+	–	2su	–	+	4su	–	+	++	–	–	–
Melanotus	–	–	+	+	–	++	–	++	4su	–	+	3su	–	–	–
Cantharoidea															
Cantharis	–	–	+	+	–	+	–	++	7su	–	+	7su	+*	–	+*
Derodontoidea															
Nosodendron	+	–	+	+	+	++	+	–	2su	–	+	3su	+*	–	+*

is semimembranous along the anterior margin. The prementum is fairly small, mostly semimembranous, and has a distinct, broad ligula with 12 sensorial papillae. One moderately long palpomere is present, with a distinct, hyaline lateral sensorial appendage (Fig. 2A). *Musculature* (Figs. 3B, 4A, Table 1). M. submentopraementalis (M. 28) originates laterally from the hind margin of the submentomentum and inserts ventromedially on a fold of the submentomentum. M. tentoriopraementalis inferior (M. 29) originates mesally from the base of the posterior tentorial arm and inserts ventrolaterally on the anterior submentomentum. M. tentoriopraementalis superior (M. 30) has its origin lateral to M. 28 and inserts laterally on the submentomentum, distinctly anterior to the insertion of M. 29. These three muscles act as retractors of the anterior labium. The function of M. praementopalpalis externus (M. 34) is unclear. It originates ventrally from the prementum, but its insertion could not be clearly identified; it is probably attached to the apodeme of the labial palp. A strong transverse muscle connects the lateral walls of the submentomentum (*ltm*, Fig. 3B), and is a contractor of the anterior labium and hypopharynx.

III. Preoral cavity

1. Epipharynx (Figs. 2A, 3A,B)

The ventral side of the labrum is semimembranous, with a dense anterior field of very fine, short hairs. A distinct median ridge separates lateral hemispherical excavations which closely fit with the upper margin of the mandibles. The cibarium is open and the posterior epipharynx is not fused with the hypopharynx laterally. *Musculature* (Fig. 3B,F, Table 1). M. clypeopalatalis (M. 43) consists of two strong bundles which originate on the anterior part of the clypeal region and insert on the posterior epipharynx. It functions as a dilator of the cibarium.

2. Hypopharynx (Fig. 2A)

The semimembranous, moderately bulging hypopharynx is separated from the dorsal wall of the prementum by a distinct fold. The upper surface is densely set with short hairs (Fig. 2A). *Musculature* (Fig. 3B,D,F). M. frontohypopharyngalis (M. 41) is composed of two closely adjacent bundles. They originate in the posterolateral frontal area, close to the attachment area of the dorsal tentorial arms, insert laterally to the anatomical mouth, and act

