External and internal structures of the head of 3rd instar larvae of Carabus coriaceus L. (Adephaga, Carabidae)

by **R.G. Beutel**

Abstract: External and internal structures of the head of 3rd instar larvae of *Carabus coriaceus* L. were examined and interpreted phylogenetically. A basal position of *Carabus* within Carabidae is supported by the following plesiomorphic character states: mandibles with 2 mesal edges, primitive preoral filter, well defined hypopharynx, presence of a complete set of hypopharyngeal, prepharyngeal and pharyngeal muscles, arrangement of antennal muscles, absence of postocular and epicranial ridges, unconstricted neck. The mandibular penicillum, and the mesal sclerite of the cardo are probably apomorphic characteristics, which have evolved early in geadephagan evolution. Both structures are absent from larvae of *Trachypachus, Metrius* and *Omophron*. The presence of a ventral labral spine suggests that Carabini, Nebriini, and Notiophilini belong to a monphylectic unit. However this interpretation would imply that the presence in larvae of *Metrius* is a result of parallel evolution. Constriction of the neck may be a synapomorphy of Nebriini and Notiophilini. The strongly protruding nasale with prominent teeth is a synapomorphy of a monophyletic group comprising *Leistus* and Notiophilini. Thus Nebriini are non-monophyletic. Distinctly prominent adnasalia, an extremely short or absent coronal suture and the strongly concave posterodorsal margin of the head capsule are synapomorphies of Carabini and Cychrini.

Key words: Coleoptera Carabidae - *Carabus coriaceus* - larva - head - morphology - phylogenetic interpretation.

I. Introduction
1. Preliminary notes

No agreement upon the phylogeny of higher taxa of Carabidae has yet been achieved according to BALL (1979). Recent studies dealing with the interrelationships of higher taxa of Geadephaga[1] are either based on the analysis of only one character system (ovipostitor: BILS, 1976; prothorax of adults; (BAEHR, 1979), or restricted to an evaluation of external structures of adults (BELL, 1967; KRYZHANOVSKIY, 1976; ERWIN, 1985).

A solid hypothesis concerning interrelationships of higher geadephagan taxa should be based however on an analysis of various character systems of different life stages. The comparative evaluation of different

---

1. The use of the terms Geadephaga and Hydradephaga does not imply that these groups are monophyletic.

character sets provides an effective control mechanism for the classification («wechselseiteige Erhellung»; HENNIG, 1950). Nonconformity of cladograms indicates misinterpretation of characters. Conformity of several cladograms based on different character analyses, confers a high probability to the resulting phylogenetic hypothesis. Furthermore, such a complex approach is appropriate to the complexity of evolution, and involves a broad scale of information, which may be useful for disciplines of entomology other than systematics.

A phylogenetic analysis of external and internal thoracic structures of Geadephaga has been worked out by BEUTEL (1992). This study, dealing with head structures of 3rd instar larvae of *Carabus coriaceus* F. is a first step towards a broader investigation of external and especially internal structures of larvae. The genus *Carabus* Linné 1758 is close to the base of the geadephagan phyletic tree, as suggested by characters of adults, especially the plesiomorphic condition of the protibial antenna cleaning organ. Therefore the results of this investigation may contribute towards the reconstruction of the groundplan of Geadephaga or Carabidae (if they are monophyletic), and clarify the systematic position of Carabini.

2. Materials and methods

Larvae of *Carabus coriaceus* were collected in a shut down quarry near Breinig (vicinity of Aachen, NRW, FRG), preserved in FAE (formol-ethanol-acetic acid), and stored in ethanol. Specimens were imbedded in Histoplast S and microtome sections were cut at 5 μm. The sections were stained with haemalaun and eosin. Drawings were carried out using an ocular grid (stereo microscope). 3rd instar larvae of *Trachypachus holmbergi* Mannerheim, *Broscus cephalotes* L. (both preserved in ethanol), and *Omophron variegatum* Olivier (preserved in FAE, stored in ethanol) were examined for outgroup/ingroup comparison.

II. Morphological results
1. Head capsule

1.1 General appearence and external structures   (Figs 1-3)
The head capsule is strongly sclerotized and pigmented. The mouthparts are in a prognathous position. The ventral wall of the head capsule
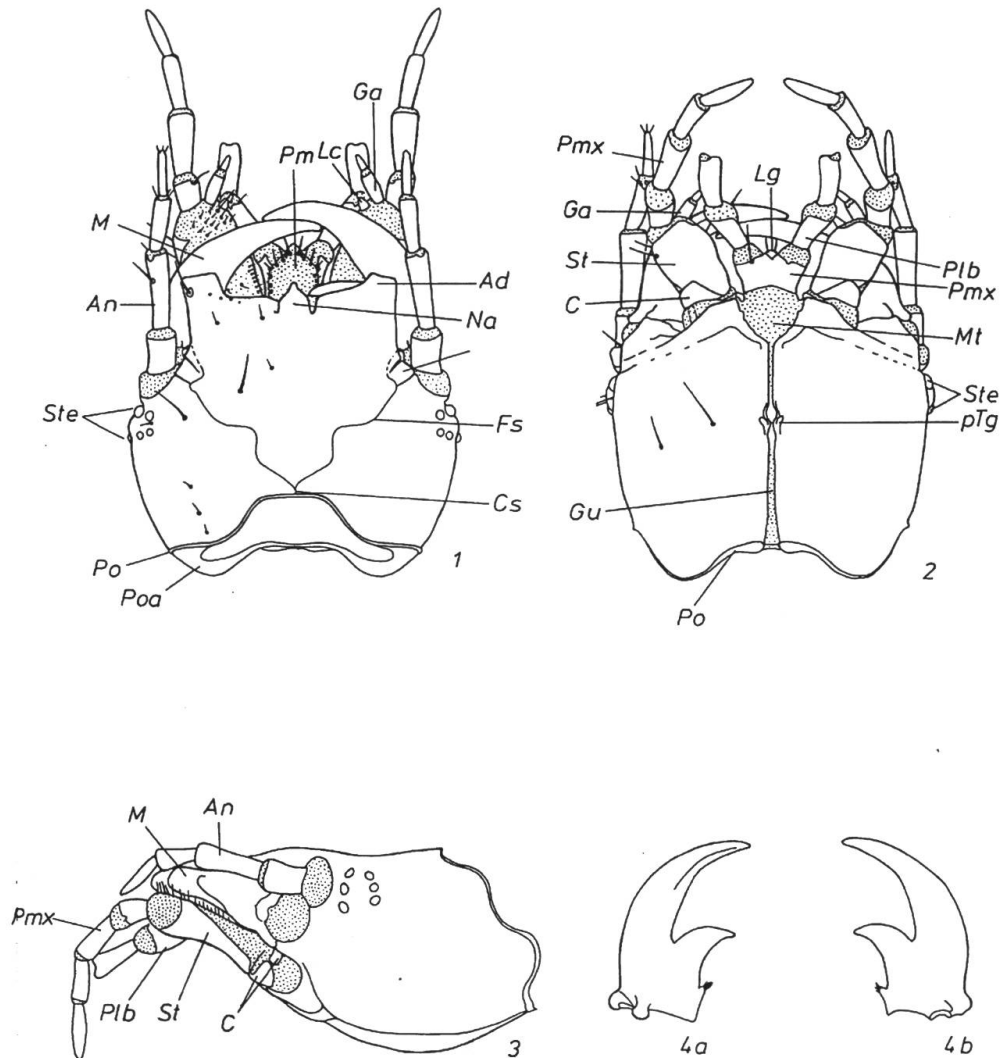
Figs 1 - 4: *Carabus coriaceus*: 1, Head, dorsal view. 2, Head ventral view. 3, Head lateral view. 4a, Mandible, dorsal view. 4b, Mandible ventral view. (Ad: adnasalia; An: antenna; C: cardo; Cs: coronal suture; Fs: frontal suture; Ga: galea; Gu: gula; Lc: lacinia; Lg: ligula; M: mandible; Mx: maxilla; Mt: mentum; Na: nasale; Pc: paraclypeus; Plb: palpus labialis; Pm: prementum; Pmx: palpus maxillaris; Po: postocciput; Poa: postoccipital apodeme; pTg: posterior tentorial grooves; Rt: retinaculum; St: stipes; Ste: stemma).

