Phylogenetic Relations Within the Hydradephaga (Coleoptera) Using Larval and Pupal Characters

by **S. Ruhnau**

Abstract: Phylogenetic analysis of numerous larval and pupal characters of the families of Hydradephaga and Trachypachidae suggests the following sister-group relationships. *Trachypachus* and Hydradephaga are sister-groups and form the Glabricornia. The Hydradephaga are separated into sister-groups, each comprising three families. One group is formed by the Gyrinidae and their sister-group Noteridae + Haliplidae. The second is composed of Amphizoidae + Hygrobiidae + Dytiscidae, which share numerous striking synapomorphies. Hygrobiidae + Dytiscidae probably form the sister-group of the Amphizoidae; the monophyly of the Dytiscidae is well-founded. Two eventually synapomorphic characters shared by the Glabricornia and the carabid *Omophron* are discussed.

Key words: Coleoptera Trachypachidae, Hydradephaga – phylogeny – larvae – pupae.

I. Introduction

The previous points of view on the phylogenetic tree of the Hydradephaga and their relationships to other adephagan beetles differ considerably (BELL, 1982; ROUGHLEY, 1981; this symposium). Some controversial issues include: Are the Hydradephaga monophyletic, including or excluding the Haliplidae? Are the Trachypachidae the sister-group of the Hydradephaga? Are Noteridae and Dytiscidae closely related?

This contribution summarizes results of my continuing comparative studies of larval and pupal characters. Only "shared derived" characters (synapomorphies after HENNIG, 1981) are regarded as evidence for a common origin (monophyly). Both studies of immatures and of adults are complementary in the understanding and reconstruction of phylogeny, and my results support BURMEISTER's (1976) phylogenetic hypothesis which was based on a detailed analysis of ovipositor structures in female adults.

In this paper, I assume that each hydradephagan family is monophyletic, except for the Dytiscidae. Evidence for the respective monophyly of the other hydradephagan families – as well as illustrations of various preimaginal characters – will be given at a later date.

Material examined in this study includes larvae of *Trachypachus*, and of all hydradephagan families and subfamilies, except those of Suphisinae, Phreatodytinae, and Notomicrinae (all currently included in Noteridae) and of the unusual gyrinid *Spanglerogyrus*; it also includes larvae of 15 carabid genera belonging to 11 tribes (*Omophron, Leistus, Nebria, Carabus, Loricera, Bembidion, Perileptus, Patrobus, Agonum, Pterostichus, Abax, Molops, Chlaenius, Oodes, Harpalus*), and of the cicindelid *Cicindela*; pupal material studied is far more restricted.

I checked all results cited on the material available to me; character states of preimaginal Rhysodidae, of cicindelid and of various carabid pupae, and of first instar larvae of *Trachypachus* and various carabids are derived solely from the literature. Many characters used in this analysis are illustrated in the studies cited. Unless otherwise stated, comparisons with the suggested adephagan ground-plan did not include the Rhysodidae, whose larval structure (BURAKOWSKI, 1975) suggests that they are the sister-group of all other Adephaga.

I designate the 1st, 2nd, and 3rd larval instars as L_1, L_2, and L_3, respectively. Unless otherwise stated, characters refer to one of the larvae. All presumed synapomorphies are successively numbered and indicated in the diagram of the phylogenetic tree (Fig. 1).

II. Phylogenetic analysis

A. Synapomorphies of Trachypachus + Hydradephaga (= Glabricornia sensu BELL [1966]; = Dytiscoidea sensu ROUGHLEY [1981][1]

1. Mandibles with two inner cutting edges enclosing a mesial groove

In all carabids and cicindelids, the prognathous mandibles possess a single cutting edge (THOMPSON, 1979: 218); in rare cases (some *Carabus* spp.) the apical-most part of mandibles shows an indication of a dorsal and a ventral edge. However, in the apparent ground-plan of the group *Trachypachus* + Hydradephaga the mandibles show an open shallow mesial groove between the (new?) dorsal and the ventral cutting edge. In the two L_3 specimens of *Trachypachus holmbergi* Mann. on hand, I observed two distinct, rather thin-bladed, similarly developed mandibular cutting edges enclosing a moderate, but distinct groove; the groove is shallowly continued dorsobasally above the retinacle and dis-

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[1] I use the name Glabricornia because of the law of priority.

appears after a short course[2]. Apparently LINDROTH'S (1960) reference to a single "cutting edge flattened into a thin plate" in his description of L_2 of *T. gibbsi* Lec. is in error.

In various hydradephagan subgroups the open shallow mandibular groove of the above mentioned ground-plan of the Glabricornia is deepened and often developed into a moderately to well-closed channel. My results indicate that closed sucking channels originated several times independently (see descussion below).

An exception among hydradephagan larvae is *Hygrobia* whose mandibles lack the ventral cutting edge and the groove. This absence is surely a secondary simplification: L_1-mandibles of *Hygrobia* still show, in addition to a marked, finely serrate, dorsal cutting edge, a well recognizable ventral cutting edge. In later instars, the ventral edge is replaced by a ventral slope. The simplification of the mandibles can be explained by extreme specializations in food choice (monophagy on tubificid worms; own results, and BALFOUR-BROWNE, 1922) and in feeding mechanism, resulting in the adoption of some of the original functions of the mandibles by other head organs: the prementum transports the worm into the prepharynx, and both mastication and predigestion are displaced caudally into the pharynx.

As my investigations reveal, *Hygrobia* uses its mandibles as grasping hooks to capture a tubificid worm by its end and then draw it onto the gutter-shaped, long, ligula-like process of the prementum. There the end of the worm presumably shows a thigmotactic response, and thus gets stuck by its apically hooked chaetae in the lumen of the transversely riffled, dorsally deeply concave, semitubular premental process. The latter becomes covered dorsally during the subsequent premental retraction by a movable flap, placed basally of the ligula-like process. The worm is then drawn into the masticating pharynx (see comments under character 26), first by the retraction of the highly retractile prementum, and then by the suction effected by the immensely developed pharyngeal dilator muscles. The intake of the worm is accomplished stepwise,

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[2] BOUSQUET (in prep.), who read a draft of this paper, recently informed me that the larva of *Metrius contractus* Eschs. has 2 inner cutting edges on its mandible as well. However, I do not know if *Metrius* shows a mandibular groove comparable to that of *Trachypachus*, and if the mandibles of *Metrius* work similarly to those of *Trachypachus*, with their distal halves against a large hypopharynx-like swelling (cf. under character 5). Metriini + Ozaenini + Paussini are together probably a monophyletic group within the carabids; the possibility of a nearer relationship of this group to the Glabricornia is unclear (see also below appendix on *Omophron*).

(nearly) without the help of the mandibles, but assisted by a special device: the ventral portion of the labrum / anterior epipharynx shows a midventral, longitudinal pinching slit which is only opened by a orally directed pull. When the larva finishes its meal before the whole worm is swallowed the mandibles detach the rest of the worm by strong adduction movements against the ventroanteriorly exposed portion of the labral edge and by some scissor-movements (cf. also Balfour-Browne, 1922).

2. Maxillary cardo riding on a finger-like, flexible cranial process

In all carabids examined, the cardo has its own condylus that fits into a sclerotized socket of the anterior ventral cranial edge; therefore the point of articulation is fixed and immovable (Bengtsson, 1927; Das, 1937: Fig. 29). However, in the Glabricornia the point of articulation is shifted onto a narrow, flexible process, that provides the cardo (and through that the whole maxilla) with a new manœuvrability, thus enabling lateral, dorsal and dorsocaudal displacement of the craniocardinal articulation. This glabricornian condition is apomorphic and must have been derived from the carabid articulation mode, because several other characters indicate that the Glabricornia are closely related to certain carabids and that the "family" Carabidae is not monophyletic (cf. appendix below).

Maxillary movement of the apomorphic condition is easily recognized in a large series of larvae because mouthparts of different individuals are randomly fixed in different postures by fixative; however, the flexible articulating process itself is often turned up dorsally to dorsocaudally in fixed material resulting in a tilted posture of the cardo with visibility of the process restricted to an anteroventral aspect. That is probably why this novel mode of articulation shared by the Hydradephaga and *Trachypachus* has been unnoticed[3]. Lindroth (1960) omitted the cardo in his description of *Trachypachus*.

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[3] Unlike all carabids, the Cicindelidae (*Cicindela)* have a cardo which rides on a reinforced, inflexible, dorsally-bent cranial articulation process. This condition partially resembles that outlined above as characteristic for the Glabricornia; however, several other characters (of the maxilla as well as other body parts; cf. also appendix) clearly suggest that this similarity must have arisen independently. Larval Cicindelidae have retained some plesiomorphies that are not present in all other Adephaga minus Rhysodidae, e.g., the stipito-lacinial muscle (acting there as an expanded depressor of a membranous area mediodorsally on the basal third of the stipes; Ruhnau, unpubl. results). In accordance with Bils (1976), I assume that the Cicindelidae are the sister-group of all other Adephaga (minus Rhysodidae).

As exceptions, the dytiscids *Copelatus* and *Eretes* possess an unflexible, strongly sclerotized cranial articulating process; the lack of the flexibility is surely a secondary feature, and is connected with the modification of their distigalea into a strong, pointing medially "claw". Similarly, the gyrinids have a secondarily hardened cranial articulating process, and a lacinia-like, strong grasping hook on their stipes (cf. under character 10).

In *Amphizoa* and, probably independently developed, in *Hygrobia*, the articulating process is abnormally lengthened though narrow and only weakly sclerotized, and is embedded in a relatively vast membrane between the cranium and the (very) small cardo sclerite; thus their maxillae are markedly retractile. In *Amphizoa*, the cardo appears to be incorporated laterally into the base of the stipes; identity of the cardo is determined by the presence of (elastic) boundary lines between the cardo and stipes, of the typical though inconspicuous cardo seta (coded MX_1 by Bousquet & Goulet, 1984), and of the cardo abductor muscle (cf. character 23). Higher magnification reveals that the mediodistal angle of the rectangular cardo sclerite is slightly covered by the basal stipital edge, and that the mediobasal angle of the cardo is united in a bridge-like manner with the stipes. In *Hygrobia*, the cardo is seemingly not reached by the indistinct, narrow, long cranial articulating process, which disappears as a recognizable sclerotization halfway-up the especially long distance between the ventral cranial edge and the cardo sclerite (cf. character 23).

3. Size of larval mesothoracic spiracles no longer larger than that of normal lateral abdominal spiracles (a). Pupal mesothoracic spiracles presumably closed (b)

The relative size of the mesothoracic spiracles in adephagan larvae seems to be correlated with that of their pupae suggesting a combined discussion of (a) and (b).