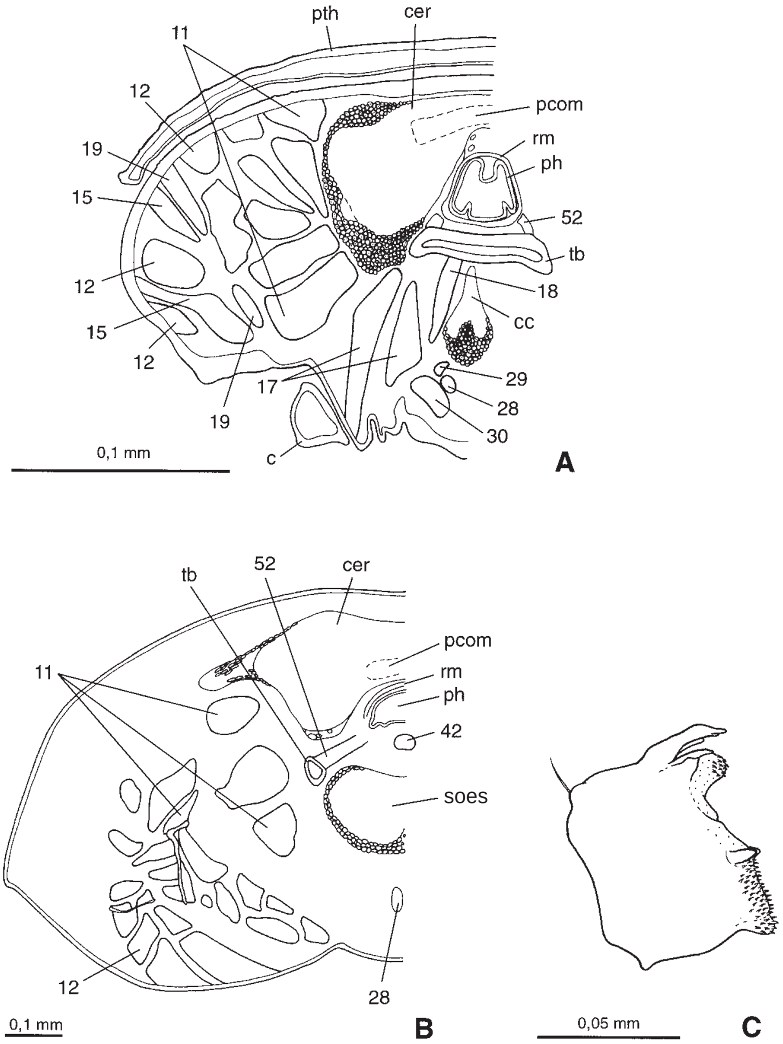

Fig. 4 A, B Cross-sections **A** *H. natans* head, cerebrum with protocerebral commissure. **B** *Acilius sulcatus* head, cerebrum with protocerebral commissure. **C** Mandible, ventral view. *c* cardo, *cer* cerebrum, *cc* circumesophageal connective, *pcom* protocerebral commissure, *ph* pharynx, *pth* prothorax, *rm* ring muscle, *soes* subesophageal ganglion, *tb* tentorial bridge, *11* M. craniomandibularis internus, *12* M. craniomandibularis externus, *15* M. craniocardinalis externus, *17* M. tentoriocardinalis, *18* M. tentoriostipitalis, *19* M. craniolacinialis, *28* M. submentopraementalis, *29* M. tentoriopraementalis inferior, *30* M. tentoriopraementalis superior, *42* M. tentoriohypopharyngalis, 52 M. tentoriopharyngalis posterior

as levators and retractors of the mouth angle. M. tentoriohypopharyngalis (M. 42), a fairly strong, median muscle, originates at the tentorial bridge, inserts ventrally on the posterior hypopharyngeal margin, and functions as a retractor of the hypopharynx.

IV. Pharynx (Fig. 3B,D,F)

The pharynx is moderately wide, with distinct dorsolateral and ventrolateral folds.

Musculature (Figs. 3B,D,F, 6A, Table 1).

M. clypeobuccalis (M. 44), composed of two thin, parallel pairs of muscles, originates on the central clypeal area, and inserts on the pharynx, immediately below the frontal ganglion. It is a dilator of the anatomical mouth. M. frontobuccalis anterior (M. 45) is composed of two moderately sized anterior bundles and two strong posterior bundles, which dilate the anterior pharynx. They originate at the frons, mesal to M. 41 and insert on the dorsolateral fold of the pharynx, posterior to the frontal ganglion and the insertion of M. 44. M. frontobuccalis posterior (M. 46) is composed of several thin bundles, arranged in two longitudinal rows. Its origin is the frons, posterior to M. 41, it inserts dorsally and dorsolaterally on the pharynx, and it dilates the pharynx. M. tentoriobuccalis anterior (M. 48) originates anteromedially from the tentorial bridge together with M. tentoriohypopharyngalis medialis and inserts ventrally on the pharynx, below the insertion area of the anteriormost bundle of M. frontopharyngalis posterior. It functions as a ventral dilator of the anterior pharynx. M. verticopharyngalis (M. 51) is absent. M. tentoriopharyngalis (M. 52) is fairly strong and is composed of two posterior subcomponents and an anterior pair of bundles. Originating laterally from the tentorial bridge (Fig. 3D,F) and inserting ventrolaterally and ventrally on the pharynx, it functions as a ventral dilator of the posterior pharynx.

A dense layer of thin ring muscles is present over the whole length of the pharynx and is used for contraction of the pharynx.