projects distincly beyond the dorsal wall posteriorly, thus resulting in an oblique position of the foramen occipitale, which has the outline of a laterally compressed oval. The neck is not constricted. The posterior margin of the head capsule is only slightly overlapped by the anterior margin of the prothorax.

The large frontoclypeolabral apotome (HINTON, 1963) is delimited by a strongly meandering frontal suture. The part anterior to the secondary mandibular joint will be referred to as clypeolabral region in the following. It is long and parallel-sided. The anterior margin is a-symmetric. The obliquely truncated adnasalia are distinctly protruding beyond the unidentate nasale. A small sclerite (Paraclypeus; BITSCH, 1966) between the cranial most section of the frontoclypeal suture and the antennal base, is bordered by a distinct suture posteriorly. A moderately long fissure, the anterior tentorial pit, divides the paraclypeus into an anterior and a posterior part. Six stemmata, which are arranged in two vertical rows, are situated on a prominence posterior to the antennal base. A postorbital ridge (Hinteraugenleiste; TRÖSTER, 1987) is not present. The part of the head capsule posterior to the stemmata appears short compared to the elongate frontoclypeal region. The sides are slightly rounded and devoid of an epicranial ridge. The frontal sutures are continuous with an extremely short coronal suture posteriorly. The hind margin of the head capsule is represented by the narrow postocciput, which is bordered by a distinct postoccipital suture. A moderately developed postoccipital apodeme arises from the postoccipital suture. It is distinctly broader ventrally and laterally than dorsally.

The postoccipital suture is continuous ventromedially with two low, internal ridges, which enclose an extremely narrow gular area. The anterior margin of the gular area is defined by the posterior tentorial pits, which lie very close together. A narrow, median, unpigmented zone, is continuous with the gular area anteriorly.

1.2. Tentorium (Figs 5-7):

The posterior tentorial arms are moderately broad and flattened. They are adjacent to each other at their base and extend dorsolaterally in a rounded curve towards the point of origin of the posteriorly directed U-shaped tentorial bridge. From the origin of the tentorial bridge the broadest part of the tentorium extends dorsolaterally towards the branching point of the dorsal and anterior tentorial arms. The dorsal arm is attached to the dorsal wall of the head capsule by means of fibrillar structures. The anterior arms, which originate from
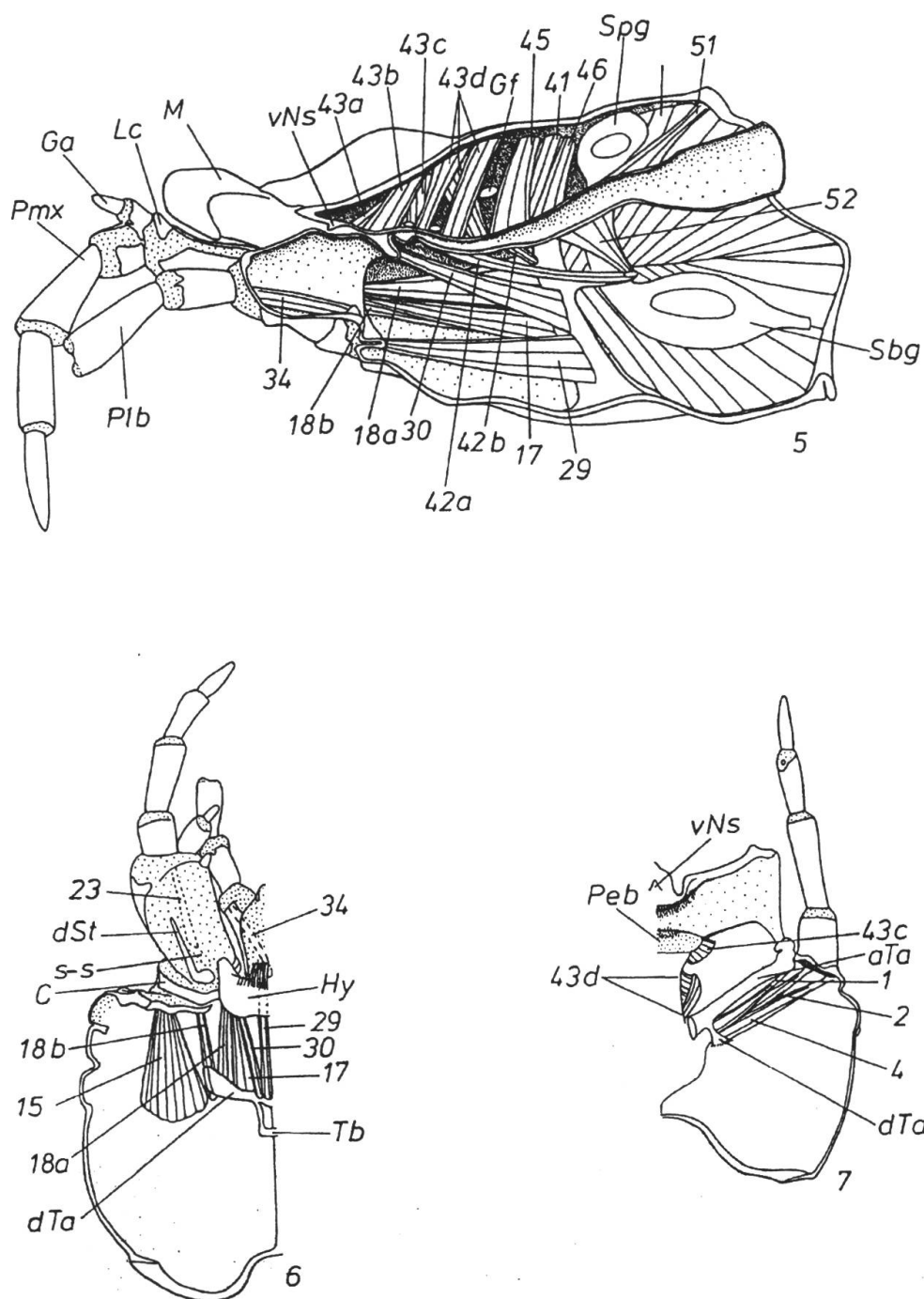
Figs 5 - 7: *Carabus coriaceus*: 5, lateral view, sagittal section. 6, Horizontal section, ventral part. 7, Horizontal section, dorsal part. (aTa: anterior tentorial arm; C: cardo; dTa: dorsal tentorial arms; Ga: galea; Gf: ganglion frontale; Hy: hypopharynx; Lc: lacinia; Peb: preepipharyngeal bulge; Plb: palpus labialis; Pmx: palpus maxillaris; pTa: posterior tentorial arms; Sbg: suboesophageal ganglion; Spg: supraoesophageal ganglion; Tb: tentorial bridge).