In rhysodids, cicindelids and carabids, the larval mesothoracic spiracles are distinctly larger than abdominal spiracles (Burakowski, 1975; van Emden, 1935; Bengtsson, 1927; this situation apparently is an adephagan ground-plan character. Larvae of *Cicindela* and many carabids also have spiracles of abdominal segment I enlarged in comparison to other posterior abdominal spiracles. Except for some trechine carabids (Jeannel, 1940), the pupal mesothoracic spiracles also are

widely open, and usually larger than those of the abdomen (Paulian, 1941: 332; Blunck, 1924: 786).

In contrast, the larval mesothoracic spiracles of *Trachypachus, Amphizoa, Hygrobia,* dytiscids, and haliplids are of the same size as the abdominal (lateral) ones; gyrinid and noterid larvae possess only reduced, unfunctional mesothoracic spiracles (Hinton, 1947). Concerning the Hydradephaga, I consider here only the L_3-conditions; in L_{1-2}, all spiracles are closed (character 6 below), except for spiracles VIII if these are shifted terminally.

Pupal mesothoracic spiracles of the hydradephagan families are presumably regularly closed (cf. Blunck, 1924: 786 for dytiscids); however, observation of this character is sometimes difficult in small pupae. The pupal stage of *Trachypachus* is unknown; however, the small mesothoracic spiracles of its larva indicate that trachypachid pupae probably have closed mesothoracic spiracles (as seen in Hydradephaga). If this assumption is eventually proven false, the closed mesothoracic pupal spiracles would presumably be a synapomorphy of the Hydradephaga, without *Trachypachus.*

4. Strong reduction in size of the 3 subapical setae on antennomere IV

Rhysodids (Burakowski, 1975), cicindelids, and carabids possess a crown of three long subapical "primary" setae (i.e. already present in L_1) on their last antennal segment, coded as AN_4, AN_5, and AN_7 by Bousquet & Goulet (1984), which is also true of the unusual carabid *Metrius* (Bousquet, pers. comm.). These three setae are strongly reduced in size in *Trachypachus* (Lindroth, 1960), and even absent in all Hydradephaga (see character 8). Convergently, some *Carabus* spp. show these setae moderately short.

Directly on the apex of antennomere IV, rhysodids, cicindelids and carabids have a group of 4 styliform sensilla. One of them is long in most carabids, and is coded as "AN_6" in the notation system, because it ressembles a "true" seta; the other three sensilla are short. However, AN_6 is short in *Metrius* (Bousquet, pers. comm.), and in *Trachypachus.* In the Hydradephaga (except Haliplidae), AN_6 and the three other sensilla are very short, minute, or absent. In the Haliplidae, AN_6 is long (Jaboulet, 1960). Additionally, in certain *Haliplus* spp., one of the three other ancestral apical sensilla is evident as a very fine "seta", closely adjoining to the long AN_6: it is short in *H. immaculatus* Gerhardt and somewhat longer in *H. lineaticollis* (Marsham).

Note: The Trachypachidae comprise two cool-temperate adapted, oligobasic genera, *Trachypachus* (Holarctic region) and *Systolosoma* (Chile). The latter genus seems to show a few adult characters more similar to hydradephagan ones than *Trachypachus* (ROUGHLEY, pers. comm.); however, because the preimaginal stages of *Systolosoma* are unknown, I cannot discuss the hitherto accepted monophyly of this family.

B. Synapomorphies of the Hydradephaga

5. Prementum moved by three instead of two paired retractor muscles

In *Cicindela,* in all carabids at hand, and, most probably , also in *Trachypachus,* only one dorsal and one ventral premental retractor are present; both originate on the posterior tentorial arm (ANDERSON, 1936, Pl. 2, B: *Cicindela,* "ventral adductors" and "retractor of hypopharynx"; DAS, 1937, Fig. 29: *Carabus;* DORSEY, 1943, Figs 20, 22: *Amara;* TRÖSTER, 1983: *Pterostichus*) [4]. These findings for *Trachypachus* are based on the study of two specimens fixed in alcohol; reexamination of material with well-preserved musculature is needed.

In all hydradephagan families the prementum is moved by three different pairs of retractor muscles. Additionally to the mentioned dorsal and ventral retractors a new median ventral retractor is present, which originates from the submental or gular region: in gyrinids, noterids, and the haliplid *Peltodytes* it arises anteriorly to, and in *Amphizoa, Hygrobia,* and all dytiscids posteriorly to the metatentorial pits (ANDERSON, 1936, Pl. 2, D: *Amphizoa;* DE MARZO, 1979: all dytiscid subfamilies; DORSEY, 1943, Figs 27, 28, and NOARS, 1956: gyrinids; first recorded in *Hygrobia* and various noterids). In *Dytiscus* the median ventral retractor pair is secondarily very thin, which is why it was overlooked by SPEYER (1922) and ANDERSON (1936, Pl. 2, E). In haliplids, these median muscles are absent in *Haliplus lineaticollis* (Marsham) (BEUTEL, 1982) and other species of this genus (the single exception among hydradephagans to my knowledge), but they are clearly present in *Peltodytes.*

I interpret the hydradephagan character state "three retractors present" as apomorphic within the Adephaga, because various other

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[4] Unlike all other carabids, *Loricera* has secondarily well-separated metatentorial pits and a broad gular region; in this genus, the origin of most or all muscle bundles of the strong ventral tentorio-premental retractor is shifted mediocaudally from the base of the metatentorial arm onto the gula.

larval characters (a part of them is discussed in this paper) suggest that the so-called Carabidae are non-monophyletic, and that *Trachypachus* + Hydradephaga are closely related to a subgroup of the carabids. Supposing that the feature "three retractors present" was a simple plesiomorphy within the Adephaga, this feature would be the unique larval character known to me in which the Hydradephaga would be more primitive than *Trachypachus,* all carabids, and cicindelids.

It is not clear how the new median ventral paired premental retractor originated. Either it could be the result of a secondary reactivation of those ancestral genes – having been unfunctional for a long period – responsible for the submento-premental muscles (no. 19 in DAS, 1937) which are present in various holometabolous larvae, even also in some polyphagan beetle larvae (cf. DAS, 1937: e.g. *Tenebrio* and elaterid *Agriotes* possess a similar pattern of three premental retractors). Or, one of the two paired premental retractors present in *Trachypachus,* carabids, and cicindelids could have "split". In this case it is possible that the median ventral retractor could have split off from the old lateroventral retractor, or the old lateroventral muscle could have migrated toward the median line and the old dorsolateral retractor gave rise to a new ventrolateral pair of muscles. Comparative studies of the corresponding nervous supply might perhaps clear up the matter.

The acquisition of a third premental retractor seems to be correlated with the distinct separation of the metatentorial pits in the ground-plan of the Hydradephaga. Unlike all other Hydradephaga, the Gyrinidae have approximate metatentorial pits, thus resembling the ground-plan condition of all Adephaga (incl. Rhysodidae?) with approximate pits, seen in cicindelids, *Trachypachus,* and all carabids (except for *Loricera*). However, I interpret the gyrinid condition as having secondarily arisen for many reasons.

Further, certain carabids, *Trachypachus,* and many Hydradephaga show a distinct hypopharynx-like swelling dorsally on their mentum (a presumed synapomorphy of these groups, cf. appendix). Though it is placed posteriorly to the dorsal premental sclerotic area, its relative position (and shape) is dependent on the respective action of the premental retractors. The swelling is clearly present e.g. in *Nebria* (SPENCE & SUTCLIFFE, 1982), *Omophron* (LANDRY & BOUSQUET, 1984), *Carabus* (BENGTSSON,

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[5] As suggested by other data, the "hypopharynx" may also be found in *Notiophilus, Opisthius,* and *Metrius;* however, it is primarily absent in cicindelids, Harpalinae s.l., *Loricera,* and, according to BENGTSSON (1927), in Elaphrini *(Blethisa).*

1927), and *Leistus*[5]; it is especially large and high in *Trachypachus*, and is well-developed e.g. in *Peltodytes* (somewhat less so in other haliplids), *Noterus, Gyrinus,* and *Copelatus.* Was the acquisition of an additional, third premental retractor associated with the transition to an aquatic mode of life? It could be that there was higher demand on labial movements in the water-inhabiting larvae so that the hypopharynx-like swelling serve to seal the front of the prepharynx during various actions of the prepharynx and mouthparts under water.

6. Spiracles in L_{1-2} very small, and closed except during ecdysis

This reductional feature of the Hydradephaga is an adaptation to the aquatic mode of life, and occurs convergently in many other aquatic holometabolous larvae (HINTON, 1947). If one regards this reduction without regard to other derived characters, it could be either a synapomorphy or the result of convergence. In those groups where the spiracles VIII become shifted into the terminal position (i.e. noterids, *Amphizoa*, dytiscids; cf. character 32), these spiracles rest open and functional even during the early instars.

7. Loss of the pygopodium (pseudopod)

Trachypachus, Cicindela[6], and most carabid tribes possess, at the end of larval abdominal segment X, a protrusible and retractile membranous, usually lobed tube which is called pygopodium, pseudopod, or anal lobes, and is mostly armed with many minute hooks (microcrochets). According to KEMNER (1918) the pseudopod corresponds to the altered remaining portion of the old segment XI.

The pygopodium is secondarily absent in all Hydradephaga. Only the Gyrinidae show their well-known 4 terminal hooks in the same position, which I believe represent secondarily enlarged remnants of the micro-hooked vestiture of the ancestral pseudopod.

8. Absence of true setae on antennomere IV (cf. character 4)

9. Loss of the fragmentated sclerite pattern of the carabid-type on ventral abdomen

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[6] THOMPSON (1979) noted for cicindelids "anal lobes absent", however, I observed a distinct, though relatively short, simple pseudopod in living and fixed specimens of *Cicindela.*

Carabids, cicindelids, and *Trachypachus* show a characteristic pattern of several distinct sclerites on the ventral and pleural sides of each abdominal segment (especially on segments I–VII); the sclerites are separated from one-another by membranes (Bousquet & Goulet, 1984, Fig. 24; Thompson, 1979; Lindroth, 1960). This pattern of separate sclerites is absent in all Hydradephaga. But, presumed secondary development of ventral abdominal sclerites is evident in haliplids, noterids, and some dytiscids; however, there is never a fragmentated pattern. The fragmentated sclerites are only slightly sclerotized in the carabids *Omophron* and *Leistus,* and in *Trachypachus.*

C. Synapomorphies of Gyrinidae + Noteridae + Haliplidae

10. Loss of the abductor muscle of the maxillary stipes

In all other adephagan groups the stipes is moved by two muscles: one outer, often dorsolaterally inserting abductor muscle, originating from the sublateral ventral cranial area, and one inner muscle, the adductor of the stipes, originating from the posterior tentorial arm. However, all gyrinids, haliplids, and noterids studied do not have the outer of these muscles, the stipital abductor (Noars, 1956; Beutel, 1982; own results).