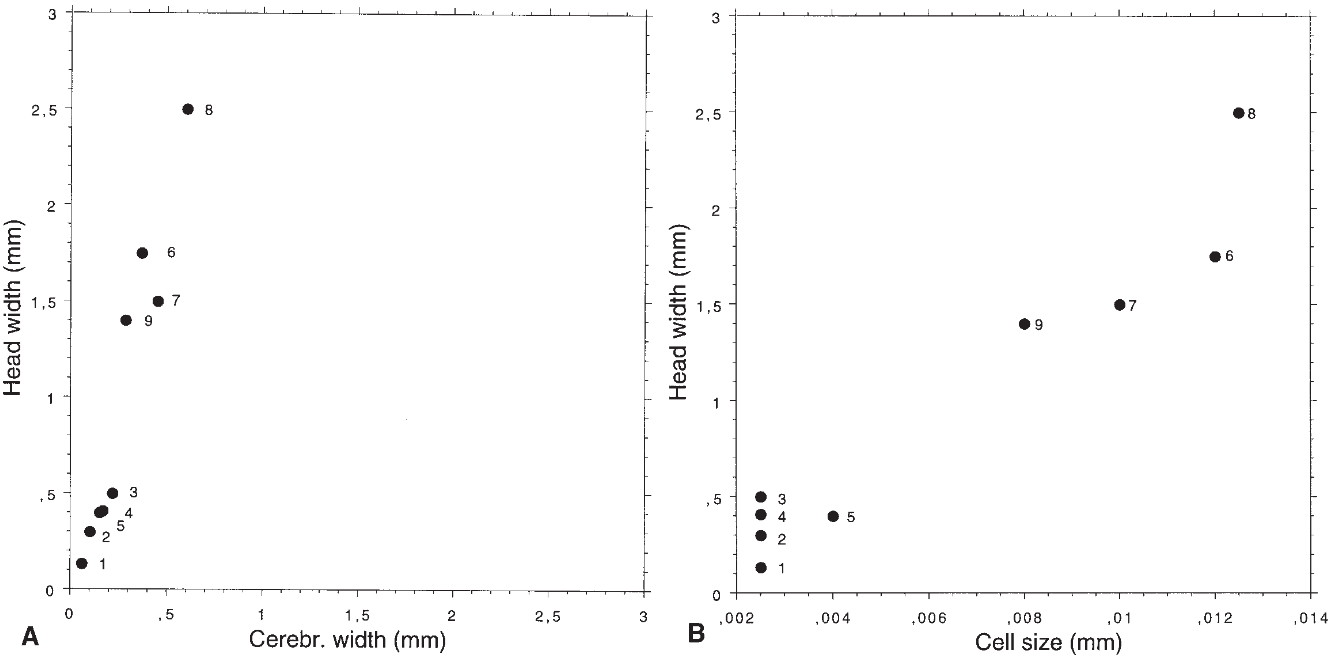

Fig. 5 **A** Head width / cerebral width. **B** Head width / cell size of neurons.*1 Microsporus*, *2 Hydroscapha*, *3 Delevea*, *4 Iapir*, *5 Ochthebius*, *6 Silpha*, *7 Acilius*, *8 Hydrochara*, *9 Staphylinus*

V. Cerebrum and subesophageal ganglion (Figs. 3A,C,E, 5A)

The suboesophageal ganglion is located in the anterior prothorax and the posteriormost region of the head, reaching the tentorial bridge anteriorly. An anterolateral processus reaches the posteroventral part of the protocerebrum. The circumpharyngeal connective is undivided posteriorly and laterally compressed. Anteriorly dividing branches are connected by a tritocerebral commissure between M. tentoriohypopharyngalis and M. tentoriobuccalis anterior (Fig. 3A). The cerebrum is unusually large in relation to body size (see Fig. 5A), strongly reclined, and the posterior globulous part of the protocerebrum is partly shifted into the anterior prothorax. The tritocerebrum is strongly extended anteriorly, curved, and connected with the circumpharyngeal connective. Very large lateral lobes of the cerebrum are separated from the tritocerebrum by broad dorsal tentorial arms (Fig. 3A,C,E).

D. Discussion

I. Characters

1. Size and shape of the head capsule

A transverse, distinctly broadened head is a characteristic apomorphic feature shared by larvae of representatives of the Hydroscaphidae and other families of the Myxophaga. A similar shape of the head capsule was not found in the other larvae examined.

2. Surface structures

Scale-like, serrate cuticular modifications, as found on the posterior head capsule of larvae of *H. natans* (Fig. 2D), are also present in the larvae of *Microsporus* species (Microsporidae), *D. namibensis*, and other species of the Torridincolidae. This is a possible autapomorphy of the Myxophaga. Similar surface structures have not yet been described for other larvae of representatives of the Coleoptera. The functional interpretation is difficult. Larvae of *H. natans* and *D. namibensis* live in hygropetric habitats, whereas larvae of *Microsporus* species live in moist substrate. The scales seem to maintain a visible, thin layer of liquid on the body surface in the larvae of *Microsporus* species (personal observation) and they may be involved in cuticular respiration in these very small larvae. Scale-like cuticular modifications on the abdominal sternites of adults of some species of the Torridincolidae were interpreted as a microplastron (Hinton 1969).

3. Tentorium

An unusually broad tentorial bridge (Fig. 3A,B) is a characteristic, presumably derived feature of the larvae of *H. natans* and larvae of other species of the Myxophaga examined. It is the main attachment area of the very strong M. tentoriocardinalis and M. stipitalis (17, 18; Fig. 3B,D). The tentorial bridge is moderately strong, very thin, or absent in other larvae of representatives of the Coleoptera examined. The origin of M. tentoriocardinalis and M. tentoriocardinalis and -stipitalis is largely or completely restricted to the posterior tentorial arms.

4. Labrum

A unique feature shared by larvae of *H. natans* and *Microsporus* species is the strongly enlarged labrum which is laterally connected with a triangular genal lobe (Figs. 1A, 2B). This semientognathous condition is a synapomorphy of the Hydroscaphidae and Microsporidae. It may have evolved as an adapation to feeding in running water. The mandible and the distal maxillary parts are almost completely enclosed in a preoral working chamber. Small lumps of algae can be removed without being washed away by the current. The presence of characteristic, flattened sensilla at the anteromedian margin of the labrum (Fig. 2A) is probably a synapomorphy of the Hydroscaphidae, Microsporidae, and Torridincolidae. Similar structures are not found in other groups of the Coleoptera.