the fissure shaped anterior tentorial pits, are moderately strong and oval in cross section.

2. Appendages of the head and their musculature
(v. Kéler's nomenclature is used for the muscles)

2.1. Labrum   (Figs 1, 5, 7):

A separate labral sclerite is not present, and has not been observed in any other adephagan larvae. However, it appears reasonable to assume that the anterior edge of the frontoclypeolabral apotome, anterior to the origin of clypeal muscles, is of labral origin. There is no reason why the labrum should have been completely reduced, and functionally replaced by the anterior clypeal margin, as already pointed out by RUNHAU (1986).

The sclerotized inflected margin of the labrum bears an anteriorly directed strongly sclerotized, thick spine (ventral nasalar spine; SPENCE & SUTCLIFFE, 1982), which acts as a prey shredding device and a physical stop for the mandibles.

Musculature: No labral muscles are present.

2.2. Antenna   (Figs 1-3, 7):

The antennal base protrudes slightly anterior to the flat elevation bearing the stemmata. Owing to the elongate clypeolabral region the antennal base appears to be located in the middle sector of the head capsule rather than at the anterolateral margin. The length ratio of the antennomeres is 1 : 1.7 : 1.1 : 1.1. Antennomere I is dinstinctly wider than the following segments. Antenomere III is not dilated distally. A minute sensorial appendage is present.

Musculature   (Fig. 7):

M. 1: M. tentorioscapalis anterior.

M. 1 originates from the proximal part of the dorsal tentorial arm, and is inserted on the anterior margin of the scapal base. This muscle is slender, and slightly flattened proximally as the following two antennal muscles.

Function: Protractor of the antenna.

M. 2: M. tentorioscapalis posterior.

M. 2 originates from the dorsal tentorial arm, dorsad of M. 1, and is inserted on the dorsal margin of the scapal base.

F: Levator of the antenna.

M. 4: M. tentorioscapalis medialis.

M. 4 Originates from the dorsal tentorial arm, posterior to M. 1 and M. 2, and is inserted on the posteroventral margin of the scapal base.

F: Extensor of the antenna.

Intrinsic muscles of the antennae are absent.

2.3. Mandible   (Figs. 4a, b):

The mandible is comparatively short, with a slender distal part, and a broad and compact base. The outer edge is evenly rounded, forming a quarter section of a circle. The apex of the left mandible is slightly less pointed than the apex of the right mandible. A distinct dorsomesal edge is extending from the tip of the mandible to the base of the retinaculum. A second, ventromesal edge is present, but does not reach the retinacular base. A third, short and weakly expressed edge is present on the upper side of the mandible. The retinacula are broad at the base. A short edge is connecting the acuminate apex of the left retinaculum with a second, less conspicuous point, which is absent from the retinaculum of the right mandible. A penicillum is present on a distinct prominence close to the mandibular base.

The mandibles articulate with the head capsule in the usual manner: a strong condyle of the ventral mandibular base forms the primary mandibular joint together with a corresponding notch, which is situated between the antennal and the maxillary articulation. A heavily sclerotized socket of the dorsal mandibular base forms the secondary mandibular joint together with a condyle of the head capsule anterior to the paraclypeal sclerite.

Musculature (Fig. 5):

M. 11: M. craniomandibularis internus.

M. 11 is the most powerful muscle of the head, and originates from large parts of the posterolateral and ventral areas of the head capsule, and from adjacent parts of the postoccipital apodeme. It is inserted on the ventral and dorsal side of the broad adductor apodeme.

F: Adductor of the mandible.

M. 12: M. craniomandibularis externus.

M. 12 originates from the lateral area of the head capsule and the adjacent part of the postoccipital apodeme. It is inserted on the abductor apodeme.

F: Abductor of the mandible.

M. 13: M. hypopharyngo-mandibularis.

An extremely thin muscle, which originates from the anterior re-

gion of the anterior tentorial arm, and is inserted on the ventral surface of the mandibular base.

F: proprioreceptor?

2.4. Maxilla   (Figs 2, 3, 5, 6):

The maxilla is comparatively short and compact. Two sclerotized parts of the cardo can be distinguished. Together the two sclerites form a ring-like structure, which is interrupted by narrow membranous zones laterally and ventromesally. The ventrolateral sclerite is broader than its counterpart and bears a strong condyle which articulates with a notch on a strongly sclerotized, conspicuous process of the anterior margin of the head capsule. The stipes is about twice as long as wide, and almost completely sclerotized on the ventral side. The dorsal side is largely membranous. A narrow dorsolateral sclerite runs parallel to the axis of the maxilla in the basal half of the stipes. It is connected with the ventral sclerite by a transverse sclerotized band at the base. Medium sized setae are distributed over most parts of the dorsal membrane in an irregular pattern. They are concentrated around the lacinia, and along the mesal edge, especially in the proximal part of the maxilla. They are absent from the lateral area of the dorsal membrane, which is adjacent with the ventral sclerite. The lacinia is represented by a small, compressed, cone-like structure, which is only lightly sclerotized, and bears a bristle at the apex. The galea is 2-segmented with a small digitiform distal segment. The four segmented maxillary palp protrudes far beyond the antennal apex. A narrow mesal section of palpomere I is unsclerotized. The length ration of the palpomeres is 1 : 2 : 1.4 : 1.7.

Musculature   (Figs 5, 6):

M. 15: M. craniocardinalis externus.

M. 15 originates from the ventral wall of the head capsule between the stemmata and the tentorial base, and is inserted on the lateral edge of the ventral sclerite of the cardo by means of a strongly sclerotized, short tendon.

F: Extensor of the maxilla.

