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The prothorax of Spanglerogyrus albiventris Folkerts, 1979 (Coleoptera, Gyrinidae) Contribution towards clarification of the phylogeny of Gyrinidae

by **R. G. Beutel**

Abstract: External and internal structures of the prothorax of *Spanglerogyrus albiventris* Folkerts, 1979, are described and used for cladistic analysis. The results clearly suggest a sistergroup relationship between the two subfamilies of Gyrinidae: Spanglerogyrinae Folkerts and Gyrininae Thomson. The following characters are considered as strong synapomorphies of Gyrininae: highly specialized notal proprioreceptive organ, triangular shape of procoxae, excavations for reception of the prolegs in repose, mesal comb of spines at the protibial apex. Further possible synapomorphies of Gyrininae are listed in the following: narrow transverse strip of the notum between the anterior and posterior evagination, posteromesal extension of the cryptopleura, presence of a of short profurcal process, loss of the ventral procoxal joint, presence of long profemoral spines, loss of the protibial spur. Some derived muscular features are shared by all members of Gyrininae examined. Some derived characters are shared by members of Orectochilini and *Dineutus:* strong posteromesal extension of the cryptopleura, fusion of the cryptopleura with the notum, strongly prolonged caudal profurcal process, M. dorsoventralis quintus divided into 2 branches, loss of M. noto-pleuralis and M. epimero-coxalis, M. pleura-trochanteralis shifted posteriorly. A proposed monophyletic group comprising Orectochilini and the enhydrine genera would imply, that the condition of the posterior prothoracic wall of members of Orectochilini, which is similar to that of *Spanglerogyrus,* is due to reversal.

Key words: Coleoptera Gyrinidae – Prothorax – *Spanglerogyrus albiventris* – phylogeny.

I. Introduction

This paper is the second in a series on the morphology and systematic position of the gyrinid *Spanglerogyrus albiventris* Folkerts, 1979. *Spanglerogyrus* was described in 1979 by FOLKERTS and a new subfamily of Gyrinidae (Spanglerogyrinae) was erected. A sistergroup relationship between Spanglerogyrinae and Gyrininae (sensu FOLKERTS) was proposed by STEINER & ANDERSON (1981), KAVANAUGH (1986), and BEUTEL & ROUGHLEY (1988). Detailed morphological studies of the head of *Spanglerogyrus* (BEUTEL, 1989), and an analysis of meso- and metathoracic structures of *Spanglerogyrus* and other gyrinid genera (Beutel, in press) correlate well with this view. However, this interpretation of gyrinid phylogeny is not sufficiently supported by morphological data at present. Biogeographic data do not confirm a sistergroup relationship between *Spanglerogyrus* and Gyrininae. To interprete *Spang-*

lerogyrus as an aberrant offshoot of the orectochiline tribe would be in agreement with the restricted distribution and the appearence of the peculiar little gyrinid. This interpretation would imply, that the beetle displays various secondarily derived characters, which appear primitive, but are the result of reversal.

The main purpose of this paper is, to clarify the systematic position of *Spanglerogyrus*. Further interpretations of gyrinid phylogeny are handicapped by a severe lack of information on internal structures of members of various gyrinid genera (see Material and methods).

It is well understood, that this is only one step towards clarification of phylogenetic relationships within Gyrinidae. Study of various body parts and as many gyrinid taxa as possible is indispensible as a sound basis for an understanding of gyrinid evolution.

II. Material and methods

All specimens of *Spanglerogyrus*, which were used for this study were collected by R. E. Roughley and R. G. Beutel at a shaded stream near Evergreen/Alabama (Conecuh County). The specimens were fixed in Kahle's fluid and preserved in alcohol. Araldite was used as embedding medium for microtome sections. The sections were cut with a glass knive at 2–5 µm and stained in methyleneblue. Drawings were carried out with an ocular reticule (stereo microscope) and with the help of SEM micrographs (Cambridge Stereoscan 250 Mk 2).

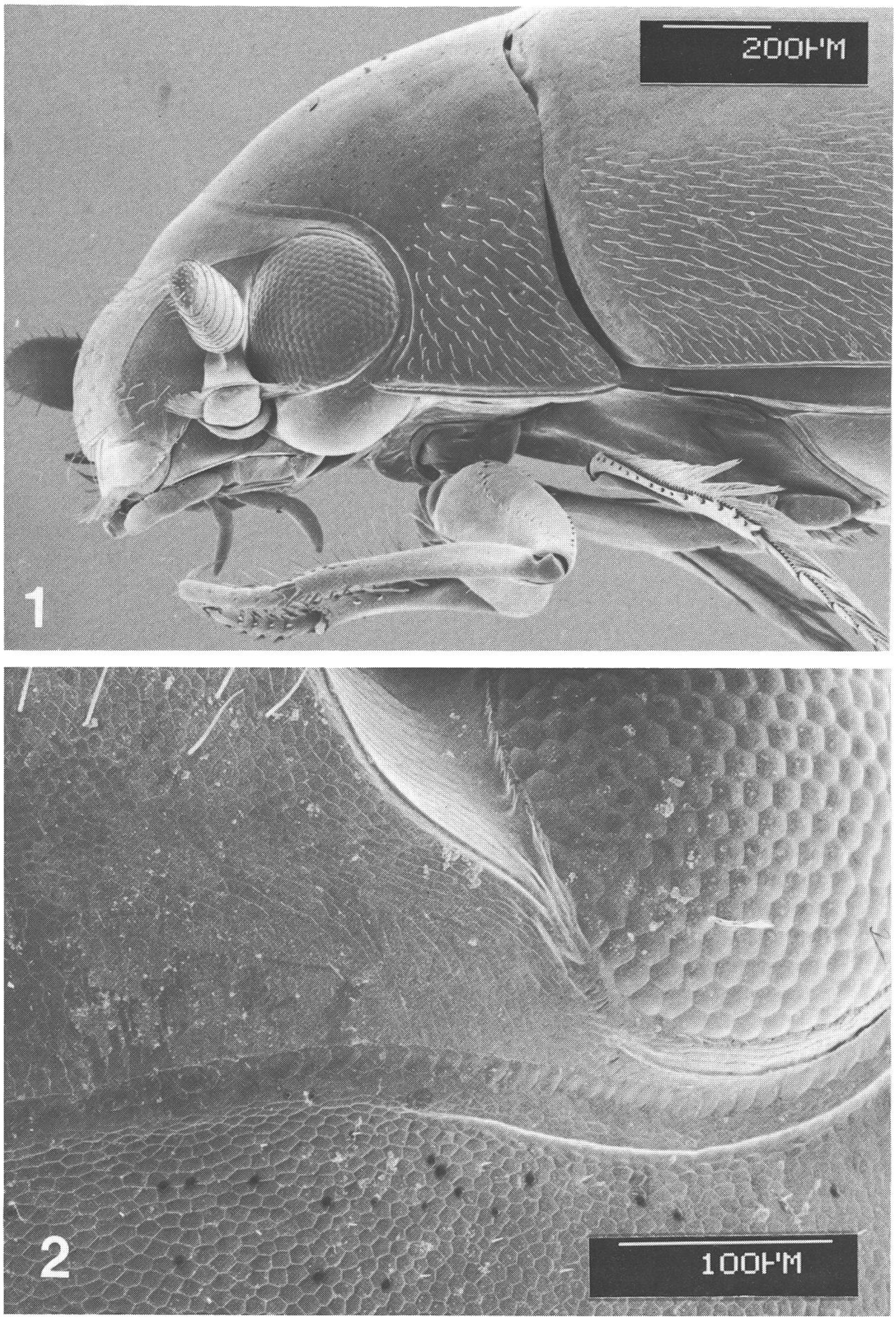
Representatives of the genera *Gyrinus, Aulonogyrus, Orectochilus, Orectogyrus, Gyretes, Andogyrus, Dineutus, Enhydrus, Macrogyrus,* and *Porrhorhynchus* were examined for external skeletal structures. Specimens of *Dineutus assimilis* Kirby, 1837, *Gyretes iricolor* Young, 1954, *Aulonogyrus coccinnus* Klug, 1833, and *Gyrinus marginellus* Fall, 1922, were examined for external and internal structures.