5. Antenna

The presence of a short larval antenna composed of two antennomeres is a shared derived feature of the Myxophaga. A causal correlation between shortened antennae (Fig. 2C; Costa et al. 1988) and life in a more or less thin film of flowing water appears possible as strongly shortened antennae are also found in the rheophilous larvae of *Brychius elevatus* (Panzer, 1794) (Haliplidae; see Beutel 1993). However, it is evident that shortened larval antennae have evolved as adaptations toward woodboring (e.g., Buprestidae, Callirhipidae; Lawrence 1991) or burrowing in sand (e.g., Limnichidae, Heteroceridae; Beutel 1995) in most cases. It cannot be excluded that shortened antennae of larvae of Myxophaga have evolved in a common ancestor which was burrowing in wet substrate and algae at the edges of streams as do adults of extant species of the Microsporidae and Lepiceridae. The presence of only two very thin antennal muscles (Fig. 3D,F) is probably an autapomorphy of the Hydroscaphidae and correlated with the extreme degree of shortening of the antennae.

6. Mandible

An unusual apomorphic mandibular feature is the presence of a subapical pseudomola in larvae of the Hydroscaphidae and Torridincolidae (Fig. 4C; Costa et al. 1988). This structure may help to break up cell structures of the ingested material. The presence or absence in the extremely small larvae of *Microsporus* species could not be verified. A similar, even though more strongly sclerotized structure has independently evolved in larvae of representatives of the Scaphidiinae (Leschen 1993).

The presence of a well-developed mola and a slender distal part in larvae of representatives of the Hydroscaphidae and Torridincolidae (and Hydraenidae) is probably a plesiomorphic feature. The mandibles of these algophagous larvae are similar to the mandibles of fungivorous larvae of representatives of the Polyphaga (e.g., Leiodidae, Scaphidiinae; Newton 1991). Microphagous and fungivorous feeding habits are probably ancestral for the Coleoptera (Lawrence 1989). A shift of the trophic behavior towards a diet of algae requires apparently little changes to the mandibular structures. This is also in agreement with observations made by Leschen (1993) in larvae of representatives of the Staphylinoidea (e.g., Oxytelinae).

The mandibular muscles and the craniomaxillary muscles of larvae of *H. natans* form a tightly packed complex which apparently allows a well-synchronized operation of both mouthparts (Fig. 3C–F). A similar muscular arrangement has not been described so far for other larvae or adults of representatives of the Coleoptera. This may be partly due to the technical difficulty of three-dimensional muscular reconstruction without computer techniques as applied in this study.

7. Maxilla

Fusion of the galea and lacinia is probably an autapomorphic feature of the Myxophaga. However, the same condition has evolved in larvae of many representatives of the Polyphaga (e.g., Scydmaenidae, Staphylinidae, Cucujiformia partim; Lawrence and Newton 1982; Newton 1991).The undivided distal part of the maxilla is well developed and hook-like. The apex is similar to the apical part of the mandibles. Both structures share the function of collecting algal material.

The complex lateral appendage of the maxillary palp of larvae of *H. natans* (Fig. 2A) is a feature not yet described for any other representative of the Coleoptera. It is distinctly different from the digitiform sensilla found on the subapical palpomeres of larvae of species of the Hydraenidae and Staphylinoidea (Newton 1991; Beutel and Molenda 1997). A chemoreceptory function seems likely, but is not yet supported by evidence.

8. Labium (maxilla 2)

The presence of a lateral, presumably sensorial appendage of the labial palp (Fig. 2a) in larvae of *H. natans* is a derived feature which has not been described so far in other groups of the Coleoptera. Fusion of the mentum and submentum is a derived character state shared with larvae of *Microsporus* species. The presence of papillae on the ligula is probably an autapomorphic feature of the Myxophaga. The latter condition may be related to specialized feeding habits. Similar ligular structures are only found in the algophagous larvae of representatives of the Hydraenidae (Beutel and Molenda 1997), but not in carnivorous aquatic larvae (e.g., species of the Gyrinidae, Noteridae, Hygrobiidae, Dytiscidae, and Hydrophilidae).

9. Preoral cavity

An open cibarium and a moderately bulging, pubescent hypopharynx which is retracted by a well-developed M.

tentoriohypopharyngalis medialis and lifted by M. frontohypopharyngalis (Fig. 3B,D; Table 1) are plesiomorphic features shared by larvae of *H. natans* and larvae of *D. namibensis* (Torridincolidae). A similar condition is found in many non-predacious larvae of representatives of the Polyphaga (e.g., Staphylinoidea excluding Paederinae and Staphylininae, Scarabaeidae, and Byrrhidae; Crome 1957; Beutel 1995; Beutel and Molenda 1997). An elongated, closed prepharyngeal tube, a more or less flattened hypopharynx, a narrow functional mouth, and a gradual reduction of the M. tentoriohypopharyngalis medialis are characteristic features of predacious larvae in several groups of Coleoptera such as Adephaga (see Beutel 1993), Helophoridae (personal observations), Hydrophilidae (Moulins 1959), Paederinae, Staphylininae (see Beutel and Molenda 1997), Histeridae (personal observations), and Cantharoidea (see Beutel 1995). However, a short prepharyngeal tube is also present in the algophagous larvae of *Microsporus* species and in larvae of most species of the Torridincolidae.