M. 17: M. tentoriocardinalis.

M. 17 originates from the lateral side of the proximal part of the posterior tentorial arm. It is inserted on the mesal edge of the ventral cardinal sclerite by means of a short tendon.

F: Flexor of the maxilla.

M. 18: M. tentoriostipitalis.

This muscle is represented by two components:

M. 18a arises from an elongate attachment area on the posterior ten-

torial arm, dorsad of M. 15. It is inserted mesally on the ventral sclerite of the stipes.

F. Acts as flexor of the maxilla together with M. 17.

M. 18b originates from the ventral wall of the head capsule between the origin of M. 15 and the tentorial base. It is inserted proximally on the narrow sclerotized bar of the dorsal side of the stipes.

F: M. 18b acts as retractor and levator of the stipes.

An intrinsic muscle of the stipes, which is not included in v. Kéler is present:

M. s-s: M. stipitostipitalis.

M. s-s originates from the ventral sclerite of the stipes, and is inserted on the narrow sclerotized bar of the dorsal side of the stipes.

F: Contraction of this muscle results in dorsoventral compression of the stipes.

M. 23: M. stipitopalpalis internus.

M. 23 originates from the ventral sclerite of the stipes, and is inserted mesally on the base of the first palpomere.

F: Flexor of the maxillary palp.

2.5. Labium   (Figs 1, 2, 5, 6):

The submentum is fully integrated into the ventral wall of the head capsule. A narrow, median, membranous zone is continuous with the triangular, unsclerotized mentum. A deep membranous fold connects the mentum with the prementum. The ventral, lateral, and dorsolateral parts of the prementum are sclerotized whereas an extensive dorsomedian area is membranous. A row of bristles is present along the margin of this membranous area. A cupola shaped ligula forms the anteromedian apex of the prementum. The two palpal segments are about equal in length. The distal segment is compressed at the apex and distinctly bilobed with two sensory areas.

A posteromedian, triangular internal apodeme of the prementum serves as muscle attachment area.

Musculature   (Figs 5, 6):

M. 29. M. tentoriopraementalis inferior.

M. 29 originates from the mesal side of the basal part of the posterior tentorial arm, and is inserted mesally on the membranous fold which connects the prementum with the mentum.

F: Retractor of the prementum.

M. 30. M. tentoriopraementalis superior.

M. 30 originates from the mesal side of the posterior tentorial

arm, dorsad to the origin of M. 29. It is inserted dorsolaterally on the base of the prementum.

F: Retractor of the prementum.

M. 34. M. praementopalpalis externus.

M. 34 originates from the median apodeme of the prementum, and is inserted laterobasally on the first palpal segment.

3. Preoral cavity

3.1. Epipharynx   (Figs 5, 7):

The anterior part of the epipharynx, which is not fused with the hypopharynx laterally will be referred to as preepipharynx in the following. The tough preepipharyngeal membrane is covered with short hairs in the anterior parts, especially along the anterior margin which is adjacent to the sclerotized inflected margin of the labrum. The bulging posterior part bears several rows of short hairs in its anteromedian region.

The posterior part of the epipharynx (postepipharynx) is fused with the hypopharynx laterally, thus forming the prepharynx as defined by BITSCH (1966). A totally unpigmented, moderately broad transverse band forms the anterior margin of this epipharyngeal section, which is fairly long and weakly sclerotized.

Musculature (Figs 5, 7):

M. 43. M. clypeopalatalis.

This muscle is divided into four clearly separated parts:

M. 43a.

Originates from the anterior clypeolabral region, and is inserted anterolaterally on the epipharynx.

F: Dilator muscle of the cibarium.

M. 43b.

Originates anteromesally to the origin of M. 43a, and is attached to the anteromesal part of the preepipharyngeal bulge.

F: Dilator muscle of the cibarium.

M. 43c.

Originates posterolaterally to the origin of M. 43b, and is attached to the posterolateral part of the preepipharyngeal bulge.

M. 43d.

M. 43d is divided into 2 mesal and 1 lateral subunit which are inserted on the lateral margin of the sclerotized part of the postepipharynx. The lateral subunit originates laterally to the anteromesal sub-

unit, and is inserted posterior to the posteromesal subunit. The attachment areas are separated by epipharyngeal transverse muscle bands.

3.2. Hypopharynx   (Figs 5, 6):

The cranial part of the hypopharynx is represented by a distinct membranous bulge with strongly pronounced lateral lobes. The anterior margin bears a dense row of long hairs. This membranous bulge is connected with the membranous mentum laterally. The posterior part of the hypopharynx, which is fused with the postepipharynx, is strongly sclerotized along its lateral edges and moderately sclerotized mesally.

Musculature:

M. 41: M. frontohypopharyngalis.

This fairly strong muscle arises from the frontal area anterior to the attachment area of the dorsal tentorial arm. It is inserted on the posterolateral margin of the hypopharynx.

F: Retractor of the mouth opening.

M. 42: M. tentoriohypopharyngalis.

M. 42 is divided into two clearly separated subunits.

M. 42a arises from the tentorial bridge and is inserted medially on the ventral surface of the hypopharynx.

F: Retractor of the hypopharynx.

M. 42b is represented by a few muscle fibres only, which arise from the mesal side of the posterior tentorial arm, and are inserted on the hypopharynx posterolaterally.

F: Antagonist to M. 41.

4. Pharynx   (Fig. 5):

The position of the morphological mouth opening is clearly defined by the insertion of M. 41. The pharynx is round in cross section and totally devoid of sclerotizations, in contrast to the prepharynx which is flattened and more or less strongly sclerotized as described above.

Musculature:

M. 45: M. frontobuccalis anterior.

M. 45 originates from the frontal area anterior to M. 41 and is inserted on the pharynx, immediately posterior to the morphological mouth opening.

F: Dilator of the pharynx.

M. 46: M. frontobuccalis posterior.

M. 46 originates from the frontal area posterior to M. 41, and is inserted on the pharynx posterior to M. 45.

F: Dilator of the pharynx.

M. 51: M. verticopharyngalis.

M. 51 originates dorsolaterally from the hind margin of the head capsule and splits up into several thin fibres which are inserted dorsolaterally on the posterior pharynx.

F: Dilator of the hind pharynx.

M. 52: M. tentoriopharyngalis.

This well developed muscle originates from the tentorial bridge and is attached over a broad region of the ventral side of the pharynx.

F: Dilator of the hind pharynx, antagonist to M. 51.