LARSÉN'S (1966) nomenclature is used for the muscles (chapter III.).

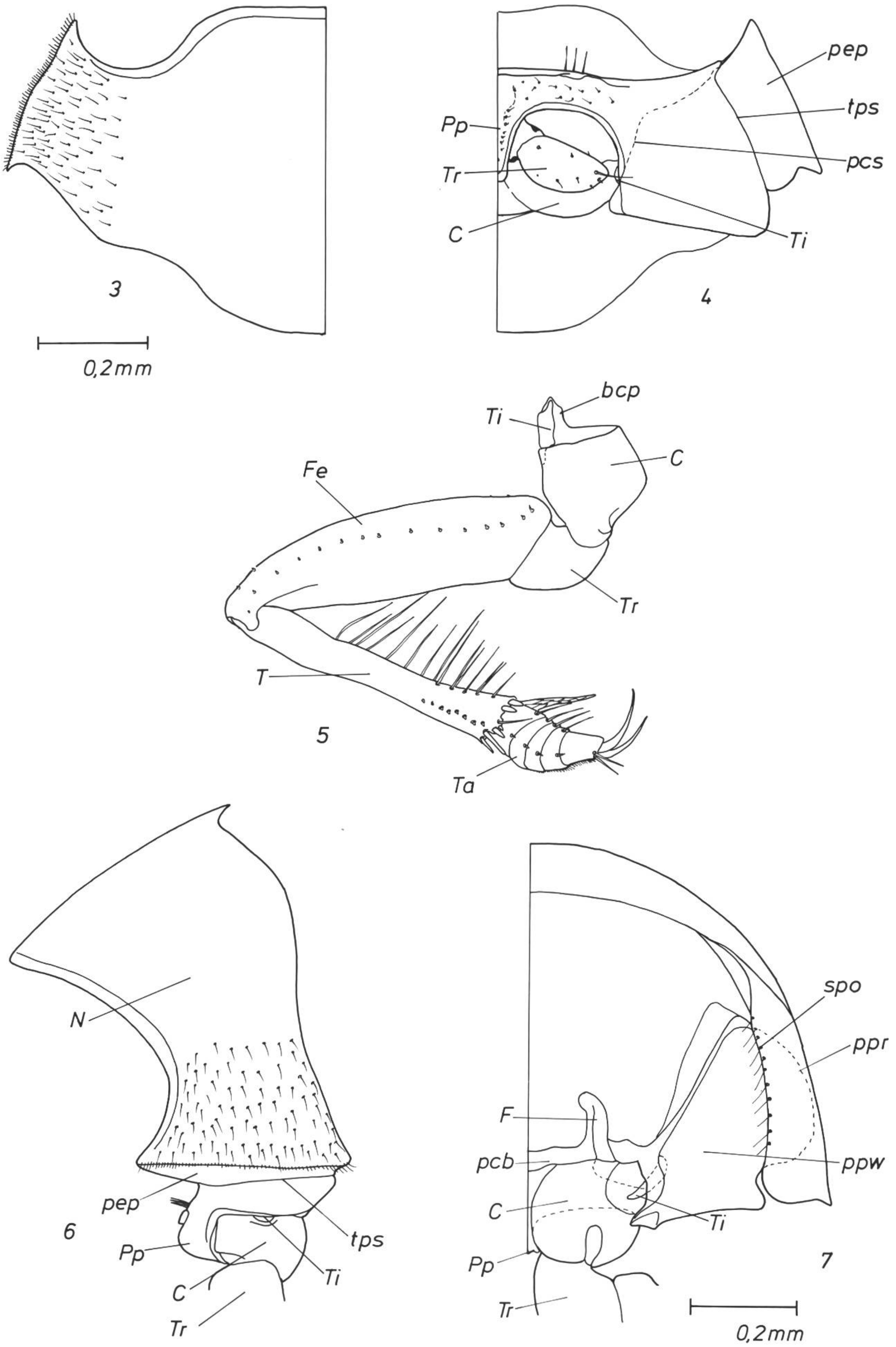
III. Prothoracic structures of Spanglerogyrus

1. Skeleton (Figs 1–7, 9)

The Prothorax of *Spanglerogyrus* is short as in other members of Gyrinidae (Figs 1, 6). The dorsal part is strongly arched, whereas the ventral surface is almost entirely flat (Figs 1, 7). The anterolateral mar-



Figs 1–2: *Spanglerogyrus albiventris*. 1, lateral view. 2, cuticular interlocking mechanism of the anterior notal margin and the head capsule.