10. Pharynx

The pharyngeal pumping apparatus of larvae of *H. natans* is unusually well developed (Table 1). A M. frontobuccalis anterior has not been described for any other larvae in the Coleoptera so far (Fig. 3B; Table 1). Its presence is a possible autapomorphy of the Hydroscaphidae. Mm. frontobuccalis anterior and posterior and M. tentoriopharyngalis are composed of several bundles each (Fig. 3B) as in other larvae of representatives of the Myxophaga. M. tentoriobuccalis anterior is also well developed in larval representatives of the Hydroscaphidae, Microsporidae, and Torridincolidae, whereas it is absent in many other larvae (e.g., Adephaga, Elateriformia, and Nosodendridae; Beutel 1993, 1995, 1996). The absence of M. verticopharyngalis in all larvae of Myxophaga species is probably the result of the posterior shift of the cerebrum. The muscle is present in the larvae of several representatives of the Adephaga (e.g., *Amphizoa lecontei*, and *Trachypachus holmbergi*; Beutel 1993), but is also absent from most larvae of the Polyphaga species examined (Dorsey 1943; Beutel 1995, 1996; Beutel and Molenda 1997; Table 1).

11. Cerebrum

The presence of very large anterolateral lobes of the protocerebrum (Fig. 3C,E) is a possible autapomorphy of the Hydroscaphidae. A similar condition has not yet been described for larvae of other representatives of the Coleoptera. The unusually large relative size of the brain and the strong extension of the tritocerebrum are shared derived features of *H. natans* (Fig. 3A,C,E) and *Microsporus* species (head length: 0.12 mm). However, the brain is almost completely shifted into the prothorax in larvae of representatives of the latter taxon. The unusual configuration of cerebral structures is probably correlated with extremely small size. A less strongly modified brain is found in the larvae of *D. namibensis* (head length: 0.33 mm) and *I. britskii* (head length: 0.26 mm).

II. Miniaturization

It can be assumed that Myxophaga species are derived from larger ancestors. The earliest fossil representatives of the Coleoptera measure about 10 mm or slightly less (e.g., *Sylvacoleus* Ponomarenko, 1963) (Ponomarenko 1969). Catiniidae, which are considered to represent a possible stem lineage of the Myxophaga (Crowson 1981), range in size between 5 and 15 mm as adults (Ponomarenko 1969).

Miniaturization does not only mean small size per se, but also has considerable effects on the anatomy, physiology, ecology, life history, and behavior (Hanken and Wake 1993). Relatively large head size and a very dense arrangement of muscles, tentorium, and other internal structures in larvae of *H. natans* are almost certainly a result of size reduction. Internal structures such as brain, tentorium, and musculature appear to be very tightly packed (Fig. 3A,C,E). This condition is clearly different from that which is found in larger coleopteran larvae such as *Acilius sulcatus* (Fig. 4B), *Dytiscus marginalis* Linné, 1758 (see De Marzo 1979), *Oryctes nasicornis* Linné, 1758 (see Crome 1957), and *Carabus coriaceus* Linné, 1758 (see Beutel 1992). In larvae of these species, fairly large internal areas are not occupied by muscles and other internal structures.

A correlation between body size and the extension of the cuticular scales is likely. The scales are conspicuous in the extremely small larvae of *Microsporus* species, but fairly indistinct in the comparatively large larvae of representatives of the Torridincolidae (body length: 2.1 mm). An intermediate condition is found in the larvae of *H. natans* (Fig. 2D).

Hanken and Wake (1993) observed in vertebrates that the most common effect of miniaturization is reduction and structural simplification. This tendency is not clearly expressed in the larvae of *H. natans*. A correlation between extremely small size (length of head of *H. natans*: 0.2 mm) and the fusion of galea and lacinia and of labial subunits cannot be excluded. However, the overall complexity of the larval head and other structures (e.g., legs) is not decreased compared with larger larvae of representatives of the Coleoptera. The presence of only one labial palpomere in the larvae of *H. natans* is probably not the result of miniaturization. Two palpomeres are present in the extremely small larvae of *Microsporus* species. Loss of one of three antennal muscles and the absence of M. frontoepipharyngalis are correlated with shortening of the antenna and fusion of the labrum, respectively, but almost certainly not with small size. Reduction of the clypeolabral suture is probably the result of an extremely extended and arched labrum. A movable labrum is present in the extremely small larvae of *Microsporus* species.

Negative allometric relationships of size and head structures were described for vertebrates by Hanken