III. Functional analysis of structures involved with feeding

The nasalar spine and the mandible, especially the retinacula, act together as an effective prey shredding mechanism. The preepipharyngeal bulge and the anterior hypopharyngeal margin fit closely together, thus closing the preoral cavity when M. 43 b and c are not contracted (functional mouth). Lifting of the epipharynx by contraction of M. 43a-d and rectraction of the hypopharnx by contraction of M. 42a opens the functional mouth and dilates the prepharnx. Prey substances which are liquified by egested mid-gut enzymes (BENGTSSON, 1927), are sucked into the preoral cavity. Adduction of the mandibles may support this process. Filtering of the predigested food is achieved by the hypopharyngeal fringe of hairs, the proximal setae of the mesal maxillary edge and the hairs of the penicillum. A certain capillary effect may support the transport of the fluid food into the preoral cavity (SPENCE & SUTCLIFFE, 1982). After relaxation of the muscles mentioned above the functional mouth closes again and the prepharynx is compressed by the elasticity of the epipharyngeal roof and by contraction of prepharyngeal transverse muscles. Compression of the prepharynx and dilation of the pharynx which is caused by contraction of dorsal and ventral pharyngeal dilators results in the passage of the food into the posterior part of the digestive channel. Closing of the anatomical mouth opening is achieved by contraction of M. frontohypopharyngalis and the posterior transverse muscle of the prepharynx.

IV. Discussion of selected characters

Determination of the polarity of character states is based on comparison with character states found in other adephagan larvae (outgroup and ingroup comparison, WATROUS & WHEELER, 1981). The choice of outgroup and ingroup is certainly problematic as long as many important questions concerning adephagan phylogeny remain unsettled, and the two categories cannot be clearly separated throughout. Gyrinidae are the sistergroup of the remaining Adephaga according to BEUTEL & ROUGHLEY (1988) and can be considered as an outgroup for the remaining Adephaga on the basis of this hypothesis. However specializations correlated with subaquatic habits may reduce the value of Gyrinidae as an outgroup in some cases. Trachypachini (+ Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae) are the sistergroup of the remaining Geadephaga according to BEUTEL (1992), (in prep.). Whether this hypothesis is accepted or not, the basal positioning of Trachypachini in the systems proposed by BALL (1960) and KRYZHANOVSKIY (1976) reflects that Trachypachini belong to a basal stock of Adephaga in any case and are therefore suitable for the determination of polarity of character states, whether as outgroup or as ingroup. The plesiomorphic terminal position of both protibial spurs demonstrates clearly that Gehringiini, Metriini and Opisthiini belong to a basal stock of Geadephaga. Therefore they are suitable for ingroup comparison. It is well understood that members of these groups may show some highly derived features absides plesiomorphic characteristics. However, character states which are shared by the larvae of these groups are almost certainly plesiomorphic.

1. Head capsule

1.1. Clypeolabral region:
A moderately long clypeolabral region, with rounded, inconspicuous adnasalia is found in larvae of *Gehringia* (LINDROTH, 1960), *Trachypachus holmbergi, Metrius* and *Opisthius*. This condition is considered as a plesiomorphic character state within Geadephaga. The presence of 4 nasal teeth as they are found in larvae of *Gehringia* (LINDROTH, 1960), *Metrius, Opisthius*, various larvae of Carabini and in larvae of Nebriini is probably a groundplan character state of Adephaga. 4 nasal teeth are also present in larvae of *Andogyrus* and *Aulonogyrus* (BERTRAND, 1972).

A distinctly prolonged clypeolabral region with strongly pro-
nounced adnasalia is characteristic for larvae of *C. coriaceus* and other
larvae of Carabini and Cychrini (LUFF, 1969) and is considered as a poss-
ible synapomorphy of these tribes (*Ceroglossus?*).

The extension of the nasale into a strongly protruding bifurcate
horn with an additional pair of basal or apical teeth suggests a closer re-
lationship between Notiophilini and the genus *Leistus* (LUFF, 1972,
1976). It is remarkable that a similar condition is also found in larvae of
Galeritini (THOMPSON, 1979).

1.2. Frontal and coronal sutures:

A moderately developed frontoclypeolabral apotome which is far
from reaching the hind margin of the head capsule, and a fairly long co-
ronal suture is characteristic for larvae of *Amphizoa*, *T. holmbergi* and
the vast majority of carabid larvae (LUFF, 1972; 1985; THOMPSON, 1979).
This condition is considered as a groundplan feature of Adephaga.

The frontoclypeolabral apotome nearly reaches, or reaches the
hind margin of the head capsule in larvae of Carbini and Cychrini (pers.
observation; LUFF, 1969). This condition is due to the strongly concave
posterodorsal margin of the head capsule and not to prolongation of
the frontal region. The coronal suture is extremely short (Carabini;
LUFF, 1969), or completely lost (Cychrini; LUFF, 1969). These characte-
ristic features of larvae of Carabini and Cychrini are doubtlessly apo-
morphic, and probably a synapomorphy of both tribes.

1.3. Epicranial and postocular ridges:

Both ridges are absent from larvae of Gyrinidae (BETRAND, 1972),
Gehringia (LINDROTH, 1960), *T. holmbergi*, *Metrius*, *Opisthius*, from lar-
vae of Carabini (LUFF, 1969), Cychrini (LUFF, 1979), Omophronini
(LANDRY & BOUSQUET, 1984), Ozaenini (*Physea setosa*), Megacephalini,
Cicindelini, Nebriini, Notiophilini, Loricerini, Elaphrini, Scaritini (in
part), Broscini (in part), Trechini (in part), Nomiini, Licinini, Chlaeniini,
Panagaeini, Pentagonicini, Masoreini, Lebiini, Zuphiini, Galeritini, Hel-
luonini, Pseudomorphini, and Brachinini (THOMPSON, 1979). The ab-
sence of both ridges is certainly a groundplan feature of Adephaga. Ho-
wever, secondary reductions may have occured. Both grooves are
present in larvae of Broscini (in part), Morionini, *Scarites*, *Bembidion*,
Pogonus, Patrobini, Pterostichini (in part), Amarini (in part), Harpalini
(in part) (THOMPSON, 1979), and in larvae of *Trechus rubens* (LUFF, 1985).
Only a cervical groove is present in Broscini (in part), Scaritini (in part),
Tachyna (Bembidiini), Pterostichini (in part), Amarini (in part), Harpa-
lini (in part), and Odacanthini (THOMPSON, 1979).

The presence of cervical and ocular grooves is doubtlessly apomorphic. The phylogenetic interpretation however is difficult due to the high variability of the character states. The presence may be considered as an apomorphic groundplan character state of Caraboidea Limbata (JEANNEL, 1941-42). This would imply, that a strong tendency towards secondary reduction is still present in Scaritini, Broscini, Nomiini, Trechini, and Bembidiini. The complete absence from larvae of Callistomorphi, Masoreimorphi, Lebiomorphi, and *Limbata Balteifera* (JEANNEL, 1941-42) may represent a common derived feature of these groups. These interpretations are certainly speculative and of minor importance for the phylogenetic reconstruction.

1.4. Neck:

The neck is not constricted in larvae of *Gehrinigia* (LINDROTH, 1960), *T. holmbergi, Opisthius, Amblycheila* (HAMILTON, 1925), Omophronini (LUFF, 1978), Carabini, Cychrini (LUFF, 1969) and the majority of the remaining geadephagan taxa. This is doubtlessly a plesiomorphic character state.