Figs 3–7: *Spanglerogyrus albiventris*. Folkerts, Prothorax: 3, dorsal view. 4, ventral view. 5, lateral view. 6, male proleg, cranial view. 7, posterior view, muscles removed.

gin of the notum is following the contour of the hind margin of the dorsal eye. The median part of the notum is considerably expanded. It reaches almost the level of the anterior margin of the dorsal eye anteriorly, and covers a part of the scutellum posteriorly. A fairly broad and distinct bead is present along the anterior notal margin (Figs 2, 3). The cuticula of the head capsule and the anteromedian notal margin is toothed and interlocked in a peculiar manner (Fig. 2). This highly uncommon condition may help, keeping the head in a defined position. Apparently, lateral movements of the head are only feasible, when the head is inclined downwards, thus releasing the locking mechanism. The dorsolateral part of the notum is covered with scattered, thin setae (Figs 1, 3, 6), as in members of Orectochilini (the terms Gyrininae, Orectochilini, Enhydrini, and Gyrinini are used in the sense of FOLKERTS (1979) throughout the paper) and *Heterogyrus* (LARSÉN, 1966). A row of lancet-like setae borders the lateral margin of the notum (Fig. 3). These setae may act as perceptive organs, registering relative movements of the water surface. The notum is sharply inflicted laterally, thus forming the lateral part of the ventral surface of the prothorax (prothoracic epipleura, LARSÉN, 1966) (Figs 4, 6). The cuticula of the lateral parts of the notum is of a pale, white coulour and translucent, as the cuticula of the ventral parts of the prothorax and the forelegs.

The evaginated collar which is surrounding the prothorax anteriorly and posteriorly (Fig. 10) is broad in the median part of the anterior notal margin, and even broader along the posterior notal margin. The notal strip between the anterior and the posterior collar, which serves as attachement area of several muscles (Fig. 8), is not as constricted as in other members of Gyrinidae (BAEHR, 1979), but still fairly narrow. The outer and inner layer of the evaginated collar are firmly attached to each other by cuticular trabeculae. The margin however is free, and bent inwards, thus forming the anterior and posterior prothoracic ridge (LARSÉN, 1966), which is fairly broad in the lateral regions. The pronotum is slightly bulged in the area covering the posterior area of the head capsule. A faint median line is corresponding with a low internal ridge, which serves as attachment area for several muscles (Figs 8, 9).

A distinct external notopleural suture separates the notum from the ventral sclerites of the prothorax (Figs 4, 11). The faint paracoxal suture separates the extensive, posterolateral katapleura from the pleurosternum (Fig. 4). The paracoxal suture is represented by a strong ridge internally (Fig. 11). The pleurosternum is composed of the preepisternum and anepisternum and may include also true sternal parts (basisternum and furcasternum) in its caudal region (Baehr, 1979). A narrow section of the procoxal cavity is formed by the katapleura, whereas the procoxa is enclosed by the pleurosternum in its anterior, medial, and most of its lateral section (Fig. 4). The whole procoxal cavity is bordered by a distinct bead. A slightly sclerotized postcoxal bridge is present as in all other aquatic Adephaga (Hlavac, 1971). The simple, stalk-like profurca arises from the postcoxal bridge. Laterally, the postcoxal bridge is adjacent with a thin and translucent sclerite which is forming the major part of the posterior prothoracic wall in *Spanglerogyrus*. This weakly sclerotized chitinous wall is continuous with the cryptopleura laterally. It is almost certainly of pleural origin. The posterior ridge of the notum is comparatively narrow in *Spanglerogyrus*, thus forming only a modest part of the posterior wall of the prothorax (Fig. 7).

The cryptopleura is about as broad as in other members of Gyrinidae in its anterior section but not expanded in its caudal section (Baehr, 1979) (Figs 8, 10, 11).

The prosternal process is short and inconspicuous as in other members of Gyrinidae (Figs 4, 11). However, an excavation is present in the lateral wall of the posternal process, forming an acessory procoxal joint with a short process of the procoxa (Fig. 11). The prosternal process is strongly curved in lateral view. It is running parallel with the lateral edge of the pronotum in its posterior part. It is adjacent with a conspicuous, wrist-band like chitinous strip, which is forming the anteromedian margin of the pleurosternum. This strip is much less distinct in the lateral parts of the pleurosternum. A conspicuous group of three fairly short, stiff setae is present on either side of the anterior pleurosternal margin (Fig. 4).

The coxae are almost globular (Figs 4, 5, 7). They are slightly flattened laterally, in order to fit with the dorsal surface of the trochanter, and the femoral basis. The movability is largeley restricted to rotation, as a second procoxal joint is present as in all other members of Adephaga except for Gyrininae (Fig. 11). The procoxal spur, which is sunk in the corresponding socket of the procoxal cavity, is directed anteromedially. The axis of rotation results from the anteromedial position of the ventral procoxal joint and the posterolateral position of the combined pleurocoxal and trochantinopleural joint (Fig. 5).

The ventral half of the rhomb-shaped trochantinus fits into an excavation of the lateral coxal basis. A small section is visible externally.

Laterally, the trochantin fits into a furrow of the lateral wall of the procoxal cavity (Figs 4–7).

The trochanter is of normal size and shape (Fig. 5).

The femur is distinctly shorter than in other members of Gyrinidae. The femuro-tibial joints is only slightly surpassing the posterolateral corner of the pronotum. No excavations on the ventral surface of the mesothorax for reception of the prolegs in repose are present in *Spanglerogyrus*. Two rows of very short setae are stretching over the whole lenght of the anterior and dorsal surface of the femorae (the directional terms are used as if the legs were stretched out laterally with the knee turned dorsally). No spines are present along the ventral edge of the femur (Fig. 5).

The tibia is slender, and about as long as the femur. The anteroventral and posteroventral edge bear a row of long spines. Two rows of short spines are present in the distal part of the anterodorsal and posterodorsal tibial edge. The apex is provided with a coronet of spines. The two outer ones are distinctly longer than the others. A conspicuous, strong spur, with a strange, scutate surface structure originates from the inner margin of the tibial apex (Fig. 5). The pentamerous tarsi of the female are slightly compressed in anteroposterior direction. The tarsi of the male specimens are only slightly dilated and possess only comparatively few adhesive hairs (Fig. 5). These adhesive hairs are shifted onto the posterior surface of the tarsomeres as in other gyrinids (LARSÉN, 1966).