(1983) and Hanken and Wake (1993). A similar effect is apparent in the larvae of *H. natans*: the cerebrum fills nearly all the space between the muscles and endoskeletal parts of the head (see above; Figs. 3A,C,E, 6A). Negative allometric relationships between body size and size of the brain may be a common feature in Coleoptera (Fig. 5A). A brain which is very small in relation to the size of the head capsule is found in large coleopteran larvae such as *Carabus coriaceus* Linné, 1758 (see Beutel 1992), *Dytiscus marginalis* (see De Marzo 1979*), Acilius sulcatus* (Fig. 4B), and *Oryctes nasicornis* (see Crome 1957). An unusually large relative size of the brain is characteristic for adults of *Spanglerogyrus albiventris* which are distinctly smaller than other Gyrinidae (approximately 2,9 mm; Beutel 1989). A medium-sized brain is present in adults of *Gyrinus substriatus* Stephens, 1829 (5–7 mm; Honomichl 1975) and a relatively small brain in adult representatives of the genera *Dineutus* Macleay, 1825 and *Andogyrus* Ochs, 1924, which are among the largest representatives of this family (between 15 and 20 mm; Beutel 1989). Very similar conditions as found in larval representatives of the Myxophaga (i.e., large relative size of brain, reclined protocerebrum; Fig. 3A,C,E) were also described for miniaturized representatives of non-coleopteran groups such as Thysanoptera (see Mickoleit 1963) and Phtiraptera (see Tröster 1990). Sensory, motor, and humoral control functions of the brain and its integration of signal inputs require a certain number of neurons. It is likely that the miniaturization of the brain, therefore, cannot go beyond a minimum limit. Other structures, however, such as muscles could be further miniaturized, for example, by reduction of fiber bundles. A limited minimal number and minimal size of neurons in the cerebrum and suboesophageal ganglion would explain corresponding modifications in taxa which are characterized by very small size, but belong to different orders of insects. The size of neurons is obviously correlated with the size of the head in the larvae of Coleoptera species, but a lower limit seems to be reached in representatives of the Myxophaga. We found the size relation of maximum head width / cerebral cell diameter to be 2.25 mm / 12 µm (= 187) in larvae of *Silpha* sp., 1.4 mm / 8 µm (= 175) in larvae of *Staphylinus* sp. (second instar), 0.4 mm / 2,5 µm (= 160) in larvae of *I. britskii*, 0.25 mm / 2,5 µm (= 100) in larvae of *H. natans*, and 0.13 mm / 2.5 µm (= 52) in the larvae of the *Microsporus* species examined (Fig. 5). A negative correlation between cell size and the morphological complexity of the amphibian tectum mesencephali was postulated by Roth et al. (1994). This does not apply to beetle larvae according to our observations.

Hanken and Wake (1993) found a consistent association between extreme phylogenetic body size decrease and derived morphological features in vertebrates. Myxophaga in general and especially larvae of *H. natans* are characterized by many apomorphic character states. However, it is difficult to evaluate which of these apomorphies can be explained by miniaturization (see above). There is obviously a complex interrelationship between morphological changes, decrease in size, and adaptation to the peculiar habitat and feeding behavior. It is plausible to assume that miniaturization in the Myxophaga has evolved in association with the unusual life style of larvae and adults in the first place. Derived structural features of larvae of Myxophaga, such as serrate cuticular scales (Fig. 2D) or ballon-like spiracular gills (Hinton 1967), are probably only functional when the larvae are very small. However, at the same time, they only make sense in insects which live among algae in running water or at least in wet interstitial conditions at the edges of streams.

III. Conclusions

Larval characters strongly suggest the monophyly of the Myxophaga (excluding Lepiceridae). A distinctly transverse head capsule, scale-like, serrate surface structures, round cuticular sensilla at the anterior labral margin, sensorial papillae on the ligula, and a very broad tentorial bridge are apomorphic character states shared by the Torridincolidae, Hydroscaphidae, and Microsporidae. The strong degree of miniaturization, the distinctly flattened head and body, and the presence of spiracular gills (Reichardt 1973) are probably further synapomorphies of these families. A sister-group relationship between the Hydroscaphidae and Microsporidae is well supported by a very characteristic, unique condition of the larval head. The labrum is strongly enlarged and connected with the genal fold, thus enclosing the mouthparts in a preoral working chamber. Fusion of mentum and submentum, the unusually dense arrangement of muscles, and the peculiar shape and large relative size of the brain are also possible synapomorphies of these families.

Several larval apomorphies found in the Hydroscaphidae + Microsporidae or Myxophaga (excluding Lepiceridae) are correlated with life on rocks with a thin film of water and an exclusive diet of algae. The proposed sister-group relationship between the Hydroscaphidae and Microsporidae suggests that the last common ancestor of the Myxophaga (excluding Lepiceridae) was living in hygropetric habitats. This implies a secondary shift of Microsporidae to the interstitium at the edges of streams. Of course the knowledge of the larval representatives of Lepiceridae is crucial for a final interpretation of the life style of immature stages of the stem species of the Myxophaga.

Miniaturization results in an unusual size and shape of the head and brain and an unusually dense arrangement of muscles in larvae of representatives of the Hydroscaphidae and Microsporidae. A negative allometry between size of head capsule and cerebrum seems to be a general feature in Coleoptera. Other derived features found in larvae of *H. natans* are probably not correlated with miniaturization (e.g., fused labrum, loss of labral and antennal muscles). The overall complexity of the head is not reduced in comparison to larvae of other representatives of Coleoptera. Besides a considerable number of specialized features, Hydroscaphidae and other Myxophaga share several, presumably plesiomorphic larval character states with non-predacious, microphagous larvae of Polyphaga. Only a few changes to the structural features of the mouthparts and musculature result from a shift from fungus feeding to a diet of algae.