A constricted neck is found in larvae of Notiophilini (LUFF, 1976), Nebriini (LUFF, 1972), and Galeritini (THOMPSON, 1979). This condition is certainly apomorphic. The presence of a constricted neck may indicate that Nebriini and Notiophilini together form a monophyletic unit. The presence of the same apomorphic feature in larvae of Galeritini is probably the result of parallel evolution.

Constriction of the neck region does also occur in hydradephagan larvae, e. g. *Andogyrus* (BACHMANN, 1966), and *Coptotomus* (THOMPSON, 1979).

2. Labral spine

A ventral labral spine which is present in larvae of *C. coriaceus, Nebria* (SPENCE & SUTCLIFFE, 1972), *Metrius, Notiophilus, Leistus* (pers. obs.) is almost certainly a character which does not belong to the adephagan groundplan. A labral spine is not found in larvae of Gyrinidae (NOARS, 1956; STAHL, 1984), Haliplidae (JABOULET, 1960; BEUTEL, 1986), *Noterus* (RUHNAU, 1985), *Amphizoa* (pers. obs.), Dytiscidae (DE MARZO, 1979), *T. holmbergi*, and *Opisthius*. It is also absent from larvae of *Cicindela campestris* (BREYER, 1989), *Pterostichus nigrita* (TRÖSTER, 1987), *Omophron variegatum* and *Broscus cephalotes*. One possible interpretation of this character is to assume that Carbini, Nebriini, and Notio-

philini form a monophyletic unit, and that the spine has independently developed in larvae of *Metrius*.

Another possible interpretation is to consider the presence of the labral spine as an apomorphic feature which has evolved early in geadephagan evolution and has been lost in the vast majority of Carabidae due to improved preoral digestion methods.

3. Antennal muscles

The arrangement of antennal muscles, as it is described for *C. coriaceus* is considered as a groundplan feature of Adephaga. A similar arrangement is found in the gyrinid larvae examined (NOARS, 1956, STAHL, 1984), *Haliplus* (BEUTEL, 1986), *Cicindela campestris* (BREYER, 1989), *Amphizoa* (pers. obs.), *Dytiscus* (SPEYER, 1922) and *O. variegatum*.

The muscle which is inserted on the posterior margin of the scapus (M. tentorioscapalis posterior; TRÖSTER, 1987) crosses the remaining two antennal muscles (M. tentorioscapalis anterior and medialis; TRÖSTER, 1987) in larvae of *P. nigrita* (TRÖSTER, 1987), and *B. cephalotes*. This is doubtlessly an apomorphic condition, which may be useful to define a large monphyletic unit within Geadephaga. However the configuration of antennal muscles of more carabid larvae needs to be studied, to provide a solid basis for phylogenetic interpretation.

4. Mandibles

4.1. Mesal edges:

Two mesal edges which enclose a more or less distinct groove, are present in the distal part of the mandibles of larvae of *T. holmbergi*, *Metrius* (1st intar), *Opisthius*, *Amphizoa* (pers. obs.), *Noterus* (RUHNAU, 1985), *Copelatus* (RUHNAU & BRANCUCCI, 1984), *C. campestris* (BREYER, 1989), and *C. coriaceus*. This condition is considered as a groundplan feature of Adephaga.

Closed mandibular channels have obviously developed independently in the larvae of Gyrinidae known at present, larvae of Haliplidae (BEUTEL, 1986), *Canthydrus* and *Hydrocanthus* (RUHNAU, 1986), and Dytiscidae excl. Copelatini (RUHNAU, 1986).

The presence of a single mesal edge, which is characteristic for the vast majority of carabid larvae (THOMPSON, 1979), is most likely

an apomorphic feature. However the reduction of the dorsal cutting edge may have taken place several times independently.

4.2. Penicillum:

A penicillum is absent from larvae of *T. holmbergi*, Hydradephaga (BERTRAND, 1972), *Gehringia* (LINDROTH, 1960), *Metrius, Physea setosa* (VAN EMDEN, 1936) and from larvae of Omophronini (pers. obs.; LUFF, 1978; THOMPSON, 1976), Megacephalini, Cicindelini, Nebriini (except for *Pelophila*), Notiophilini, Morionini, Scaritini (in part), Patrobiini (in part), Zuphiini, Galeritini, Helluonini, Pseudomorphini and Brachinini (THOMPSON, 1979). The absence of the penicillum is probably a ground-plan feature of Adephaga. However, the evident fact that it has been lost many times independently reduces the value of the character decisively. Whether the absence of the penicillum in larvae of Omophronini, Cicindelini, and others is a primitive feature or due to secondary loss, is a matter of speculation.

5. Maxilla

5.1. Cardo:

Only a ventrolateral cardo sclerite is present in larvae of *T. holmbergi, Metrius, Opisthius* and *O. variegatum*, whereas and additional mesal sclerite is present in the vast majority of geadephagan larvae, e. g. *C. campestris* (BREYER, 1989), *P. nigrita* (TRÖSTER, 1987), *C. coriaceus, Blethisa multipunctata, B. cephalotes, Scarites* sp. (pers. obs.). It is quite obvious that the mesal sclerite has newly developed within Geadephaga. The presence of a mesal cardo sclerite may prove useful to define a monophylectic unit within Carabidae. The value of this character however is reduced by the possibility of secondary loss.

5.2. M. stipito-stipitalis:

This muscle is described only for larvae of *C. campestris* (BREYER, 1989) and *C. coriaceus* so far. The muscle is absent in the larvae of Gyrinidae examined (NOARS, 1956; STAHL, 1984), in larvae of *Haliplus lineatocollis* (BEUTEL, 1986) and in larvae of *Dytiscus marginalis* (SPEYER, 1922). The homology of this unusual muscle is unclear and more information is required for a phylogenetic evaluation. The presence seems to be plesiomorphic within Geadephaga.

6. Preoral cavity

6.1. Hypopharynx:

A well defined hypopharynx, which is clearly separated from the dorsal wall of the prementum by a deep fold, is present in larvae of *T. holmbergi, Amphizoa, C. coriaceus, O. variegatum* and *C. campestris* (BREYER, 1989). This is certainly a plesiomorphic condition within Geadephaga. The hypopharyngeal platform is continous with the dorsal wall of the prementum on one level in larvae of *Amara* (DORSEY, 1943), *P. nigrita* (TRÖSTER, 1987), and *B. cephalotes* (pers. obs.). This is certainly a derived feature which may characterize a larger unit within Geadephaga as monophyletic.

Anterior and posterior epipharyngeal ridges as described for *P. nigrita* by TRÖSTER (1987), are also present in larvae of *B. cephalotes*. It is quite obvious that they represent a functional substitution for the reduced hypopharynx in these taxa (a brief explanation will be given below). The presence of these ridges may be a significant synapomorphy of a large monophyletic unit within Carabidae. The character needs to be studied in more taxa.