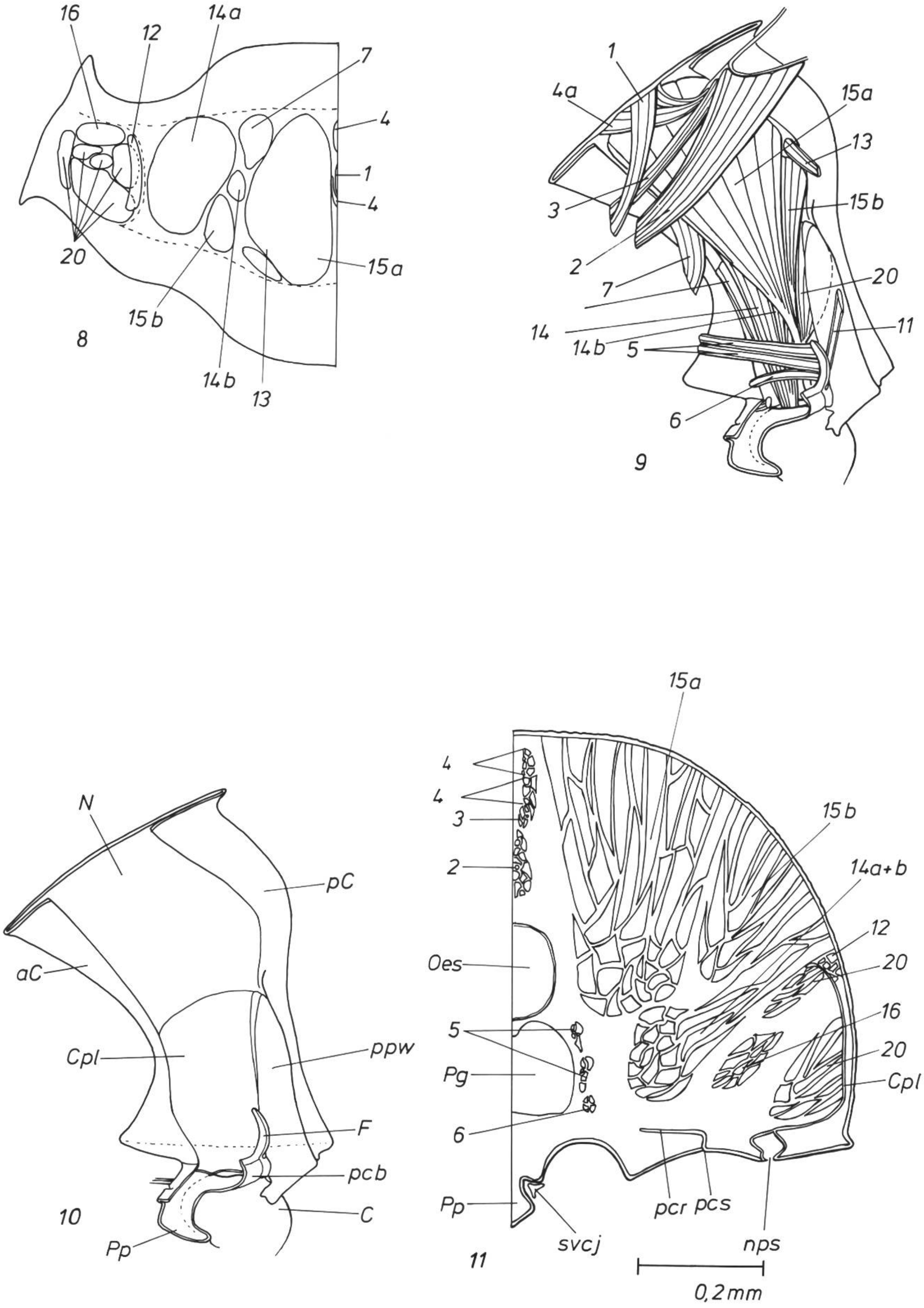
Long setae are present at the anteroventral and posteroventral apices of the tarsomeres 1–4. Together with the long tibial setae, they may act as grasping mechanism. The posteroventral elongate setae are supported by short, flat and strong setae. The tarsomeres 1–4 bear a strong, flattened spine at their posterodorsal apex, one fairly thin, short seta on the anterior and another thin, short seta on the posterior surface. A pair of thin setae is present at the apex of tarsomere 5. The claws are about as long as the tarsomeres 4 + 5 (Fig. 5).

2. Musculature (Figs 8, 9, 11)

a. Dorsal muscles. Musculi pronoti

M 1: M. pronoti primus

A compressed muscle, which originates from the low median ridge



Figs 8–11: *Spanglerogyrus albiventris.* Folkerts: 8, dorsal view, dorsal muscle attachments. 9, median transverse section, musculature. 10, median transverse section, muscles removed. 11, Cross section, the section is slightly inclined backwards. Ventral procoxal joint, paracoxal ridge, notopleural suture, cryptopleura.

of the pronotum, and is attached to the postoccipital ridge laterally. Present in all members of Coleoptera examined by LARSÉN (1966) except for *Gyrinus* and *Aulonogyrus*. However, the muscle is described for *Gyrinus substriatus* Stephens, 1829 (HONOMICHL, 1975). It is also present in *Hygrobia tarda* (Herbst, 1779) (M. 60; BEUTEL, 1986).

M 2: M. pronoti secundus

A strong muscle, which stretches from the medial parts of the 1st phragma to the apodemal plate of the postoccipital ridge. Present in all members of Coleoptera examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

M 3: M. pronoti tertius

This fairly slender muscles originates from the 1st phragma laterally from M 2 and is inserted dorsolaterally on the cervical membrane. Present in the gyrinids examined by LARSÉN (1966), some carabids, and some members of Polyphaga (LARSÉN, 1966).

M 4: M. pronoti quartus

This muscle is divided into 2 components in *Spanglerogyrus*. Both parts originate from the 1st phragma laterally from M 3. M 4 a originates from the median notal ridge anterior to M 1. M 4 b is attached to the notum posterolaterally from M 1. Present in all members of Coleoptera examined by LARSÉN (1966) except for Gyrinidae. However, the muscle seems to be present in *Gyrinus substriatus* (HONOMICHL, 1975, Figs 5, 6). It is also present in *Hygrobia tarda* (BEUTEL, 1986).

b. Ventral muscles. Musculi prosterni

M 5: M. prosterni primus

This muscle is represented by two fairly strong branches, which originate from the lateral side of the profurca. They are inserted medially on the caudal section of the gular ridge. Present in all members of Adephaga and most members of Polyphaga examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

M 6: M. prosterni secundus

M 6 originates ventrally from M 5 and is inserted ventrolaterally on the cervical membrane. Present in all members of Coleoptera examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

c. Dorsoventral muscles. Musculi dorsoventralis

M 7: M. dorsoventralis primus

A strong muscle, which originates from the anterior notal region and inserts on the lateral section of the postoccipital ridge. This muscle is present in all members of Coleoptera examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

M 8: M. dorsoventralis secundus

Absent in *Spanglerogyrus* as in the members of Gyrinidae examined by LARSÉN (1966), in *Cicindela campestris* Linnaeus, 1758, some carabids, and some dytiscids (LARSÉN, 1966).

M 9: M. dorsoventralis tertius

Absent in *Spanglerogyrus* as in all members of Adephaga examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

M 10: M. dorsoventralis quartus

This muscle is very short in *Spanglerogyrus*. It arises from the internal ridge of the paracoxal suture and is inserted ventrolaterally on the cervical membrane. The muscle is present in all members of Coleoptera examined by LARSÉN (1966), and in *Hygrobia tarda* (BEUTEL, 1986).