The gyrinid maxillae and correlated mouthparts are remarkably specialized. The cardo is exceptionally elongate (its length about 1.2 to 2.5 times that of stipes), and the shortened stipes is capable of extensive adduction movement; it bears a fixed long, strong, compressed lacinia-like "claw". Thus the maxillae are adapted to assist the mandibles in squeezing the prey dorsally (!) against the medially broadly depressed labral edge by means of the lacinia-like claws. Because of this novel mode of seizing the prey (together with predigestion and suction through the mandibular channels), the labial prementum ceased functioning as a lower lip, allowing its complete median bifurcation. The novel pair of premental palp-like articles each moved by the three premental "retractors" (cf. character 5), improves the manœuvrability of the actual two-segmented palps, movable in turn by the palpal abductor muscle (cf. Noars, 1956).

11. Brain elongated and extended far rearward, shaped like two parallel water drops wich are connected at the thickest parts

This very characteristic shape of the supraoesophageal ganglion is unique among Adephaga. The brain of the other hydradephagan and geadephagan larvae is transversely and somewhat dorsally extended in the middle of the head (NOARS, 1956; BEUTEL, 1982; DE MARZO, 1979; BEIER, 1927; own results).

12. Loss of the egg-bursters on the head of L_1

Although BERTRAND (1928: 192) reports egg-bursters (frontal hatching tubercles) as present in noterid L_1, I can detect no trace of them on L_1 of *Noterus crassicornis* (Müller) by light and scanning electron microscopic examination. They are lacking in haliplids and gyrinids (BERTRAND, 1972; SAXOD, 1964). However, in cicindelids, most or all carabids, *Trachypachus* (BOUSQUET & GOULET, 1984), *Amphizoa, Hygrobia*, and all dytiscids, egg-bursters are present (in *Cybister* only minute ones).

13. Pupae: Complete loss of urogomphi

In haliplids and gyrinids (BERTRAND, 1972; SAXOD, 1965), and, first recorded here, in *Noterus* (pupae of other noterid genera are unknown), the pupal urogomphi are absent. However, they are present without exception in the three other hydradephagan families, and even conspicuously elongated compared with the short urogomphi seen in carabids (cf. character 34). Rhysodids (BURAKOWSKI, 1975) and cicindelids lack pupal urogomphi.

From this paper I call the dorsal outgrowths of segment IX in beetle larvae and pupae urogomphi in preference to "cerci". There are hardly any grounds for their derivation from true cerci, and even from segmental limbs at all (cf. CROWSON, 1981: 119f.; HENNIG, 1981: 301, 303).

14. Pupae: Peristigmatic glands probably lost

However, carabids, dytiscids, *Hygrobia,* and presumably *Amphizoa* possess segmental glands close to their spiracles, each with a small or minute opening to the exterior (BRANCUCCI & RUHNAU, 1985; additionally, I regularly found them in numerous dytiscid genera of all subfamilies).

15. Pupae: Tibio-tarsal joint of hind legs straightened, and tibiae and tarsi converge posteroventrally

In haliplids and *Noterus,* the hind legs meet each other only at the tips of the metatarsi. In known gyrinid pupae the hind legs are so short that they do not meet (BERTRAND, 1972); in the unknown pupal *Spanglerogyrus,* whose adults have much longer hind legs than other gyrinids, the hind leg posture might look like in haliplids and noterids.

The plesiomorphic hind leg posture is seen in *Amphizoa* (KAVA-NAUGH, pers. comm.), *Hygrobia,* dytiscids, and many carabids: the tibio-tarsal joint is flexed, and the metatarsi are paralleled in the ventral midline, often adpressed (and seemingly glued by dried ecdysial fluid) to one-another. (Note that a fixative solution sometimes alters the natural posture of pupal wings, legs, etc.)

D. Synapomorphies of Haliplidae + Noteridae

16. Prepharynx with at least 7 transverse cibarial compressor muscles

The prepharynx in *Haliplus* and *Noterus* is comparatively long, distinctly crescentic in cross-section, and is constricted by the contraction of an increased number of transverse dorsal prepharyngeal compressors. *Haliplus* has 7 very thin compressors (BEUTEL, 1982). *Noterus,* showing the same number of (better developed) transverse muscles, has in the posterior half of its prepharynx a few additional muscle fascicles which cross another obliquely, placed just below the normal transverse compressors. The compressors alternate with a series of dorsal dilators. In *Haliplus* these dilators have transverse, narrow, serially arranged submedio-dorsal origins on the clypeal region, and insert, by pairs, with joint attachments along the midline of the prepharynx. In *Noterus* these paired dilators have relatively far-anterolateral origins on the clypeal region, and insert in two ranks submedially along the prepharynx (which is broader than in *Haliplus*). Anterior to those series of compressors and alternating dilators, both families additionally show two pairs of "vertical" dorsal dilators arranged in a transverse line.

The plesiomorphic number of cibarial compressors apparently is 3–4. *Orectochilus* (NOARS, 1956) and *Gyrinus* show three slender compressors in the posterior half of the elongate prepharynx. Carabids, e. g. *Pterostichus* (TRÖSTER, 1983), *Omophron, Carabus, Nebria, Leistus,* and *Loricera,* have four compressors in the posterior half of the prepharynx; however, the two intermediate compressors are (very) thin. In *Nebria,* only the fourth compressor, placed at the end of the

prepharynx, is well-developed; SPENCE & SUTCLIFFE (1982), who apparently did not notice the presence of the three very thin preceding compressors, call the fourth compressor, according to its function, as "unpaired closer of the mouth". (The prepharyngeal muscles in the two alcohol-fixed specimens of *Trachypachus* on hand are poorly preserved and thus not clearly distinguishable.)

In the Gyrinidae, the prepharynx is elongate as in their probable sister-group Haliplidae + Noteridae; however, the constriction of the anterior parts of the prepharynx is achieved in a different way. The haliplid and noterid prepharynx shows the increased number of transverse compressors, and this series already begins within the anterior part of the prepharynx. In gyrinids, the long anterior part of the prepharynx is markedly trough-shaped in cross-section, and is endowed with special, extended filtering devices; it is compressed by a series of muscles which insert far laterally on the upper side of the prepharynx, and originate dorsally on the clypeal region close to the midline. These muscles, which function as compressors, are, in the morphological sense, modified anterior dorsal cibarial dilator muscles (cf. NOARS, 1956: "constricteurs de l'atrium").

However, dytiscids (DE MARZO, 1979), *Hygrobia,* and *Amphizoa,* show a completely different situation. There the characteristically short and transverse prepharynx is covered with only one compact, large mass of compressor muscle, through which a group of thin dorsal cibarial dilator muscle bundles is running on both sides of the midline; correspondingly, the pharynx itself is long and increases in importance for sucking and pumping tasks (cf. characters 25 and 26).

17. Only one paired trachea cephalica enters the head from behind

This apomorphic feature probably is unique among adephagan larvae. I observed the plesiomorphic presence of two pairs of tracheae cephalicae in *Cicindela,* various carabids and all hydradephagan groups except of haliplids and noterids: the two head trunks of each side arise from a common trunk cranially of its junction with the mesothoracic spiracular trachea (cf. ALT, 1912, for *Dytiscus*). (*Trachypachus* which was not dissected for this special test by reason of limited material presumably shows the same conditions.) In *Hygrobia,* which unusually possesses two pairs of (proportionally thin) principal longitudinal tracheal trunks running the length of the body (probably a secondary[7] condition,

correlated with the novel mode of respiration by means of ventral thoracic and abdominal gills, and with a marked increase in volume of the body, especially in its anterior half), the two head trunks of each side simply represent the continuation of the respective principal body trunks.

Further, my dissections reveal that the adults of haliplids and noterids show about the same unusual modification of the tracheal head supply as their larvae. Adults of *Cicindela*, various carabids examined, and all hydradephagan groups except of haliplids and noterids possess two paired, well-developed principal head trunks, called trachea cephalica superior and tr. ceph. inferior; additionally, in *Gyrinus* (and possibly other gyrinids) a third, proportionally thin ventral head trunk is present.

However, in adults of *Haliplus* and *Peltodytes* the trachea cephalica superior is thin. In adults of noterids examined (*Noterus*, *Canthydrus*, *Suphisellus*, and *Hydrocanthus*), the trachea cephalica superior obviously is lacking; they have only one paired principal head trunk which enters the head directly laterally along the oesophagus. It may be noted that other (even small-sized) water beetles (members of dytiscid Hydroporinae) constantly show two well-developed pairs of tracheae cephalicae.

18. Midgut straight throughout its length

This similarity is surprising considering the different nutrition in the two families. Haliplid larvae ingest the contents of algae (secondary strict algophagy), while *Noterus* (and presumably similarly other noterid) larvae feed on the body contents of chironomid larvae and (very) small oligochaetous worms, using preoral predigestion and a special filter placed anteriorly in the prepharynx.

In all other hydradephagan (and presumably generally in adephagan) larvae, the posterior part of the comparatively longer midgut forms a hairpin bend or loop, so that a midgut section running in cranial direction is present.

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[7] Other adephagan larvae examined show 1 pair of longitudinal trunks, except of the Cicindelidae (*Cicindela)* where all spiracles are connected by 2 pairs of main tracheae; in rare other cases, two successive spiracles are connected by two tracheae instead of one: in the carabid *Patrobus* (between abdominal spiracles I and II) and in the dytiscid *Copelatus* (between those of mesothorax and abdominal segment I).

19. Ventral mandibular articulation shifted onto a dorsomedially inwards bent, narrowing lobe

That is why the maxilla of haliplids and noterids conceals the ventral mandibular condylus in the ventral aspect of head. Only in the more derived noterids (*Hydrocanthus* and Suphisini), which show a secondarily very broad and comparatively flat head shape and a less broad mandibular base than other noterids, is the ventral mandibular articulation again visible in ventral aspect, though being shifted as described. I have not seen such a dorsomedially shifted ventral mandibular articulation in any other examined adephagan larvae.

The dorsomedially inwards bent, narrowing lobe and its thin, stiff, bar-shaped prolongation separate the mandibular and maxillary cavities of the head capsule. This feature as such is only a certain modification of a structure which is part of the ground-plan of all adephagan larvae (probably except of Rhysodidae) (cf. e. g. NOARS, 1956, Fig. 3: "barre ventrale à la mandibule, fenestra mandibularis, and fenestra maxillaris"). A strengthened bar between the base of the mandible and the maxilla ("inter-mandibulo-maxillary bar") is present in *Cicindela,* all carabids examined (sometimes more or less shortened, e. g. in *Patrobus* and *Agonum*), and all Glabricornia; in *Omophron* and *Amphizoa* it is modified into a firm separation wall, and in *Hygrobia* it is indistinct and semimembranous (see also below under appendix).