6.2. Hypopharyngeal filter apparatus:

A moderately broad fringe of longer hairs is present along the anterior margin of the hypopharynx of larvae of *Nebria* (SPENCE & SUTCLIFFE, 1982) and *C. coriaceus*. This filter apparatus is distinctly improved in larvae of *P. nigrita* (TRÖSTER, 1987) and *B. cephalotes* (pers. obs.). A dense field of numerous specifically arranged long hairs (TRÖSTER, 1987) is present on the surface of the anterior hypopharyngeal region. These hairs are branched in case of *P. nigrita* (TRÖSTER, 1987). The improved filter mechanism may represent another synapomorphic feature of a higher category of carabids.

6.3. M. tentorio-hypopharyngalis:

The presence of two components of M. tentoriohypopharyngealis is considered as a plesiomorphic feature within Adephaga. The part which arises from the tentorial bridge is present in larvae of *C. coriaceus* and *T.holmbergi*. It is absent from larvae of *C.campestris* (BREYER, 1989), *Nebria* (SPENCE & SUTCLIFFE, 1982) and *P.nigrita* (TRÖSTER, 1987). The loss is possibly correlated with the interrupted tentorial bridge in the case of *Nebria*. A correlation between reduction of the hypopharynx and loss of M. tentoriohypopharyngalis (a) in other carabid larvae is quite obvious.

7. Pharynx

7.1. Precerebral dorsal dilator muscles:

The presence of two precerebral dorsal dilator muscles of the pharynx as they are found in larvae of *Cicindela campestris* (BREYER, 1989) and *C. coriaceus* is probably a plesiomorphic feature within Geadephaga. Precerebral dilator muscles are absent from larvae of *P. nigrita* (TRÖSTER, 1987). This is certainly an apomorphic feature. The loss of one or both precerebral dilator muscles may be characteristic for larger groups within Carabidae.

7.2. M. verticopharyngalis:

The presence of M. verticopharyngalis is undoubtedly primitive. The muscle is present in larvae of *C. coriaceus, T. holmbergi, C. campestris* (BREYER, 1989) and in the dytiscid larvae examined (DE MARZO, 1979). It is absent from larvae of *Nebria* (SPENCE & SUTCLIFFE, 1982), and larvae of *P. nigrita* (TRÖSTER, 1987). The loss is a derived character state of minor importance for phylogenetic analysis.

7.3. M. tentoriopharyngalis:

The presence of M. tentoriopharyngalis is certainly a primitive characteristic as well. The muscle is present in larvae of *C. coriaceus, Nebria* (SPENCE & SUTCLIFFE, 1982) and in larvae of Dytiscidae (DE MARZO, 1979), *Haliplus* (BEUTEL, 1986) and *Noterus* (RUHNAU, 1986). It is absent in larvae of *C. campestris* (BREYER, 1989) and represented by a few fibrillar structures only in larvae of *P. nigrita* (TRÖSTER, 1987).

V. Concluding remarks

It is obvious from the results presented within this paper that *Carabus* belongs to a basal stock of Geadephaga. The feeding apparatus is characterized by various plesiomorphic features such as the 2-edged mandibles, the rather primitive preoral filter apparatus, the well defined, voluminous hypopharynx, and the complete set of hypopharyngeal, prepharyngeal and pharyngeal muscles. The trend within Geadephaga (excl. Trachypachini) goes clearly towards improvement of the filter mechanism levelling of the hypopharynx, newly developed closing mechanisms, and reduction of muscles connected with the alimentary channel. An increasing elaboration of the larval feeding apparatus plays certainly a crucial role in the evolution of Geadephaga. Even though parallelisms due to parallel selective pressure cannot be ex-

cluded, close attention should be paid to these structural changes. They may be helpful for definition of larger monophylectic units within Geadephaga after examination of a broader spectrum of larvae. A basal positioning of *Carabus* is further supported by the plesiomorphic arrangement of antennal muscles and the absence of cranial ridges.

The presence of a mandibular penicillum and a mesal cardo sclerite may turn out as synapomorphies of a monphyletic unit comprising the major part of Anisochaeta (JEANNEL, 1941-42). The position of Opisthiini, Omophronini and Cicindelinae remains unclear.

Carabini and Cychrini seem to form a well founded monophyletic unit, as suggested by the elongated clypeolabral region with strongly pronounced adnasalia and the strongly concave posterodorsal margin of the head capsule.

The presence of a ventral labral spine, which acts as a crushing device, may point towards a close relationship between Carabini, Cychrini, Nebriini and Notiophilini. However a similar structure is also present in the 1st instar larvae of *Metrius*. It is evident that this is a highly problematic character state which needs further investigation.

The monophyly of a group comprising Notiophilini and Nebriini is substantiated by the constricted neck of the larvae. The presence of a strongly prolonged nasale with prominent teeth is strong evidence for a monophyletic unit comprising *Leistus* and Notiophilini. The nasale is moderately protruding in larvae of *Nebria* but not in larvae of *Eurynebria*. The latter two observation strongly suggest the non-monophyly of Nebriini.

V. Acknowledgements

VI. Literature

BAEHR, M. (1979): *Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax der Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta).* Zoologica *44* (130): 1-76.
BALL, G. E. (1960): *Carabidae (Latreille, 1810). In: Beetles of the United States*

genetischen Beziehungen der Adephaga (Coleoptera, Insecta). Zoologica *44* (130): 1-76.

BALL, G. E. (1960): *Carabidae (Latreille, 1810). In: Beetles of the United States* (ARNETT, R. H., ed.). The Catholic University of America Press, Washington D.C. pp. 55-181.

BALL, G. E. (1979): *Conspectus of carabid classification: history, holomorphology, and higher taxa.* In: *Carabid beetles: their evolution, natural history, and classification* (ERWIN, T. L., BALL, G. E., WHITEHEAD D. R. & HALPERN, A. L., eds.). W. Junk, The Hague, pp. 63-111.

BELL, R. T. (1967): *Coxal cavities and the classification of the Adephaga (Coleoptera).* Ann. entomol. Soc. Amer. *60*: 101-107.

BENGTSSON, S. (1927): *Die Larven der norwegischen Arten von Carabus Lin. Eine morphologische Studie.* Lunds Univ. Arsskr. *N.F. (2) 24(2)*: 1-89.

BERTRANDT, H. (1972): *Les larves et nymphes des Coléoptères aquatiques du globe.* 804 pp. F. Paillart, Abbeville.

BEUTEL, R. G. (1986): *Skelet und Muskulatur des Kopfes der Larve von Haliplus lineatocollis Mrsh. (Coleoptera: Haliplidae). Stuttg. Beitr. Naturk. (A) 390*: 1-15.