M 11: M. dorsoventralis quartus

This is a fairly slender muscle which originates from the postcoxal bridge, lateral to the furcal basis, and is attached to the intersegmental membrane close to be the anterolateral mesonotal margin. The muscle is present in all members of Coleoptera examined by LARSÉN (1966), and *Hygrobia tarda* (BEUTEL, 1986).

d. Lateral muscles. Musculi lateralis

M 12: M. noto-pleuralis

This muscle with very short fibres arises from the lateral region of the notum, and is attached to the upper part of the cryptopleura. It is present all along the dorsal margin of the cryptopleura. The muscle is present in most cicindelids and carabids, rhysodids, in amphizoids, hygrobiids, *Noterus,* most dyticids, and in *Gyrinus* and *Aulonogyrus* (BAEHR, 1979).

M 13: M. pronoto-mesepisternalis

M 13 arises from the posterior notal area, and is inserted on the intersegmental membrane. Present in *Hygrobia tarda* (Beutel, 1986) and all members of Coleoptera examined by Larsén (1966) except for *Haliplus confinis* Stephens, 1828.

e. Leg muscles. Musculi pedalis

M 14: M. noto-trochantinalis

This strong muscle is divided into 2 components. The powerful M 14 a originates from the notum medially from the cryptopleura. M14 b, which is not by far as strong as M 14 a, originates from the notum between M 14 a, M 15 a, M 15 b, and M 7. Both branches are inserted on the cranial edge of the trochantin. The muscle is present in all members of Adephaga examined by Baehr, (1979), but absent in various members of Polyphaga (Baehr, 1979). The muscle is divided into two components in all members of Adephaga examined by Baehr (1979) except for *Clinidium* and *Rhysodes*. It is also undivided in *Priacma serrata* (LeConte, 1861) (Baehr, 1979).

M 15: M. noto-coxalis

This powerful muscle is divided into 2 components. M 15 a arises from large parts of the median notal area. M 15 b, which is distinctly less stronger than M 15 a, originates from the posterior notal area between M 15 a and M 14 a. The muscle is present in all members of Coleoptera examined by Baehr (1979), and composed of 2 or 3 components.

M 16: M. episterno-coxalis

This fairly strong muscle arises from the anterolateral area of the cryptopleural ridge, stretches along the medial side of the trochantin, and inserts on the coxal base laterally. It is present in all members of Coleoptera examined by Baehr (1979), except for *Sphaeridium*.

M 17: M. epimero-coxalis

Absent in *Spanglerogyrus*. The muscle is also absent from members of the gyrinid genera *Dineutus*, *Orectochilus*, *Orectogyrus* and *Gyretes*, but present in members of *Gyrinus* and *Aulonogyrus* (Larsén, 1966; Baehr, 1979). It is also reduced in many carabids, hygrobiids, *Haliplus*, *Peltodytes*, *Noterus*, and several representatives of Dytiscidae (Baehr, 1979).

M 18: M. sterno coxalis

M 18 is absent in *Spanglerogyrus* as in all other members of Gyrinidae examined by LARSÉN (1966) and BAEHR (1979). The muscle is also absent from *Rhysodes,* some cicindelids and some carabids (BAEHR, 1979).

M 19: M. Furca-coxalis

This muscle originates from the lateral side of the furcal basis and is inserted on the base of the coxa medially. This muscle is present in all members of Adephaga except for members of Orectochilini (LARSÉN, 1966; BAEHR, 1979).

M 20: M. pleura-trochanteralis

M 20 is subdivided into several components. The area of attachment of this powerful muscle extends over most parts of the cryptopleura. M 20 is inserted on the base of the trochanter by means of a strong tendon. Present in all members of Coleoptera examined by LARSÉN (1979).

M 21: M. coxo-trochanteralis medialis

M 21 originates from the anteromesal wall of the coxa and is inserted on the tendon of M 20. Present in all members of Coleoptera (LARSÉN, 1966).

M 22: M. coxo-trochanteralis lateralis

M 22 is composed of 4 components, which originate from the anterior coxal wall, the mesal coxal wall, the mesal coxal basis, and the lateral coxal wall. All components insert on the lateral lip of the base of the trochanter. Present in all members of Coleoptera (LARSÉN, 1966).

IV. Discussion of characters

1. Anterior and posterior notal margin

The median part of the anterior and posterior margin of the pronotum is conspicuously extended in *Spanglerogyrus*. This is considered as an autapomorphous character state of *Spanglerogyrus* as a similar condition is not found in members of other adephagan families. The plesiomorphic condition is also found in the members of Gyrininae examined (BAEHR, 1979, personal observation).

2. Pronotal-occipital cuticular interlocking mechanism

The cuticula of the anterior notal margin of *Spanglerogyrus* is interlocked with the cuticula of the occipital region of the head capsule. This condition is not described for any member of other gyrinid genera or other adephagan families, and considered as an autapomorphous character state of *Spanglerogyrus*.

3. Size and shape of the notal area between the anterior and posterior evagination

The notal area, which is reserved for muscle attachment, is distinctly narrower in *Spanglerogyrus* than in members of other adephagan families. This is considered as a derived groundplan character of Gyrinidae (char. 3 a). The extreme contraction of this area in *Gyrinus natator* Linnaeus, 1758, *Dineutus aereus* (Klug, 1834) and *Orectochilus villosus* Müller, 1776 (BAEHR, 1979) is considered as a possible synapomorphy of Gyrininae (char. 3 b).

4. Pronotal epipleura

The pronotal epipleura are broad in *Spanglerogyrus* and members of *Gyrininus* and *Aulonogyrus* (LARSÉN, 1966; personal observation), but fairly narrow in members of Orectochilini and the enhydrine genera (LARSÉN, 1966; personal observation). As a gradual modification, this character is of little significance. Following the in-group comparison criterion, the narrow epipleura may be considered as a possible synapomorphy of enhydrine genera and Orectochilini.

5. Pubescence of the lateral notal area

The lateral area of the notum is covered with setae in *Spanglerogyrus,* members of Orectochilini (personal observation), and *Heterogyrus* (LARSÉN, 1966). These short hairs carry a store of air between them when the beetles dive, thus increasing their buoyancy and enabling them quickly to reestablish their contact with the water surface when they have been washed over by waves or submerged by falling water (LARSÉN, 1966). The presence of these setae is interpreted as a derived ground-plan character of Gyrinidae, and the absence in members of the enhydrine genera and the genera *Gyrinus* and *Aulonogyrus* as an apomorphic character state within Gyrinidae (in-group criterion). The loss of these setae has probably occured several times independently. It may be correlated with the preference of still water habitats in the case of *Gyrinus* and *Aulonogyrus*.