20. Only two of the ancestral four labral sensory pegs present, shifted medially closely side by side

In cicindelids, carabids, *Trachypachus* (BOUSQUET & GOULET, 1984: coded as FR_{10-11}), as well in gyrinids, there are nearly always four (= two pairs) special, anteriorly projecting setae or pegs arising on the edge of the labrum (cf. SPENCE & SUTCLIFFE, 1982; ALTNER & BAUER, 1982). As exceptions, the carabid *Omophron* obviously has three pairs of such pegs (BOUSQUET, in litt.; LANDRY & BOUSQUET, 1984: Fig. 2), and *Loricera* has lost these structures completely.

However, in *Haliplus, Noterus,* and *Hydrocanthus* there are only two such pegs (= 1 pair): they are small, cylindrical, and apically rounded, and are visible in front view, medially placed, adjacent and parallel to each other, comparatively ventrally directed, and sunk to some extent into the cuticula. They probably represent the inner pair of the ancestral two pairs, coded as FR_{11}. (As scanning electron micrographs reveal, *Noterus* has submedially in a fully ventral position, concealed by

the labral edge, a very small, acute, spine-shaped seta pointing post-eromedially which eventually corresponds to the modified and shifted remainder of the outer paired peg FR_{10}.)

In Amphizoidae, Hygrobiidae, and Dytiscidae, the number of labral pegs is strongly multiplied (character 27 below).

Concerning *Haliplus,* DE MARZO & NILSSON (1986: Fig. 9) interpret two longer, comparatively dorsally situated hair-shaped setae on each anteriorly projecting sublateral lobe of the cranial fore-edge as being the exact counterparts of those four labral – they call them clypeal – pegs seen in gyrinids and illustrated by their figure 8. In my view these long anterodorsal setae of *Haliplus* actually correspond to those setae coded by BOUSQUET & GOULET (1984) as FR_{8-9}. The two specialized, anteriorly pointing pegs of *Haliplus* are very small, and placed medially on a somewhat deeper level on the strongly downward sloped, broad median excavation of the cranial fore-edge; they are therefore not visible on the micrograph given by DE MARZO & NILSSON.

21. Cranium without ventral ecdysial line

HINTON (1963) showed that, in many larval Holometabola, ecdysial lines, previously often confused with gular sutures, are present on the ventral surface of the cranium. In the great majority of the Adephaga, there is a single, straight, medioventral preformed line of weakness from the occipital foramen to the base of the more or less membranous mentum (most carabids, *Trachypachus, Amphizoa,* and all dytiscids except of Laccophilinae and Hydroporinae); at each ecdysis this line splits. SPENCE & SUTCLIFFE (1982, *Nebria*) and THOMPSON (1979: 219, *Amphizoa*) take this line for a median gular suture. In *Cicindela* this line is distinct only up to the "connate" metatentorial pits, and in *Scarites* it is forked anteriorly (HINTON, 1963: 43); in *Loricera* with its broad submentogular region (cf. footnote to no. 5) the line seems to be absent (check on shed cuticles is needed).

In haliplids and noterids, a ventral ecdysial line is absent, and the head is not split below at larval-larval or larval-pupal ecdyses. (Shed cuticles of *Noterus* rarely show a minute, irregular ventral rent at the cranial hind-edge in the region of the midline.) As a result of convergences, the line/split also is absent in *Hygrobia* and, among dytiscids, in Laccophilinae (except of *Agabetes*) and all Hydroporinae; in *Copelatus* the ventral split only reaches up to the metatentorial pits.

In gyrinids, a partial reduction of the ventral ecdysial line is evi-

dent. My observations confirm those made by Saxod (1965: Pl. 2), but differ to some extent from those given by Hinton (1963). The line is distinct only up to the metatentorial pits (Noars, 1956: Fig. 2, "suture gulaire"); at larval-larval ecdyses this line splits, but usually not at the larval-pupal ecdysis.

22. Metatentorial pits very broadly separated and shifted rearward

    This feature is unknown from other Adephaga.

E. Synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae

23. Cardo lost its medioventral sclerotized part, including the adductor muscle

    As shown above, the maxilla of the Glabricornia (=*Trachypachus* + Hydradephaga) rides on a novel cranial process and thus is more manœuvrable than that of carabids (character 2). Possibly this evolutionary step was a pre-condition which then, within the Hydradephaga, allowed the reduction of one of the four ancestral maxilla-moving muscles. In the group Gyrinidae + Noteridae + Haliplidae, one of the two stipes-moving muscles – the stipes abductor – is lost (character 10). On the other hand, in the group *Amphizoa* + *Hygrobia* + Dytiscidae, another of the four ancestral maxilla-moving muscles is lost, namely, the cardo adductor muscle, and this reduction also concerns the medioventral sclerotized part of the cardo. I refer the reader to figures of Speyer (1922) and De Marzo (1979), and to my remarks on the conditions in *Amphizoa* and *Hygrobia* above under character 2. The dytiscid *Copelatus* shows a peculiarly modified cardo: the insertion of the cardo abductor is exceptionally shifted medioventrally onto the tip of a novel, inward curved, internal cardinal ridge; this modified insertion which is correlated with a somewhat modified shape of the cardo, and, together, with the secondarily un-flexible cranial articulating process (cf. character 2), results in the cardo abductor being secondarily able to partly replace the function of the lost cardo adductor.

24. Tentorium with a pair of novel, long, parallel caudal arms which arise from the vertical posterior arms and extend toward ventral attachment points in the rear of the head capsule; the caudal arms bear the tentorial bridge

This unique tentorial condition among Adephaga is well illustrated by SPEYER (1922) for *Dytiscus* and by DE MARZO (1979) for all dytiscid subfamilies. In *Amphizoa* and in *Hygrobia,* I observed the tentorial bridge originating from the rear of the caudal arms and forming a forward-directed, strongly pointed arch. *Copelatus* (eventually the whole "tribe" Copelatini) has a similar but roundly arched bridge arising from the caudal arms slightly behind their middle (DE MARZO, 1979; RUHNAU & BRANCUCCI, 1984). All the other Dytiscidae possess a strongly narrowed pharynx and relatively approximate tentorial halves, and a tentorial bridge which is rectilinear and arises from the caudal arms far anteriorly to their middle; secondarily, all Hydroporinae lack the bridge (cf. footnote to character 28).

Distinct caudal arms are absent among other Adephaga.

25. Mandibular adductor apodeme completely forked into a dorsal and a ventral branch, allowing for the passage of new postcerebral dorsolateral pharyngeal dilator muscles

Presence of the furcation of the adductor apodeme was so far only described for *Dytiscus* by SPEYER (1922); however, it is distinctly evident throughout all three families considered. The series of postcerebral dorsolateral dilators, which pass nearly horizontally between the two apodeme branches to their lateral attachments in the upper temporal margin of the head, are called "dilatatores pharyngis VIII" by SPEYER (1922) or "dorsal dilator muscles of the posterior pharynx" by DE MARZO (1979). In all other Adephaga, the mandibular adductor apodeme is unforked and flat (in *Cicindela* it is heavily sclerotized and crooked), and dorsolaterally originating postcerebral pharyngeal dilators are absent.

However, the latter muscles probably are derived from those postcerebral dilators which originate middorsally from the hind cranium, and are primitively present though only poorly developed in very few adephagan groups. So far, I observed one pair of such dilators in *Cicindela, Omophron* (in both genera slightly divided into 2 fine bundles), and *Leistus* (1 fine bundle); I presume their presence in *Trachypachus,* but reexamination of material with well-fixed musculature is needed. The muscles are absent in the group Gyrinidae + Noteridae + Haliplidae (possibly a synapomorphic reduction), and in most carabid tribes.

Unlike those postcerebral dilators, precerebral dorsal pharyngeal dilators are present in all Hydradephaga (SPEYER, 1922; DE MARZO, 1979; NOARS, 1956; BEUTEL, 1982), and in *Trachypachus, Cicindela,* and a certain part of carabids, e. g. in *Nebria* (SPENCE & SUTCLIFFE, 1982), *Leistus, Omophron,* and *Carabus.* However, they are lost in *Pterostichus* (TRÖSTER, 1983) and other Harpalinae sensu lato.

26. Prepharynx shortened but transversely extended; frontal ganglion shifted forward; transverse cibarial compressor muscles strongly condensed; pharynx long, very roomy

DE MARZO (1979) called the condensed compressor muscle the "mouth depressor muscle". See above character 16 for further explanations, and note the opposite development of compressor muscles – an increased number! – in haliplids and noterids. – Among dytiscids the large, roomy pharynx is only retained in the "tribe" Copelatini; in all other dytiscids (as already stated above, character 24) the pharynx is strongly narrowed (RUHNAU & BRANCUCCI, 1984). BALFOUR-BROWNE (1922), despite noticing presence of powerful dilator muscles, misinterpreted the very roomy pharynx of *Hygrobia* with its strange masticating bars as "oesophagus" and "proventricular spines".

27. Labral pegs multiplied from '2 + 2' to '2 + a basic number of 12'

In dytiscids these multiple pegs are often called clypeal lamellae, or lamelliform or paddle-like setae of the clypeus. There are several reasons why I interpret position of these pegs labral instead of clypeal. They are inserted, in the Adephaga, directly on the cranial fore-edge, pointing forward. In my view the functionally important fore-edge is always of labral origin, even if labrum and clypeus are completely fused; I see no reason to suggest a complete loss of the labrum, functionally replaced by the clypeus. Following HINTON (1963), the fore-part of the head capsule in front of the dorsal ecdysial lines, as it is fused into one piece in Adephaga, should correctly be called frontoclypeolabral apotome. DE MARZO (1979) does not mention the term labrum; in his view the dytiscid clypeus extends wholly forward to include the cranial fore-edge. MEINERT (1901) and BLUNCK (1924: 498f., and 523, Fig. 33) likewise take the cranial fore-edge for clypeal area, but assume that the actual labrum is strongly tilted as a whole in oral direction and thus is present though wholly ventrally exposed (DE MARZO, 1979, calls the latter area "palato" = epipharynx). In my view the labral area in dytiscids

comprises the narrow, transverse, not exactly definable dorsal cranial strip in front of the origins of the cibarial dilators, the cranial fore-edge itself, which bears the multiple pegs, and the mentioned ventrally exposed sclerotic area visible in anteroventral aspect of head (cf. character 28).

As outlined under character 20, other Adephaga show 4 labral pegs in sum (one outer pair, coded by BOUSQUET & GOULET, 1984, as FR_{10}, and one inner pair, FR_{11}), except for the Haliplidae + Noteridae, where the outer pair is reduced, thus showing only two medially placed pegs.