The enormous lack of the knowledge of internal structures of immature and adult Coleoptera (e.g., Archostemata) is certainly a serious impediment to a reliable clarification of the interrelationships of higher groups of Coleoptera. Computer techniques as applied in this study will faciliate detailed morphological reconstructions which were so far neglected because of small size or other reasons.

Acknowledgements We are greatly indebted to Dr. E. Arndt (Universität Leipzig), Dr. C. Costa (Museu de Zoologia, Sao Paulo), Dr. S. Endrödy-Younga (Transvaal Museum, Pretoria), Prof. Dr. M. Sato, and Dr. P. J. Spangler (Smithsonian Institution, Washington, D.C.) for the gift of valuable specimens. We also wish to thank Dr. R. E. Roughley. Study of selected valuable specimens was made possible by the Natural Sciences and Engineering Research Council of Canada, operating grant number A0428 held by R. E. R. (Department of Entomology, University of Manitoba). Valuable comments and criticisms by Prof. Dr. O. Kraus and Dr. R. A. B. Leschen are gratefully acknowledged.

References

Beier M (1949) Körperbau und Lebensweise der Larve von *Helodes hausmanni* Gredler (Col. Helodidae). Eos 25: 49–100

Beutel R (1997) Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. Abh Naturwiss Ver Hamburg (NF) 31:1–164

Beutel RG (1989) The head of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga. Zool Jahrb Anat 118:431–461

Beutel RG (1992) External and internal structures of the head of 3rd instar larvae of *Carabus coriaceus* L. (Adephaga, Carabidae). Entomol Basiliensia 15:147–168

Beutel RG (1993) Phylogenetic analysis of Adephaga (Coleoptera) based on characters of the larval head. Syst Entomol 18: 127–147

Beutel RG (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. J Zool Syst Evolut Res 33:145–171

Beutel RG (1996) Study of the larva of *Nosodendron fasciculare* (Olivier 1790) (Coleoptera: Nosodendridae) with implications for the phylogeny of Bostrichiformia. J Zool Syst Evolut Res 34:121–134

Beutel RG, Molenda R (1997) Comparative morphology of larvae of Staphylinoidea (Coleoptera, Polyphaga) with phylogenetic implications. Zool Anz 236:37–67

Britton EB (1966) On the Larva of *Sphaerius* and systematic position of the Sphaeriidae (Coleoptera). Aust J Zool 14:1193–1198

Costa C, Vanin SA, Casari-Chen SA (1988) Larvas de Coleoptera do Brasil. Museo de Zoologia, Universidade de Sao Paulo, Sao Paulo

Crome W (1957) Zur Morphologie und Anatomie der Larve von *Oryctes nasicornis* L. (Col. Dynastidae). Dtsch Entomol Z (NF) 4:228–262

Crowson RA (1955) The natural classification of the families of Coleoptera. Lloyd, London

Crowson RA (1981) The biology of Coleoptera. Murray, London

Delachambre J (1965) Squelette et musculature céphaliques de la larve de *Limnius volkmari* Panz. (Col. Elminthidae). Trav Lab Zool Fac Sci Dijon 65:1–54

De Marzo L (1979) Studi sulle larve dei Coleotteri Ditiscidi X. Anatomia e funzionamento dell'apparato succhiante cibario-faringeo in alcune forme larvali delle subff. Dytiscinae, Colymbetinae, Laccophilinae e Hydroporinae. Entomologica 15: 5–72

Dorsey CK (1943) A comparative study of the larvae of six species of *Silpha* (Coleoptera, Silphidae). Ann Entomol Soc Am 33:120–139

Hanken J (1983) Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae). II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. J Morphol 177:255–268

Hanken J, Wake DB (1993) Miniaturization of body size: organismal consequences and evolutionary constraints. Annu Rev Ecol Syst 24:501–519

Hinton HE (1967) On the spiracles of the larvae of the suborder *Myxophaga* (Coleoptera). Aust J Zool 15:955–959

Hinton HE (1969) Plastron respiration in adult beetles of the suborder *Myxophaga*. J Zool 159:131–137

Honomichl K (1975) Beitrag zur Morphologie des Kopfes der Imago von *Gyrinus substriatus* Stephens, 1829 (Coleoptera, Insecta). Zool Jahrb Anat 94:218–295

Kéler S von (1963) Entomologisches Wörterbuch. Akademie Verlag, Berlin

Kelsey LP (1954) The skeleto-motor mechanism of the dobson-fly *Corydalus cornutus*. Head and prothorax. Cornell Univ Agric Exp Stat Mem 334:1–52

Klausnitzer B (1975) Probleme der Abgrenzung von Unterordnungen bei den Coleoptera. Entomol Abh Staatl Mus Tierkde Dresden 40:269–275

Kukalová-Peck J, Lawrence JF (1993) Evolution of the hind wing in Coleoptera. Can Entomol 125:181–258

Lagoutte S (1966) Squelette et musculature céphaliques de la larve de *Cantharis rustica* Fall. (Col. Cantharidae). Trav Lab Zool Stat Aquic Grimaldi Fac Sci Dijon 70:1–29