6. Proprioreceptive organ of the prothorax

The proprioreceptive organ of the prothorax (LARSÉN, 1966) is represented by a tuft of specialized, spatulate setae in the members of Gyrininae examined by LARSÉN (1966). This condition is considered as derived and a synapomorphy of *Gyrininae*. A row of fairly long, unspecialized setae extends along the margin of the notal part of the posterior prothoracic wall in *Spanglerogyrus*. This is almost certainly a preceeding stage of the proprioreceptive organ as found in members of Gyrininae, and therefore a plesiomorphic character state.

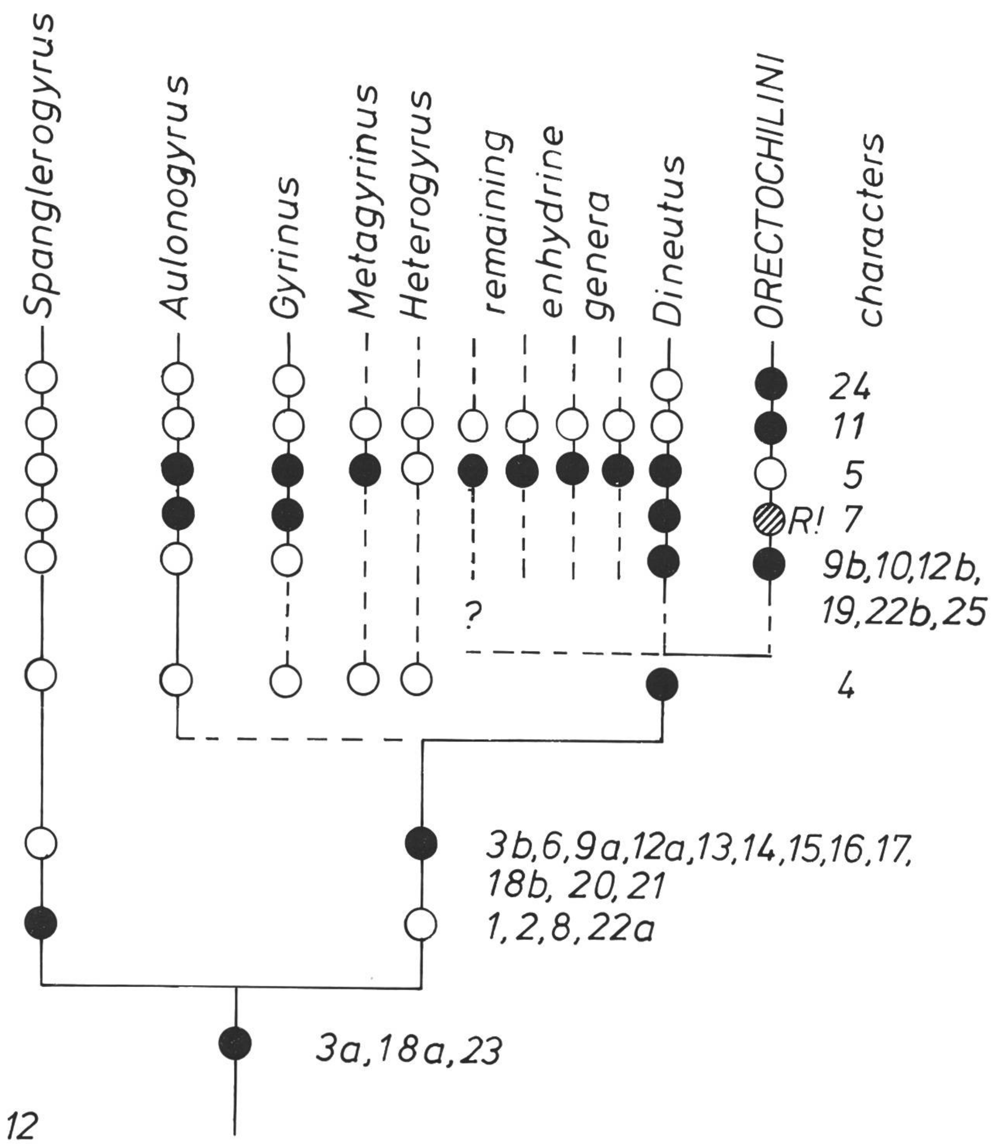


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Fig. 12: Proposed phylogeny of Gyrinidae; Reversal is indicated as R!.

7. Posterior prothoracic wall

The notal part of the posterior prothoracic wall (posterior ridge of the prothorax, LARSÉN, 1966) is fairly narrow in *Spanglerogyrus,* and devoid of a medially projecting edge or process. Large parts of the posterior prothoracic wall are represented by a weakly sclerotized, triangular plate, which is continuous with the postcoxal wall, and the katapleura. This is probably the plesiomorphic condition among Gyrinidae (character correlation criterion).

The posterior ridge is of very modest size in members of Orectochilini (LARSÉN, 1966; personal observation), but a distinct, medially projecting process, carrying the proprioreceptive organ, is present. The posterior wall of the prothorax is almost exclusively represented by a weakly sclerotized plate. No stronger sclerotized katapleural area is marked off from this transparent chitinous wall. This type of posterior protoracic wall appears similar to that of *Spanglerogyrus,* except for the medially directed process of the posterior ridge. It is correlated with the lateral expansion of the dorsal region of the mesothoracic anepisternum in members of Orectochilini according to LARSÉN (1966), and therefore most likely a secondary condition.

The posterior prothoracic ridges in members of *Dineutus, Gyrinus* and *Aulonogyrus* are extensive, with a conspicuous, medially projecting edge, carrying the proprioreceptive organ (LARSÉN, 1966, personal observation). A strongly sclerotized katapleural area is clearly separated from the weakly sclerotized, transparent part of the posterior prothoracic wall, which is continuous with the postcoxal bridge. This is considered as an apomorphic character state. It appears most plausible, to assign this derived character state to the groundplan of Gyrininae. This implies that the condition found in members of Orectochilini is not plesiomorphic but secondarily derived as pointed out above.

8. Coloration

The lateral portions of the pronotum, the ventral surface of the prothorax and the prolegs of *Spanglerogyrus* show a bright, white coulour. Muscles are clearly visible through the translucent cuticle. Such a coloration is not described for any other member of Gyrinidae or Adephaga, and is considered as an automorphic character state of *Spanglerogyrus.* The white coulour of the ventral side may yield a certain protection from attacks by fishes.

A yellowish brown or darker brown is characterirstic for other members of Gyrinidae. Bright yellow epipleurae and lateral margins of the pronotum are known from representatives of Orectochilini (*Orectogyrus,* personal observation), enhydrine genera (*Porrhorhynchus,* personal observation) and Gyrinini (*Aulonogyrus,* personal observation). Whether this is the primitive condition among Gyrinidae, or a derived character state, which has evolved several times independently, remains open to question.

9. Shape of the cryptopleura

The cryptopleura of *Spanglerogyrus* is about as broad in the anterior as in the posterior region. The cryptopleura is distinctly extended mesally in the caudal section in members of *Gyrinus* and extremely extended in members of Orectochilini and *Dineutus* (Baehr, 1979).