As a surely synapomorphic feature, *Amphizoa, Hygrobia,* and Dytiscidae possess a high number of labral pegs. *Amphizoa lecontei* Matthews has 24 conspicuous, pointed pegs in L_{1-3} (in L_3 slightly flattened), and *Hygrobia tarda* (Herbst) shows 12 relatively small, somewhat pointed pegs in L_1, and 24 very small, somewhat blunt, cylindrical pegs in L_{2-3}. In both genera, the pegs are arranged in a transverse line just below the labral cranial edge. (In *Amphizoa* the peculiar conspicuous microspinular vestiture of its dorsal body extends on the head to the cranial fore-edge where these tubercle-based cuticular outgrowths, which are trichomes, not true setae, become more and more spiniform thus simulating (a) further row(s) of "pegs" just above the series of true pegs.) The primitive dytiscid genus *Copelatus* possesses cylindroconical pegs, 12 in L_1, 24 in L_2, and 36 (=24 longer and 12 smaller ones) in L_3. In the three just-mentioned genera, but also in various (other) dytiscids, there is one additional, usually obliquely anteromedially directed spiniform peg evident, laterally on each side of the peg series. Therefore I suspect that only the inner two peg-like setae (FR_{11}) of the ancestral pattern were multiplied to a basic number of 12, and that the additional paired peg represents the ancestral outer pair (FR_{10}) which was not involved in the multiplication process. That is what I refer to in the heading as being multiplied from '2 + 2' to '2 + a basic number of 12'.

For further information on the labral peg series in dytiscids, which is usually derivable from the basic number 12, I refer to BERTRAND (1928: Figs 13–31), DE MARZO & NILSSON (this volume), and DE MARZO (1979) and his other papers cited therein. As curious exceptions within dytiscids, the L_1 of *Laccophilus* (cf. DE MARZO & NILSSON, this volume: Fig. 7), *Lancetes,* and *Coptotomus* possess the old adephagan 4-peg-pattern; the multiple peg pattern appears only from L_2 on. The Copelatini (*Copelatus*) are plesiomorphic in having cylindrical pegs. Lamelliform, instead of cylindrical pegs, with a special unilateral mobility (i. e. capable of being strongly tilted, but only into the oral direction), are charac-

teristic of the Dytiscidae excluding Copelatini (RUHNAU & BRANCUCCI, 1984; cf. BLUNCK, 1924: 488f.).

The cylindrical pegs of *Hygrobia* (and probably also those of *Copelatus*) show an inner cavity over most of their length; this also is true for the carabids *Notiophilus* (ALTNER & BAUER, 1982) and *Nebria* (SPENCE & SUTCLIFFE, 1982). In the flattened, lamelliform modification of these pegs, this cavity is probably always restricted to their base (DE MARZO & NILSSON, this volume); at most a very subtle central channel remains recognizable in microscopical sections as remainder of the formation process (BLUNCK, 1924: 488f.).

Based on some experimental work with living colymbetine larvae, I believe that the flattened pegs probably function as mechanocontactreceptors for prey (handling) as in other Adephaga, but additionally act as barbs and possibly as sensors for the turgescence condition of the prey item. They are not deflectible by fine water movements produced by a pipette, as are the various fine sense hairs distributed especially laterally on the head (cf. character 42).

28. Mandibles working against a well-sclerotized, obliquely ventrally exposed, widely transverse strip of labrum, resulting in the loss of the retinacula

The mandible(s) press a captured prey item against this specialized part of the labrum (cf. BERTRAND, 1928; BLUNCK, 1924: 498f.; many figures in DE MARZO, 1979). The loss of the mandibular retinacle in *Amphizoa* was also noticed by MEINERT (1901: 425); cf. LINDROTH (1960: Fig. 7B).

The ventral sclerotic labral strip of *Hygrobia* is secondarily narrowed and medially altered (cf. BALFOUR-BROWNE, 1922, and my remarks under character 1), and in *Copelatus* it is in its medial part further backwardly tilted into the horizontal plane (DE MARZO, 1979: Figs 33–34). In Hydroporinae it forms the large underside of the clypeolabral horn, against which their uniquely obliquely suspended mandibles are pressing the prey[8].

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[8] In all Hydroporinae, the ventral mandibular articulation is modified allowing transverse gliding of the mandibular condylus, and the ventral cranium is destabilized and elastic, thus enabling a considerable amount of controlled rotation of the mandibles for more or less dorsally orientated adduction movements against a prey item and the venter of the protruding clypeolabral horn. These new results easily explain the above mentioned absence of the tentorial bridge and of the ventral ecdysial line in this subfamily (cf. under no. 21 and 24). The above discussed complete bifurcation of the mandibular adductor apodeme (character 25) surely was a prerequisite for the evolution of a controlled mandibular rotation in the Hydroporinae.

29. Temporal horizontal keel behind eyes developed

This feature, belonging to the ground-plan of the three families, is completely lacking among other Hydradephaga and *Trachypachus*. In *Hygrobia* the keel is clearly developed only in L_1 while its disappearance in later instars is probably correlated with the more and more bloated head shape in L_{2-3}. Secondarily, within dytiscids, the keel becomes indistinct several times, and sometimes it is even absent.

30. Abdominal ganglion chain considerably condensed

The plesiomorphic condition is evident in the three other hydradephagan families, *Trachypachus,* carabids, and cicindelids: the ganglion chain is fully extended, and each ganglion lies in its corresponding segment (except for the last ganglion mass VIII which mostly is advanced to segment VII).

In the apomorphic condition, all connectives between the metathoracic and the VIIIth ganglion are very short. The condensed ganglion chain lies in the fore part of the abdomen, such that in *Amphizoa,* the ganglion VIII lies in the second half of segment IV, in *Hygrobia* even in the second half of segment III, and in dytiscids at least at the beginning of segment III, often in segment II (BEIER, 1927: *Cicindela,* carabids, dytiscids; SPEYER, 1922: *Dytiscus;* own results).

31. Development of a trochanteral annulus

MEINERT (1901) and BERTRAND (1928) have already observed that a peculiar subdivision of the trochanter by an annular line, which is not due to the presence of a joint, is a characteristic of the three families considered. The annulus lacks in all other Adephaga (as a certain convergence *Haliplus* spp. show somewhat like a transverse line of weakness in the posterior wall of their trochanters).

The trochanteral annulus looks under the compound microscope like an internal transverse ridge, but this impression seems (partly) to be due to a change of the refraction of light by the cuticula forming the annulus (see below). In *Amphizoa,* a comparatively weakly visible "ridge structure" is evident only in the posterior wall of the trochanters, but a yellowish transverse line runs around at this level (in one specimen I additionally observed a slight external groove in correspondence to the internal "ridge" in the mesotrochanteral posterior wall). In *Hygrobia* and the Dytiscidae, this internal "ridge" is better developed and annular, forming at least ⅔ of a ring (character 38).

It is interesting that muscles moving the femur and the tibia, which wholly or partly originate within the trochanter (cf. under character 45), have their origins always distally of this annulus in the three families considered, i. e., never in the basal part of the trochanter. However, in various other groups lacking an annulus (e. g. noterids, carabids), there are muscle bundles which originate basally in the trochanter (cf. VERHOEFF, 1903: Pl. 17, Fig. 13).

The nature of the annular ridge or line is difficult to see clearly. Many trichopterous larvae possess a highly similar trochanteral annulus. TINDALL (1963: 457), after studying thin microscopical sections stained with azan of the trochanteral annulus of *Limnephilus*, states that the annular line probably consists of elastic material which is wider internally than externally, and not extending through the thin surface layer. He writes: "Possibly this line is one of elasticity, which, combined with the trochantero-femoral muscle, gives a springiness between the thorax and coxa and the rest of the leg." Similarly detailed investigations of the trochanteral annulus present in three hydradephagan families are needed to decide whether their annulus is a line of springiness as seen in Trichoptera, or whether it is a line of strengthening along a line of stress.

32. Last abdominal segments: segment X lost, IX largely reduced, VIII completely ringlike sclerotized from L_1 on; spiracles VIII shifted into the terminal position while displacing the urogomphi into a ventral position

Hygrobia, although lacking terminal spiracles, shows similarly reduced last segments and ventrally situated urogomphi, as seen in the two other families. It is curious that the last segments of *Hygrobia* are reduced. In other water-inhabiting holometabolous larvae, the loss of the last abdominal segments is always correlated with the use of the spiracles VIII as terminal respiration organs. I presume that the spiracles VIII were in the terminal position in the last common stem-species of the three families considered, and that the terminal spiracles were secondarily lost during the evolution of the modern Hygrobiidae, which breathe by means of a number of gills which are ventrally placed on their thoracic and anterior three abdominal segments.

That a secondary complete reduction of terminally placed spiracles can in fact take place is demonstrated by the dytiscid *Macrovatellus* (Hydroporinae, Vatellini) (SPANGLER, 1963). In certain respects this

larva is an interesting parallel to *Hygrobia*. In both genera the urogomphi and the terminal part of segment VIII are immensely drawn out into three similar, thin "tails".

Noterid larvae have terminally placed spiracles like *Amphizoa* and dytiscids; however, many other characters (see no. 10–22) suggest that the noterids are closely related to haliplids and gyrinids, and that the similarities between the former result from convergence.

33. Maxillary and labial apical palpomeres, each with a medially placed
     primary seta

These primary setae, evident throughout the three families considered, are lacking in other adephagan groups (DE MARZO, 1979, and his papers cited therein; LINDROTH, 1960: fig. 7A, maxilla of *Amphizoa;* NOARS, 1956; JABOULET, 1960; BOUSQUET & GOULET, 1984; own results). As exceptions, a few geadephagans show similarly placed primary setae: *Metrius* (on maxilla and labium) and *Brachinus* (on labium) (BOUSQUET & GOULET, 1984), and cicindelids (on labium, but more ventrally than medially placed) (THOMPSON, 1979).

Secondarily, certain dytiscids (*Eretes,* most or all Hydroporinae) bear more than one single medial primary seta (usually three) on their second (= apical) labial palpomere.

34. Pupae: Urogomphi elongated, extending in lateral view the arched
     silhouette of the pupal back; probably preferred resting position
     with dorsal side up

In the plesiomorphic condition, seen in carabid pupae (the pupa of *Trachypachus* is unknown), the urogomphi are small and dorsocaudally directed. In the group Haliplidae + Noteridae + Gyrinidae the pupal urogomphi are completely lost (apomorphic character 13). However, the three families considered here show another apomorphic condition: the urogomphi are comparatively long and ventrocaudally directed (BERTRAND, 1972; BLUNCK, 1924: 777, Fig. 32; KAVANAUGH, concerning *Amphizoa,* pers. comm.).

Based on various data (i. e. observations by me and others in living pupae of members of all dytiscid subfamilies and of *Copelatus;* pronounced development of setae on the anterior pronotal edge and or on dorsal head surface), I assume that dytiscid pupae generally prefer a special resting position: they rest, if undisturbed, in a position of labile equilibrium, propped solely on their urogomphi and, on the other side,

on their setae of the anterior pronotum and head (cf. BLUNCK, 1924: 788, and 776, Fig. 31, "natürliche Schwebelage" of *Dytiscus),* and thus their convex dorsal side is exposed upward. (Disturbance elicits rotation of abdomen, often resulting in an intermediate phase of resting upon the dorsal side.) According to BLUNCK (1924: 794) the special balanced resting position is maintained during the imaginal ecdysis as well; the loss of this position during this phase would entail deformation of the adults.