Lawrence JF (1989) Mycophagy in the Coleoptera: feeding strategies and morphological adaptations. In: Wilding N, Collins NM, Hammond PM, Webber JF (eds) Insect-fungus interactions. Academic Press, London, pp 1–23

Lawrence JF (1991) Classification. Cupedidae (Archostemata) (= Cupesidae). Micromalthidae (Archostemata). Eucinetidae (Eucinetoidea). Clambidae (Eucinetoidea) (including Calyptomeridae). Dascillidae (Dascilloidea) (including Karumiidae). Byrrhidae (Byrrhoidea) (including Syncalyptidae). Derodontidae (Derodontoidea) (including Laricobiidae, Peltasticidae). In: Stehr FW (ed) Immature insects, vol 2. Kendall/Hunt, Dubuque, Iowa, pp 182–184, 298–302, 364–366, 431–432

Lawrence JF, Newton AF (1982) Evolution and classification of beetles. Ann Rev Ecol Syst 13:261–290

Lawrence JF, Newton AF (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In: Pakaluk J, Slipinski SA (eds) Biology, phylogeny, and classification of coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warsaw, pp 634–797

Lawrence JF, Reichardt H (1991) Torridincolidae (Myxophaga), Microsporidae (Myxophaga) (= Sphaeriidae), Hydroscaphidae (Myxophaga). In: Stehr FW (ed) Immature insects, vol 2, Kendall/Hunt, Dubuque, Iowa, pp 302–304

Leschen RAB (1993) The evolutionary patterns of feeding in selected Staphylinoidea (Coleoptera): shifts among food textures. In: Schaefer CW, Leschen RAB (eds) Functional morphology of insect feeding. Proceedings of the Entomological Society of America, Thomas Say Publications in Entomology, Lanham, Md., pp 59–104

Mickoleit E (1963) Untersuchungen zur Kopfmorphologie der Thysanopteren. Zool Jahrb Anat 81:101–150

Moulins M (1959) Contribution a la connaissance de quelques types larvaires d'Hydrophilidae (Coléoptères). Trav Lab Zool Stat Aquic Grimaldi Fac Sci Dijon 30:1–46

Newton AF (1991) Agyrtidae (Staphylinoidea). Leiodidae (Staphylinoidea) (= Anisotomidae, Liodidae, including Camiaridae, Catopidae, Cholevidae, Colonidae, Leptodiridae). Leptinidae (Staphylinoidea) (including Platypsillidae). Scydmaenidae (Staphylinoidea). Micropeplinae (Staphylinoidea). Dasycerinae (Staphylinoidea). Scaphidiinae (Staphylinoidea). Silphidae (Staphylinoidea). Pselaphinae (Staphylinoidea) (including Clavigeridae). Histeridae (Hydrophiloidea) (including Niponiidae). In: Stehr FW (ed) Immature insects, vol 2, Kendall/Hunt, Dubuque, Iowa, pp 324–341, 353–354

Ponomarenko AG (1969) The historical development of archostematan beetles (in Russian). Tr Paleontol Inst Akad Nauk SSSR 125:1–238

Reichardt H (1971) Three new Hydroscaphidae from Brazil (Coleoptera, Myxophaga). Entomologist 104:290–292

Reichardt H (1973) A critical study of the suborder Myxophaga, with a taxonomic revision of the Brazilian Torridincolidae and Hydroscaphidae (Coleoptera). Arq Zool Sao Paulo 24:73–162

Reichardt H (1976) Revision of the Lepiceridae (Coleoptera, Myxophaga). Pap Avulsos Zool Sao Paulo 30:35–42

Reichardt H, Hinton H (1976) On the New World beetles of the family Hydroscaphidae. Pap Avulsos Zool Sao Paulo 30:1–24

Reichardt H, Vanin SA (1976) Two new Torridincolidae from Serra do Cipó, Minas Gerais, Brazil (Coleoptera, Myxophaga). Stud Entomol 18:211–218

Röber H (1942) Morphologie des Kopfes und des Vorderarmes der Larve und Imago von *Sialis flavilatera*. Zool Jb Anat 67: 61–118

Roth G, Blanke J, Wake DB (1994) Cell size predicts morphological complexity in the brains of frogs and salamanders. Proc Natl Acad Sci USA 91:4796–4800

Tröster G (1987) Skelet und Muskulatur des Kopfes der Larve von *Pterostichus nigrita* (Paykull) (Coleoptera: Carabidae). Stuttg Beitr Naturkde (A) 399:1–23

Tröster G (1990) Der Kopf von *Hybophtirus notophallus* (Neumann) (Phtiraptera: Anoplura). Eine funktionsmorphologische und konsequent-phylogenetische Analyse. Stuttg Beitr Naturkde (A) 442:1–89

Vanin SA (1991) *Ytu cleidei*, a new species of torridincolid from Mato Grosso, Brazil (Coleoptera, Torridincolidae). Rev Bras Entomol 35:573–576