The shape of the cryptopleura found in *Spanglerogyrus* is considered as plesiomorphic character state, as a similar condition is found in *Priacma* and all members of Adephaga examined by Baehr (1979) except for some dytiscids.

A modest extension of the cryptopleura is considered as a derived groundplan condition of Gyrininae (9 a), and the further extension as a possible synapomorphy of the enhydrine genera and Orectochilini (9 b).

10. Fusion of the cryptopleura with the notum

The cryptopleura is fused with the notum in members of *Dineutus* and Orectochilini (Larsén, 1966). This is considered as a possible synapomorphy of the enhydrine genera and Orectochilini.

11. Prosternal process

The prosternal process is short in *Spanglerogyrus* and members of Enhydrini and Gyrinini. It does not reach the hind margin of the procoxae. This is considered as a primitive groundplan character state of Gyrinidae (Beutel & Roughley, 1988). The extremely reduced posternal process of members of Orectochilini (Hatch, 1927; personal observation) is considered as a synapomorphy of this tribe.

12. Caudal profurcal process

A long, caudally directed process arises from the posterior surface of the profurca in members of *Dineutus* and Orectochilini (Baehr, 1979). This process is only indicated in members of *Gyrinus* and *Aulonogyrus* according to Baehr (1979) and totally absent in *Spanglerogyrus* (personal observation). A short profurcal process is considered as a derived groundplan character of Gyrininae (12 a), whereas the long process may represent a synapomorphy of the enhydrine genera and Orectochilini (12 b). The bisectional condition of M. dorsoventralis quintus (M 11) in members of *Dineutus* and Orectochilini (BAEHR, 1979) is correlated with the prolongation of the caudal profurcal process. The absence of this process in *Spanglerogyrus* and the members of other adephagan families (BAEHR, 1979) is clearly plesiomorphic.

13. Ventral procoxal joint

A ventral procoxal joint is absent in the members of Gyrininae examined by BAEHR (1979), and in members of the genera *Enhydrus, Porrhorhynchus, Andogyrus, Macrogyrus,* and *Orectogyrus* (personal observation). This is considered as synapomorphy of Gyrininae. The presence of the ventral procoxal joint in *Spanglerogyrus* is considered as plesiomorphic, as it is also present in the members of the remaining adephagan families (BAEHR, 1979).

The loss of the ventral procoxal joint is probably associated with the necessity of cleaning the elytra and abdominal segments with the prolegs (LARSÉN, 1966). For these purposes, an increased moveability of the procoxae is indispensible. The middle and hind legs of members of Gyrininae are converted into short, broad paddles, which are perfect as locomotor organs, but of little use as cleaning devices.

14. Procoxal shape

The procoxa of *Spanglerogyrus* is roughly globular in shape, as in most members of other adephagan families (BAEHR, 1979). This is considered a primitive groundplan character of Gyrinidae and as a groundplan character of Adephaga. The procoxae of members of Gyrininae are distinctly triangular in shape, which is achieved by caudolateral extension (LARSÉN, 1966; BAEHR, 1979; personal observation). Such a condition is not found in any other members of Adephaga (BAEHR, 1979; personal observation) and is considered as a synapomorphy of Gyrininae.

15. Excavations for reception of the prolegs in repose

A distinct excavation for reception of the prolegs in repose, extending over the mesothoracic anepisternum and epimeron, the metathoracic anepisternum and the anterior part of the elytral epipleura, is present in the members of Gyrininae but absent from *Spanglerogyrus*. The presence of these excavations is considered as a synapomorphy of Gyrininae.

The absence in *Spanglerogyrus* is clearly plesiomorphic, as similar excavations are not known from any other members of Adephaga.

These excavations improve the streamline of the ventral body surface.

16. Femoral spines

The ventral side of the femorae of members of most gyrinine genera is provided with an anterior row of short spines, and a posterior row of longer spines (LARSÉN, 1966; personal observation), which are probably a part of a grasping mechanism. The row of longer spines is functionally replaced by a serrate, ventral profemoral edge in some representatives of Enhydrini (*Enhydrus, Dineutus, Macrogyrus*), and two rows of acuminate bunches of setae are present in *Porrhorhynchus* (personal observation).

The profemorae of *Spanglerogyrus* are devoid of any longer setae. Following the in-group criterion, the absence of longer profemoral setae should be considered as plesiomorphic, and their presence as synapomorphy of Gyrininae (with secondary reduction in several genera). This interpretation would be in agreement with a stepwise improvement of the profemoral-protibial grasping mechanism within Gyrinidae. However, a secondary reduction of longer profemoral setae in *Spanglerogyrus,* resulting from an unfavourable size relationship between prey and predator is another possible interpretation.

17. Apical spines of the protibia, mesal comb of spines

The apex of the protibia of *Spanglerogyrus* bears a coronet of spines, with two fairly long spurs on the outer edge. Members of Gyrininae are characterized by a conspicuous, dense mesal comb of spines and absent or extremely reduced lateral spurs or spines (LARSÉN, 1966; personal observation). This condition is considered as an apomorphic character state and synapomorphy of Gyrininae. It is a highly specialized arrangement of the apical protibial spines, compared to that of *Spanglerogyrus,* which is more similar to that of other members of Adephaga.

18. Tibial spur

One strong spur, with an unusual fir-cone like surface structure is present at the mesal apex of the tibia of *Spanglerogyrus* (meso- and metatibial spurs show the same surface structure). A more or less distinct, tuft-like concentration of setae is present at the mesal apex of the tibia of members of Gyrininae. This setal tuft is fairly strong and conspicuous in all members of enhydrine genera examined (personal observation), well isolated, but composed of few long setae only in the members Orectochilini examined (personal observation), and very slightly indicated or obsolete in members of *Gyrinus* and *Aulonogyrus* (personal observation).

The presence of two protibial spurs is considered as a primitive groundplan character state of Adephaga. The presence of only one spur, as found in *Spanglerogyrus,* is considered as a derived groundplan character of Gyrinidae (18 a), and the reduction of this spur as a synapomorphy of Gyrininae (18 b).

19. M. noto-pleuralis (M 12)

M 12 is present in members of *Gyrinus* and *Aulonogyrus* (BAEHR, 1979), and in *Spanglerogyrus,* but absent in the members of *Dineutus* and Orectochilini examined by BAEHR, (1979). The presence is certainly a primitive groundplan character of Gyrinidae, as the muscle is present in most representatives of other adephagan groups (BAEHR, 1979). The loss, which is most likely connected with the fusion of the mesal cryptopleural area with the notum, is a possible synapomorphy of enhydrine genera and Orectochilini.