Judging from the elongate shape and characteristic orientation of the urogomphi in *Amphizoa* and *Hygrobia,* I suggest that their pupae likewise prefer a balanced resting position with dorsal side up. If this is true, the three families considered would differ therein from the behaviour of other adephagan pupae which (as also most polyphagan pupae, except for many hydrophilids) constantly show a resting position upon their dorsal side, with ventral side up.

F. Synapomorphies of Hygrobiidae + Dytiscidae

35. Antennomere I elongated (i. e. in L_3 at least two times longer than broad)

In other Hydradephaga and in *Trachypachus* the basal antennal segment is scarcely longer than broad; in noterids, as a relative exception, antennomere I can be somewhat longer, up to 1.4 times longer than broad, but this is still distinctly different from *Hygrobia* and the dytiscids.

36. Tarsi laterally compressed from L_1, showing a ventral dense comb of thin spinulae along the ventral keel

Such a tarsal feature is unique to Hygrobiidae and Dytiscidae ("peigne de tarse" of BERTRAND, 1928; cf. character 40). In L_2, and even more so in L_3, of *Hygrobia* the comb of small spinulae is superimposed by some moderately long stiff, upright setae in the keel line so that the primary comb of spinulae comes to be inconspicuous.

37. (?) Presence of a vertical line directly behind eyes

Hygrobia has a dorso-ventrally running carina (dark, strengthened line) behind the stemmata (BERTRAND, 1928: 201), and dytiscids show a

series of fine long hairs in the same position from L_2 on (cf. character 42). Both features are unknown in other Hydradephaga, but I am not certain whether these features have a common origin. The similarly situated "ocular groove" seen in a number of carabid tribes (THOMPSON, 1979) is surely a convergent development.

38. Trochanteral annulus completed to at least ⅔ of a ring

Cf. character 31.

G. Synapomorphies of the family Dytiscidae.

In this paper I have assumed all examined hydradephagan groups except of Dytiscidae were monophyletic at the family level. I will substantiate this generally accepted view at a later date using preimaginal characters. However, for the Dytiscidae, it is useful to conclusively demonstrate monophyly at this point. It adds further evidence that the Noteridae cannot be considered as forming a dytiscid subfamily "Noterinae", as is still done by some recent authors. As already shown, the distribution of numerous derived preimaginal characters among the hydradephagan families (i. e. all the characters 10–38, possibly except of character 32) totally contradict such a view, as also the traditional opinion about a close relationship of Noteridae and Dytiscidae. Additionally, it is important to show that the Dytiscidae including Copelatini form a well-founded monophyletic group because the Copelatini differ from other dytiscids in many larval characters. For example, copelatines possess only very shallowly grooved mandibles, a roomy pharynx, a crop and proventriculus, etc. (ref. RUHNAU & BRANCUCCI, 1984, where it is shown that Copelatini and Dytiscidae excluding Copelatini are sister-groups).

Dytiscidae (excluding the Noteridae!) share the following synapomorphies.

39. Abdominal segment VII completely sclerotized from L_2, ringlike

Cybister and *Dytiscus* show this segment secondarily medio-ventrally semi-membranous. A completely ringlike sclerotized segment VII is also present in Hydrocanthinae and Suphisinae, but not in *Noterus* and other, less derived noterids, and thus it is not part of the noterid ground-plan and surely a simple convergence to the dytiscid condition.

40. Tibiae with ventral keel bearing a dense comb of spinulae (from L_1)

The principal duty of these combs on tibiae (BERTRAND, 1928) and their counterparts on tarsi (cf. character 36) is apparently for cleaning of the body surfaces of the larva from impurities or "Aufwuchs". I watched diverse dytiscid larvae use the distal parts of their legs to groom their heads and bodies. Additionally, the combs may contribute to the leg's grasp in locomotion.

The tibial comb is absent in all Dytiscinae being replaced by ventral swimming hairs; it is also lost in *Oreodytes* (Hydroporinae). The tibiae of L_{2-3} of *Hygrobia* also have a (moderate) ventral keel bearing some long, strong setae, but a comb of spinulae is absent.

41. Presence of a series of temporal spines (from L_2 on)

The spines are lost secondarily in a few genera (BERTRAND, 1928, 1972); such a reduction seems to occur more often in inhabitants of running water than in those dwelling in lenitic habitats. I have observed by manipulating these spines in living and dying colymbetine larvae with a very thin needle that they are only movable anteriorly. I presume that these spines are of importance in the grooming behaviour. Dytiscid larvae clean their heads and mouthparts, especially after a meal, by wiping actions of their fore legs (cf. BLUNCK, 1924: 645), and while doing so the temporal series of spines might serve to re-clean the fore legs and their combs.

42. Vertical line behind eyes represented by a series of about 10 fine long hairs (from L_2)

This series of upright hairs at the lateral-most part of the head directly behind the stemmata (cf. character 37) might be important to sense fine water movements produced by prey items or enemies. Experimentally produced deflexion of these long grouped hairs (as also of other long hairs distributed over the body) by a pipette or fine needle very easily elicits larval reactions such as a special alert phase (cf. following paragraph), or immediate attacks with the mandibles, or even an escape behaviour.

43. Larvae respond to (slight) tactile stimuli by assuming a posture where the mandibles are widely spread apart for long periods

I observed this characteristic dytiscid behaviour in no other hydradephagan family; admittedly, I do not know the respective behaviour of *Amphizoa*. This is a special alert phase enabling the larvae to attack instantly the "stimulator" (prey/enemy) after it has been more clearly located (and identified) (cf. BLUNCK, 1924: 639).

44. Principal tracheal trunks enlarged, laterally "compressed", with a
       dorsal and a ventral elastic, keel-like taenidial strengthening

In the dytiscid ground-plan the enlargement and the keel-like strengthenings of principal tracheae are only developed in the pair of abdominal trunks of L_3 (cf. RUHNAU & BRANCUCCI, 1984). Such modified tracheae, if air-filled to a normal extent, are oval in cross-section and possess in the dorsal and the ventral line elastic, buckle-like dark strengthenings of the tracheal taenidia, thus forming a rounded dorsal and ventral keel. PORTIER (1911: 227, 251) already described this peculiarity for some larval Dytiscinae. I believe that these specialized tracheae are unusually apt to collapse and to re-expand in a minimum of time thus increasing speed and volume of the tracheal ventilation during respiration at the water surface. The tracheal enlargement itself serves as air store and gives those larger and heavier larvae with swimming abilitiy the necessary buoyancy.

In Noterinae, even more in Hydrocanthinae and *Amphizoa,* the pair of principal longitudinal trunks is markedly enlarged in the abdomen, but their trunks are circular in cross-section and lack the keel-like strengthenings, as is the case with all other non-dytiscid adephagan larvae as well. In noterids the enlarged trunks simply serve as air store, while in *Amphizoa* they additionally give sufficient buoyancy so that a larva which has lost its foot-hold is able to float by assuming a characteristic "rolled-in" posture with its posterior dorsum and terminal spiracles at the water surface (cf. BERTRAND, 1972).

45. Femoro-tibial flexor muscle: all its branches originate within the
       femur, no ones extend into the trochanter

In the legs of all other Hydradephaga, *Trachypachus, Cicindela and* carabids examinedthe plesiomorphic state is present: 1–2 thin bundles of the tibial flexor extend (far) into the trochanter (i. e. the "Brückenmuskel b" in terms of VERHOEFF, 1903, present in various insects). There they originate anteroventrally, i. e., somewhat dorsal and in most of the genera proximal to the ventrally placed origin of the strong

trochantero-femoral muscle (rotator/remotor of the femur). I refer to illustrations given by VERHOEFF (1903: Pl. 17, Figs 13, *Pterostichus,* and 18, *Dytiscus*), MEINERT, (1901: Pl. 6, Fig. 157, *Noterus*), and SPEYER (1922).

46. Pupae: Bases of both wing pairs dorsally with a few setae

My observations confirm BERTRAND's (1928, 1972) results that this characteristic of dytiscids is lacking in other Hydradephaga, and to my knowledge in carabids, too (exceptionally a few species of *Gyrinus* show similarly placed setae, cf. SAXOD, 1965). Only in the Dytiscinae are these setae secondarily lost (RUHNAU & BRANCUCCI, 1984: character 4 e'). As to the presumed absence of these setae in *Amphizoa,* I admit that my present knowledge about its pupa (KAVANAUGH, pers. comm. incl. a drawing) is still incomplete.

47. Pupae: Sternal region with setae

In the dytiscid ground-plan eventually only one pair is present (on sternum VII of *Copelatus haemorrhoidalis* (F.), cf. RUHNAU & BRANCUCCI, 1984). This characteristic of dytiscids (BERTRAND, 1972) is lacking in other adephagan pupae.


III. Discussion

A. Phylogenetic conclusions

Larval and pupal characters help to reconstruct the phylogenetic relationships among the hydradephagan families and *Trachypachus.* Fig. 1 shows the phylogenetic tree issuing from my findings and the suggested conclusions; the characters employed are listed in the legend.

a. *Trachypachus* and the Hydradephaga share four, most probably synapomorphic preimaginal ground-plan characters (no. 1–4): 1) mandibles with two cutting edges enclosing an open mesial groove, 2) cardo riding on a flexible cranial process, 3) larval mesothoracic spiracles small and pupal mesothoracic spiracles closed, and 4) subapical setae on antennomere IV strongly reduced (no. 3 and 4 are reductions). These new findings support the hypothesis that the Hydradephaga and Trachypachidae together form a monophyletic group, called the Glabricornia sensu BELL, 1966. Up to now, this hypothesis was based