BEUTEL, G.G. (1992): *Phylogenetic analysis of thoracic structures of Carabidae (Coleopt. Adephaga).* Z.zool. Syst.-Evolut.-forsch. *30*:53-74.

BEUTEL, R. G. & R. E. ROUGHLEY (1988): *On the systematic position of the family Gyrinidae (Coleoptera: Adephaga).* Z. zool. Syst.-Evolut.-forsch. *26*: 380-400.

BILS, W. (1976): *Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung für die Phylogenie.* Zoomorph. *84*: 113-193.

BITSCH, J. (1966): *L'évolution des structures céphaliques chez les larves des coléoptères.* Ann. Soc. entomol. Fr. *(N.S.) 11 (2)*: 255-324.

BOUSQUET, Y. & H. GOULET (1984): *Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga).* Can. J. Zool. *62*: 573-588.

BREYER, S. (1989): *Skelet und Muskulatur des Kopfes der Larve von Cicindela campestris L. (Coleoptera: Cicindelidae).* Stuttgarter Beitr. Naturk. *(A) 438*: 1-60.

BURAKOWSKI, B. (1975): *Description of larva and pupa of Rhysodes sulcatus (F.) (Coleoptera, Rhysodidae) and notes on the bionomy of this species.* Ann. Zool. (Warsz.) *32*: 271-287.

DAS, G. M. (1937): *The musculature of the mouth-parts of insect larvae.* Quart. J. microsc. Sci. *80*: 39-80.

DE MARZO, L. (1979). *Studi sulle larve dei Coleotteri Dytiscidi. X. Anatomia e funzionamento dell'apparato succhiante cibariofaringeo in alcune forme larvali delle subff. Dytiscinae, Colymbetinae, Laccophilinae e Hydroporinae.* Entomologica (Bari) *15*: 5-72.

DORSEY, C. K. (1943): *The musculature of the labrum, labium, and pharyngeal region of adult and immature Coleoptera.* Smithson. misc. Coll. *103 (7)*: 1-42.

EMDEN, F. VAN (1936): *Eine interessante, zwischen Carabidae und Paussidae vermittelnde Käferlarve.* Arb. phys. angew. Entomol. Berlín-Dahlem *3*: 250-256.

ERWIN, T. L. (1985): *The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles.* In: *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants.* (G. E. BALL, ed.). W. Junk, Dordrecht.

HENNIG, W. (1950): *Grundzüge einer Theorie der phylogenetischen Systematik.* 370 pp. Deutscher Zentralverlag, Berlín.

JEANNEL, R. (1941-42): *Coléoptères Carabiques*. Parts 1-2. Faune de France. Librairie de la Faculté des Sciences, Paris. 1173 pp.

KÉLER, S. VON (1963): *Entomologisches Wörterbuch*. 3. Aufl., Akademie Verl., Berlin, 774 pp.

KRYZHANOVSKIY, O. L. (1976): *An attempt at a revised classification of the family Carabidae (Coleoptera)*. Entomol. Rev. *1*: 80-91.

LANDRY, J.-F. & BOUSQUET Y. (1984): *The genus Omophron Latreille (Coleoptera: Carabidae): Redescription of the larval stage and phylogenetic considerations*. Can. Entomol. *116(11)*: 1557-1569.

LINDROTH, C. H. (1960): *The larvae of Trachypachus Mtsch., Gehringia Darl., and Opisthius Kby. (Col. Carabidae)*. Opusc entomol. *25*: 30-42.

LUFF, M. L. (1969): *The larvae of the British Carabidae (Coleoptera). I. Carabini and Cychrini*. Entomol. *102*: 245-263.

LUFF, M. L. (1972): *The larvae of the British Carabidae (Coleoptera) II. Nebriini*. Entomol. *105*: 161-179.

LUFF, M. L. (1976): *The larvae of the British Carabidae (Coleoptera) IV. Notiophilini and Elaphrini*. Entomol. Gaz. *27*: 51-67.

LUFF, M. L. (1978): *The larvae of the British Carabidae (Coleoptera) V. Omophronini, Loricerini, Scaritini and Broscini*. Entomol. Gaz. *29*: 265-287.

LUFF, M. L. (1980): *The larvae of the British Carabidae (Coleoptera) VI. Licinini, Panagaeiini, Chlaeniini and Oodini*. Entomol. Gaz. *31*: 177-194.

LUFF, M. L. (1985): *The larvae of the British Carabidae (Coleoptera) VII. Trechini and Pogonini*. Entomol. Gaz. *36*: 301-314.

NOARS, R. (1956): *Contribution à la connaissance de la larve d'Orectochilus villosus (Coléoptères Gyrinidés)*. Trav. Lab. Zool. Fac. Sci. Dijon *17*: 1-32.

RUHNAU, S. (1985): *Zur Morphologie und Biologie der praeimaginalen Stadien des Wasserkäfers Noterus crassicornis (Müller, 1776) (Coleoptera, Hydradephaga, Noteridae)*. Unpubl. Diplomarbeit, Fakultät f. Biol., Univ. Tübingen, 99 pp.

RUHNAU, S. (1986): *Phylogenetic relations within the Hydradephaga (Coleoptera) using larval and pupal characters*. Entomol. Basiliensia *11*: 231-271.

RUHNAU, S & BRANCUCCI, M. (1984): *Studies on the genus Lancetes. 2. Analysis of its phylogenetic position using preimaginal characters (Coleoptera, Dytiscidae)*. Entomologica Basiliensia 9: 80-107.

SPENCE, J. R. & SUTCLIFFE, J. F. (1982): *Structure and function of feeding in larvae of Nebria (Coleoptera: Carabidae)*. Can. J. Zool. *60(10)*: 2382-2394.

SPEYER, W. (1922): *Die Muskulatur der Larve von Dytiscus marginalis L. Ein Beitrag zur Morphologie des Insektenkörpers*. Z. wiss. Zool. *119*: 423-492.

STAHL, J. (1984): *Skelett und Muskulatur des Kopfes der Larve von Gyrinus substriatus STEPH. (Gyrinidae, Coleoptera)*. Unpubl. Diplomarbeit, Fakultät f. Biol., Univ. Tübingen, 47 pp.

THOMPSON, R. G. (1979): *Larvae of North American Carabidae with a key to the tribes*. In: *Carabid Beetles: their evolution, natural history, and classification* (ERWIN, T. L., BALL, G. E., WHITEHEAD, D. R. & HALPERN, A. L., eds.). W. Junk, The Hague. pp. 209-291.

TRÖSTER, G. (1987): *Beiträge zur Kenntnis des Skeletts und der Muskulatur des Kopfes der Larve von Pterostichus nigrita (Paykull 1790)*. Stuttg. Beitr. Naturk. (A) *399*: 1-23.

Author's address:
Dr Rolf Georg Beutel
Institut für Biologie II (Zoologie)
RWTH Aachen
D-W 5100 Aachen (FRG)