20. Origin of M. dorsoventralis primus (M 7)

The mesal origin of M 7 as described for members of *Dineutus, Gyrinus, Aulonogyrus* and Orectochilini by BAEHR (1979), is considered as a synapomorphy of Gyrininae. The origin of M 7 between M 15a and M 14 a, as found in *Spanglerogyrus,* is considered as a primitive groundplan character of Gyrinidae. A similar condition is found in many carabids, *Leoglymmius lignarius* Oliff, 1835, *Haliplus ruficollis* (Degeer, 1774) and *Noterus crassicornis* (Müller, 1776) (BAEHR, 1979). The mesal position of M 7 in *Amphizoa isolens* LeConte, 1853, *Hygrobia tarda,* and members of Dytiscidae, is considered as an apomorphic character state, which has evolved independently from Gyrininae, and as a possible synapomorphy of Amphizoidae, Hygrobiidae and Dytiscidae. The posteromesal position of M 7 in *Hygrobia tarda* and dytiscids (BAEHR, 1979) may be considered as synapomorphy of Hygrobiidae and Dytiscidae.

21. M. noto-coxalis (M 15)

The strong mesal component of M 15 in *Spanglerogyrus,* which is also found in rhysodids *(Leoglymmius lignarius)*, many carabids, haliplids (*Haliplus ruficollis*) and noterids (*Noterus crassicornis*) (Baehr, 1979), is considered as a plesiomorphic character state.

The area of attachment of M 15 a in the members of Gyrininae examined by Baehr (1979) is transverse, and shifted in a posterolateral position. This is considered as a synapomorphy of Gyrininae. A similar position of M 15 a is found in *Amphizoa insolens, Hygrobia tarda,* and members of Dytiscidae (Baehr, 1979). This is considered as a result of parallel evolution and as a possible synapomorphy of Amphizoidae, Hygrobiidae, and Dytiscidae.

22. M. epimero-coxalis (M 17)

M 17 is present in members of *Gyrinus* and *Aulonogyrus,* but is absent in members of *Dineutus, Orectogyrus, Orectochilus, Gyretes* (Baehr, 1979), and in *Spanglerogyrus.* We assume, that the loss of M 17, which is certainly a derived character state, occured at least two times independently (22 a, loss in *Spanglerogyrus;* 22 b, loss in members of Orectochilini and enhydrine genera). M 17 is also absent from many other representatives of Adephaga (Baehr, 1979).

23. M. sterno-coxalis (M 18)

The absence of M 18 from *Spanglerogyrus* and the members of Gyrininae examined (Larsén, 1966; Baehr, 1979) is considered as a synapomorphy of Gyrinidae. As a loss, this character is of little relevance. M 17 is also reduced in members of other adephagan families (Baehr, 1979).

24. M. furca-coxalis (M 19)

The absence of M. furca coxalis is considered as a synapomophy of Orectochilini. The muscle is present in other members of Gyrininae examined by Baehr (1979), and in *Spanglerogyrus.*

25. Position of M. pleura-trochanteralis (M 20)

Large parts of M 20 are shifted in a posteromesal position in the members of *Dineutus* and Orectochilini examined by Baehr (1979). This is considered as a possible synaypomorphy of Orectochilini and enhydrine genera. Such a position of M 20 is not described for members of other adephagan families (Baehr, 1979). A lateral position of M 20 is found in members of Gyrinini (Baehr, 1979) and in *Spanglerogyrus.*

V. Conclusions

The results of this study point clearly towards a sistergroup relationship between *Spanglerogyrus* and Gyrininae, even if those characters, which are not very reliable as chars. 3 and 9 (gradual modifications), char. 13 and 18 (losses) and char. 16 (doubtful determination of the polarity of character states) are not taken into consideration. The following characters are convincing synapomorphies of Gyrininae: highly specialized proprioreceptive organ (char. 7), triangular shape of the procoxae (char. 15), excavations for the prolegs in repose (char. 16), and the mesal comb of spines of the protibia (char. 18). The monophyly of Gyrininae is further supported by common derived features of the mesal origin of M 7 (char. 20), and the posterolateral position of M 15 a (char. 21).

The relationships within Gyrininae remain rather unclear. The absence of lateral notal pubescençe (char. 5) is a common derived character of the genera *Gyrinus* and *Aulonogyrus* and of members of the enhydrine genera. As a loss, this character is of little significance. A common derived character state of *Gyrininus, Aulonogyrus* and *Dineutus* (remaining enhydrine genera?), which seems more significant, is the composition of the posterior prothoracic wall (char. 7; large notal posterior ridge, strongly sclerotized katapleural component). However, as pointed out above, there is good evidence, that the condition of the posterior prothoracic wall in members of Orectochilini is not primitive, but secondarily derived.

The following apomorphic characters are shared by members of Orectochilini and *Dineutus:* conspicuous posteromesal extension of the cryptopleura (char. 9 b, gradual modification), fusion of the cryptopleura with the notum (char. 10), strongly prolonged caudal process of the profurca (char. 12 b, gradual modification), M 11 divided into 2 branches (char. 12 b), loss of M 12 (char. 21), loss of M 17 (char. 22; parallel loss in *Spanglerogyrus*), and the posteromesal displacement of M 20 (char. 25). It is not clear at present, whether these derived character states are shared by all the remaining enhydrine genera.

Despite of the lack of information on internal structures of members of the enhydrine genera other than *Dineutus,* a working hypothesis of a monophyletic unit comprising Orectochilini and enhydrine genera may be appropriate. This hypothesis would be in agreement with the results of a study of gyrinid meso- and metathoracic structures (BEUTEL, in press).

Characters 1, 2, 8, and 24a are interpreted as autapomorphies of *Spanglerogyrus*.

Characters 11 and 24 are possible synapomorphies of Orectochilini. Characters 3a, 18a and 23 are synapomorphies of Gyrinidae.

No synapomorphies are given for Enhydrini and Gyrinini. Further studies may reveal, wheter Enhydrini and Gyrinini are monophyletic or not.

Abbreviations used in the figures

aC	anterior evaginated collar
bcp	basal coxal process
C	coxa
Cpl	cryptopleura
F	furca
Fe	femur
N	notum
nps	notopleural suture
Oes	oesophagus
pC	posterior evaginated collar
pcb	postcoxal bridge
pcr	paracoxal ridge
pcs	paracoxal suture
pep	prothoracic epipleura
pg	prothoracic ganglion
Pp	prosternal process
ppr	prothoracic posterior ridge
ppw	pleural part of the posterior prothoracic wall
spo	seta of the proprioreceptive organ
svcj	spine of the ventral procoxal joint
T	tibia
Ta	tarsus
Ti	trochantinus
Tr	trochanter

Muscles are indicated by numbers (Larsén's nomenclature)

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