Fig. 1: Phylogenetic tree of the Glabricornia. Synapomorphies are indicated by ●, and listed below; the respective symplesiomorphic alternatives, if not deducible, are briefly noted by (pm: ...). Pure reductions are marked with R in the figure; L means larvae, P pupae. – 1. L, Mandibles with 2 (pm: 1) inner cutting edges enclosing a groove (pm: without groove). 2. L, Cardo riding on a flexible cranial process (pm: cardo with condylus that fits into a cranial socket). 3. Mesothoracic spiracles: small in L, closed in P (pm: large, open in L and P). 4. L, Strong reduction in size of the 3 subapical setae on antennomere IV. – 5. L, Prementum moved by 3 (pm: 2) paired retractor muscles. 6. L, (Lateral) spiracles in L_{1-2} very small, closed (pm: of normal size, open). 7. L, Pygopodium lost. 8. L, Antennomere IV without setae (cf. 4.). 9. L, Loss of the carabid-type fragmentated sclerite pattern on ventral abdomen. – 10. L, Stipital abductor muscle lost. 11. L, Brain caudally elongated, of highly characteristic shape (pm: transversely and dorsally extended near middle of head). 12. L_1, egg-bursters lost. 13. P, Urogomphi lost. 14. P, Peristigmatic glands lost. 15. P, New posture of hind legs. – 16. L, Prepharynx with 7 or more (pm: 3–4) transverse cibarial compressor muscles. 17. L, Only one (pm: 2) paired trachea cephalica enters the head (similar in the adults!). 18. L, Midgut straight throughout its length (pm: with hairpin bend / loop in its posterior part). 19. L, Ventral mandibular articulation shifted onto a dorsomedially inwards bent, narrowing lobe. 20. L, Two (pm: 4) labral sensory pegs present, placed medially side by side. 21. L, Ventral cranial ecdysial line lost. 22. L, Metatentorial pits very broadly separated and shifted rearward. – 23. L, Cardo lost its medioventral sclerotized part, including the adductor muscle. 24. L, Tentorium highly characteristic, with a novel pair of long parallel caudal arms. 25. L, Mandibular adductor apodeme completely forked, allowing for the passage of new postcerebral dorsolateral pharyngeal dilators (pm: apodeme unforked). 26. L, Prepharynx shortened but transversely extended; cibarial compressors condensed to one mass; pharynx long and very roomy (secondarily narrow in 'Dytiscidae excluding Copelatini'). 27. L, Labral pegs multiplied from '2 + 2' to '2 + a basic number of 12'. 28. L, Mandibles working against a well-sclerotized, ventrally exposed transverse strip of labrum; retinacula therefore lost. 29. L, Temporal horizontal keel behind eyes (pm: absent). 30. L, Abdominal ganglion chain condensed. 31. L, Development of a trochanteral annulus. 32. L, Abdominal segments X and IX reduced, VIII ringlike sclerotized; spiracles VIII terminal (secondarily lost in *Hygrobia* and few dytiscids); urogomphi in ventral position. (Similar in noterids!). 33. L, Maxillary and labial apical palpomeres, each with a (new) medially placed primary seta. 34. P, Urogomphi elongated (pm: short), extending in lateral view the arched silhouette of the pupal dorsum (pm: projecting dorsally); presumably preferred resting position with dorsum up (pm: venter up). – 35. L, Antennomere I elongated. 36. L, Tarsi with ventral keel bearing a dense comb of spinulae (from L_1). 37. (?) L, Vertical line behind eyes present (pm: absent). 38. L, Trochanteral annulus completed to at least $^2/_3$ of a ring (cf. 31.). – 39. L, Abdominal segment VII ringlike sclerotized (from L_2). 40. L, Tibiae with ventral keel bearing a dense comb of spinulae (from L_1). 41. L, Series of temporal spines (from L_2). 42. L, Vertical series of about 10 fine long hairs just behind eyes (from L_2). 43. L, Tactile stimuli cause a posture with widely spread apart mandibles for long periods. 44. L, Tracheal trunks enlarged, laterally "compressed", with dorsal and ventral keel-like strengthenings (at least in abdomen of L_3). 45. L, Femoro-tibial flexor muscle: all its bundles originate within the femur, no ones extend into the trochanter. 46. P, Bases of both wing pairs dorsally with a few setae. 47. P, Sternal region with setae.
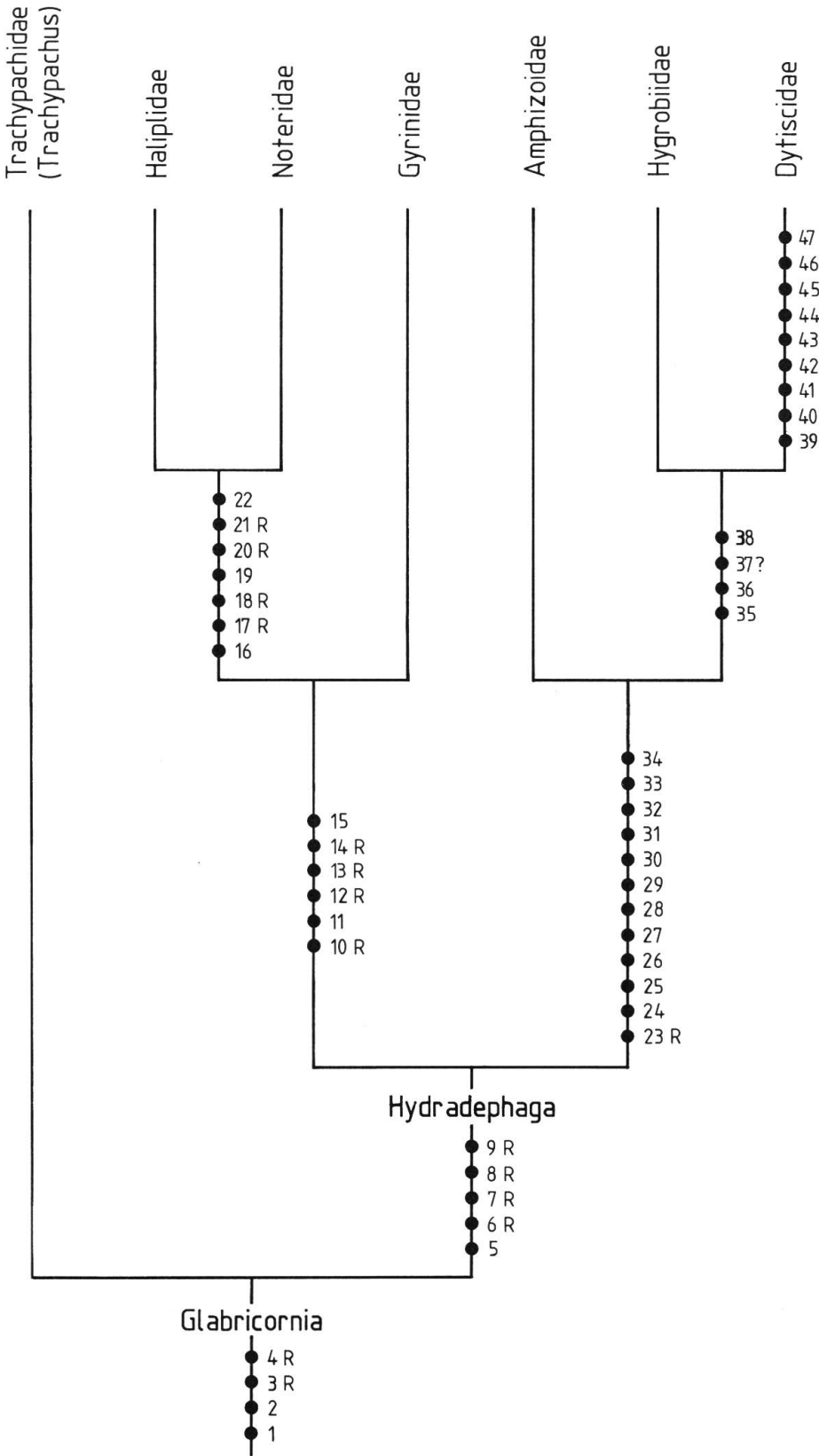
only on evidence from various adult characters (cf. Roughley, 1981; Bell, 1982; Hennig, 1981: 394f.). Lindroth (1960:35) stressed three similarities shared by larval *Trachypachus* and *Amphizoa;* one of those, the lack of a ligula, could be a further, though not very reliable synapomorphy of the Glabricornia: the ligula is convergently lacking in the carabids *Cychrus, Gehringia,* and Brachinini, and it secondarily reappears in *Hygrobia* and many Dytiscinae. Further studies are needed to reveal whether the unexpected presence of two cutting edges in the larva of the carabid *Metrius e footnote to character 1) is the result of a convergence or a close relationship.*

b. The monophyly of the Hydradephaga is suggested by five larval synapomorphies (no. 5–9). One of those five, the presence of a third premental retractor muscle, is very remarkable. Unfortunately the other four are character losses or reductions and therefore not as reliable. However, I did not find any character which would indicate that a part of the Hydradephaga – doubts stated concern the Gyrinidae and especially the Haliplidae, cf. Roughley (1981) – could be more closely related to *Trachypachus* or even to any geadephagan group than other Hydradephaga.

c. As suggested by the characters 10–15 and 23–34, the six currently recognized hydradephagan families can be separated into sister-groups each comprising three families (sensu Burmeister, 1976). Unfortunately, I could not study the phylogenetically interesting genus *Notomicrus,* whose immatures are unknown. Eventually this genus, "which surely does not belong to the Noteridae" (Burmeister, 1976: 166, 252) and even presumably not to the group Noteridae + Haliplidae + Gyrinidae, represents a further, monogeneric (?) hydradephagan family.

d. The families Gyrinidae + Noteridae + Haliplidae share six preimaginal synapomorphies (no. 10–15); particularly interesting are the highly characteristic shape and position of the supraoesophageal ganglion, the loss of the stipital abductor muscle, and the loss of the pupal urogomphi. Four of those six characters are character losses, however, together with Burmeister's (1976) results on female adults, the monophyly of this family group appears substantiated. The occurrence of terminally placed larval spiracles VIII in the Noteridae and in the ground-plan of the group *Amphizoa* + *Hygrobia* + Dytiscidae has to be explained as a convergent development.

e. The Noteridae and Haliplidae share seven larval synapomorphies (no. 16–22), among them the increased number of prepharyngeal compressors, the loss of the trachea cephalica superior, the shifted ventral mandibular articulation, and the loss of the outer paired labral sensory peg. I conclude that Haliplidae + Noteridae together form the sister-group of the Gyrinidae.

f. *Amphizoa, Hygrobia,* and the Dytiscidae share 12 preimaginal synapomorphies (no. 23–34); most of them are striking character gains. These findings justify the definite conclusion that this group is monophyletic, and rule out the close relationship of the Noteridae to the Dytiscidae which is currently presumed. So far only few synapomorphies of the adult stage, characterizing this group, are known (e. g. the ventromedial trough-like fusion of the genital appendages VIII, i. e. gonapophyses VIII, Burmeister, 1976).

g. Larvae of *Hygrobia* and the Dytiscidae share three or four presumable synapomorphies (no. 35–38); especially the presence of a ventral tarsal keel bearing a comb of spinulae (no. 36) appears to be a convincing synapomorphy. My assumption that the Hygrobiidae + Dytiscidae form the sister-group of the Amphizoidae, is additionally supported by some synapomorphies in the adult stage (Beutel, pers. comm.; prothoracic defence glands). Some similarities shared by larval *Amphizoa* and Dytiscidae are obviously already part of the ground-plan of the group *Amphizoa* + *Hygrobia* + Dytiscidae; these features are secondarily effaced in *Hygrobia* due to autapomorphic specializations (head shape, mouthparts, respiration mode).

h. The family Dytiscidae, composed of the two subgroups Copelatini and 'all remaining dytiscids' (Ruhnau & Brancucci, 1984), is monophyletic, as shown by nine synapomorphies (no. 39–47).

B. Independent origins of the mandibular tubular sucking channel[9]

Many larval Hydradephaga possess a more-or-less distinctly closed mandibular channel. This development is in my view a significant step, so that its secondary loss appears most unlikely. It is derivable from the situation seen today in *Trachypachus,* but also (primitively) retained in

Amphizoa, and, approximately, in the Noterinae among noterids, in L_1 of *Hygrobia,* and in the dytiscid *Copelatus* (cf. character 1; *Hygrobia* has lost the ventral cutting edge from L_2 on). Although most dytiscid larvae possess a more-or-less distinctly closed channel, this character state cannot be ascribed to the ground-plan of the Dytiscidae: *Copelatus* (and presumably its allied genera of the "tribe" Copelatini) has only very shallowly grooved manibles, and *Agabetes* has broadly open, but deep grooves (RUHNAU & BRANCUCCI, 1984; DE MARZO & NILSSON, 1986, and various papers of the senior author cited therein). Similarly, a closed channel surely does not belong to the ground-plan of the Noteridae; however, I observed it in more derived noterids: *Canthydrus* and *Hydrocanthus* possess a very fine, closed channel located medially in the proximal half of the mandibles (RUHNAU, unpubl. results; the Suphisini with similarly flattened, slender mandibles might show the same condition). As is already known, both Haliplidae and Gyrinidae *(Spanglerogyrus?)* possess closed channels in their respective ground-plan (the Gyrininae have only very imperfectly closed channels, in contrast to Enhydrinae and especially Orectochilinae, cf. NOARS, 1956).

These results indicate that a tubular channel has developed several times independently. Within the Dytiscidae, a deep mandibular sucking groove (i. e. an intermediate stage toward a tubular channel, already correlated with modifications of other head organs) can be ascribed to the group 'Dytiscidae without Copelatini'; an extensive closure of the deep groove has probably evolved independently along three paths: in the group '*Lancetes* + Colymbetinae + Dytiscinae', in the Hydroporinae, and, within the Laccophilinae s. lat., in the group 'Laccophilinae without *Agabetes*' (RUHNAU & BRANCUCCI, 1984). Further, my conclusion that Noteridae + Haliplidae are the sister-group of the Gyrinidae, based on seven other characters (Fig. 1), has the consequence that the closed mandibular channel developed three times independently in these three families.

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[9] I omit a discussion on the sensorial appendage placed distally on antennomere III, which is usually present in carabids. It may be small, or very prolonged, or (externally) absent within the Hydradephaga, and was obviously subject to independently developed enlargements, reductions, and even character reversal. The value of this character appears low for the scope of this paper.

IV. Appendix

Are Omophron and the Glabricornia closely related?

As seen above, my interpretation of characters found in the Glabricornia is often influenced by my result that the family Carabidae (even without the Cicindelidae) minus Trachypachidae is a non-monophyletic cluster. The secondary formation of a hypopharynx-like swelling (see under character 5), as well as other characters not discussed in the present paper, suggest that a certain subgroup of carabids (which includes Carabini, Nebriini, Omophronini) is more closely related to the Glabricornia than to other carabid subgroups.

Supplementary to my results on the glabricornian phylogeny, I add here the notice and discussion of two larval apomorphies shared by *Omophron* and the Glabricornia, but absent in other carabids studied, and finally discuss a peculiar dorsal keel on the mandible of *Omophron*.

a. Maxillary cardo well-sclerotized only on ventral side (1 sclerite)

In the cicindelids and the majority of carabids, the ring-shaped cardo shows two separate sclerites: the main piece which provides the craniocardinal articulation, and the medial piece called "basimaxillary sclerite" by DAS (1937). These two sclerites are separated by membranes: on the ventral side of the cardo, there is a narrow, oblique "slit", medially of the craniocardinal articulation, and the dorsal side shows a more or less broad membranous area (cf. BOUSQUET & GOULET, 1984: Figs 6, 7).

I observed two different, apomorphic modifications of this condition. In the Carabini and Nebriini (plus *Notiophilus? Opisthius?),* the two sclerites are completely fused dorsally, thus forming a sclerotic ring whose rigidity is mitigated only by the (medio)ventral membranous slit (BENGTSSON, 1927, incorrectly ascribed this situation to all carabids). Further, these carabids show a secondary, dorsal articulation point between the cardo ring and the inter-mandibulo-maxillary bar (see under character 19), in addition to the usual ventral craniocardinal articulation (cf. SPENCE & SUTCLIFFE, 1982).

The other modification of the cardo is found in *Omophron, Trachypachus,* and the hydradephagan ground-plan. There the "basimaxillary sclerite" is not apparent, and the (medio)ventral slit is lacking (or possibly shifted onto the mesial side). The cardo shows only one

sclerite which extends ventrally from the medial to the lateral side, and the whole dorsal side is (semi)membranous[10] (cf. THOMPSON, 1979: Fig. 33b). In their detailed description of the larva of *Omophron,* LANDRY & BOUSQUET (1984) do not mention this feature, and their Fig. 4 (dorsal aspect of maxilla) is misinterpretable concerning this point. This modification of the cardo sclerotization seems to be a prerequisite for the evolution of the glabricornian craniocardinal articulation mode (character 2).

b. Mode of articulation in the femoro-tibial joint different from (other) geadephagans

JEANNEL (1925: 42f., Figs 4, 5) reported that in larval adephagan legs all the joints distally of the bicondylar coxo-trochanteral joint show an identical mode of articulation throughout all Adephaga: dorsally the distal end of a leg segment and the proximal end of the next segment each show a short, longitudinal strengthening; between the distal and the following proximal strengthening there is a direct tight contact. My observations reveal the following results. Concerning the trochantero-femoral and the tibio-tarsal joints, I confirm that their mode of articulation is of a constant type as described by JEANNEL (1925). As to the femoro-tibial joint, JEANNEL's generalization is only true for all cicindelids and carabids examined except *Omophron,* but not for *Omophron* and the Glabricornia. Correspondingly to this directly dorsal tight articulation mode in the knee-joint of cicindelids and carabids (except for *Omophron*), the femoro-tibial extensor muscle is inserted on the proximal rim of the tibia slightly to distinctly posteriorly of the dorsal articulation point (a directly dorsal insertion would make no sense!); thus the extensor tibiae functions to a certain extent as remotor tibiae.

However, in *Omophron* and the Glabricornia, the femoro-tibial extensor is inserted directly dorsally at a strengthened point of the proximal rim of the tibia. This dorsal insertion point is drawn somewhat into the femur when the knee-joint is straightened; a dorsal tight and invariably direct contact of two hard points as seen in other Adephaga is lacking.

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[10] As a secondary exception within the Hydradephaga, the dorsal side of the secondarily very elongate cardo of the Gyrinidae is relatively well sclerotized (see also under character 10).

Omophron larvae, which dig in moist, fine sand, seemingly have special devices to compensate mechanically the loss of the invariably direct dorsal articulation point in the knee-joint of other carabids. Besides that the tibiae are exceptionally short, they possess presumable stop mechanisms preventing excessive extension by the extensor tibiae or by the substratum: the protibiae bear a sub-basal marked dorsal protuberance (from L_2 on), and the meso- and metatibiae show two strong primary setae which in other carabids are distally situated, completely shifted into the dorsobasal position (LANDRY & BOUSQUET, 1984: Fig. 13, "TI_{2+7}"). Within the Hydradephaga, an obviously secondary modification of the knee-joint articulation is evident in larger dytiscids and also indicated in *Amphizoa:* the distal end of their femur bears two more-or-less distinctly developed, inflected sclerotized points (in the dorsoanterior and dorsoposterior position, best visible in end-on view of the femur) on which the proximal rim of the tibia pivots.

c. Is the dorsal keel on the mandible of *Omophron* a forerunner of the dorsal, second inner cutting edge evident in Glabricornia?

The closing motion of the mandibles in carabid larvae is mostly terminated by special, physical stop devices which serve to mitigate the impact of the mandibles against the medial part of the labral fore-edge, or against the hypopharynx-like swelling. In diverse Harpalinae s. lat., the termination of mandibular closing motion is largely achieved as follows: a convex, robust area dorsomedially near the mandibular base meets a special, strongly sclerotized, ventrolaterally exposed area of the lateral labrum or "adnasale". In the Carabini, Nebriini, and presumably Notiophilini, the mandibular cutting edge distally of the retinaculum runs against a solid, sharp tooth located medially on the underside of the cranial fore-edge. This anteroventrally directed "hypodon" (BENGTSSON, 1927) or "ventral nasalar spine" (SPENCE & SUTCLIFFE, 1982) protrudes from the rear of a narrow, transverse, strongly sclerotized cuticular stripe, which slopes posteroventrally and belongs to the labrum; the spine acts not only as a physical stop for the mandibles, but also as a prey crushing device.

In *Omophron* the cutting edge of the mandibles passes directly below the fore-edge of the medially strongly protruding "horn-like" labrum during the adduction motion; the horizontal venter of the labrum lacks the "hypodon". The mandibular motion is stopped by the contact between the labral horn and a special keel-like edge dorsally on

the mandible. This stopping device may also serve for prey crushing. The keel is not drawn in figure 3 (mandible) of LANDRY & BOUSQUET (1984); it is developed in the distal half of the mandible, in the dorsal "midline" of this part, running from the apex basalward, passing medially closely the pore MN_c, and disappearing just mediobasally of this pore[11].

My speculation is that such a dorsal mandibular keel could have been the forerunner of the second, i. e., dorsal inner cutting edge present in the Glabricornia (cf. character 1). If this is true, the evolution of the mouthparts toward the ground-plan conditions of recent Glabricornia might be understood as a functional complex, characterized by the following developments: 1. the migration of the dorsal stopping (and prey crushing) keel toward the mandibular inner side, so that it became the dorsomesial, second cutting edge; 2. the enlargement of the hypopharynx-like swelling, against which the mandibles are working; 3. the adaptation of feeding on soft prey (ROUGHLEY, pers. comm., has reared *Trachypachus* larvae on brachypterous mutants of *Drosophila;* he partly injured the latter, so that the L_1 of *Trachypachus* could feed on them). Further, the development of the novel craniocardinal articulation mode (character 2) could be correlated with the enlargement of the "hypopharynx".

Essentially, this short, supplementary chapter on *Omophron* and its possibly close relationship to the Glabricornia can only be a stimulus for future research. For instance, comparisons with larval *Metrius* which possesses mandibles with two cutting edges (cf. footnote 2), might contribute to a better understanding, not only of the significance of my observations on *Omophron,* but also of the origin of the Glabricornia.

V. Acknowledgements

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[11] The hyperprognathous mandibles of cicindelids convergently show such a keel.

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