PHYLOGENETIC ANALYSIS OF THE FAMILY GYRINIDAE (COLEOPTERA) BASED ON MESO- AND METATHORACIC CHARACTERS

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ABSTRACT

Thirty six characters of the meso- and metathorax of adults of Spanglerogyrus albiventris *Folkerts and other members of Gyrinidae were examined and analyzed phylogenetically. The acquired data suggest that Spanglerogyrinae are the sister-group to the remainder of Gyrinidae; oar-like tibial processes, feather-like swimming hairs, and the presence of one tibial spur only are autapomorphies of* Spanglerogyrus. *Members of Gyrininae are characterized by a large number of synapomorphic character states. Some of these are: anepisternal-elytral opening, excavations for the prolegs in repose, paddle-like middle- and hind legs, swimming lamellae, metanotum extended laterally, metapostnotum inflected below the scutellum, metasternal transverse-ridge completely reduced, metafurca arising from the fused medial metacoxal walls, lateral metafurcal projections reduced, medial metacoxal walls fused, loss of several flight muscles, loss of Mm. furca-coxalis anterior and lateralis (M 81 and M 82), presence of M. noto-trochanteralis (M 84). The absence of M. sterno-episternalis (M 72) is considered as a possible synapomorphy of* Gyrinus *and* Aulonogyrus (+ Metagyrinus, Heterogyrus ?). Orectochilini *and the enhydrine genera seem to form a well-founded monophyletic unit. The following characters are interpreted as synapomorphies of this assemblage: anterior and posterior walls of tibiae and proximal tarsomeres connected by cuticular columnae, markedly developed elytral glossula, median metanotal area only half as broad as lateral parts, metanotum without membranous area. The modified shape and position of metatarsomeres 4 + 5 is considered as a synapomorphy of the genera* Dineutus, Porrorhynchus, Macrogyrus, Andogyrus *and* Orectochilini. *Consequently,* Enhydrini *are not monophyletic. The concealed mesoscutellar lobe in members of* Dineutus *and* Porrorhynchus *is a possible synapomorphy of both genera. The modified shape and position of mesotarsomeres 4 + 5 is considered as a synapomorphy of a monophyletic group comprising* Macrogyrus, Andogyrus *and* Orectochilini. *The attachment of the anterior metacoxal wall to the hind margin of the ventral sclerite of the metathorax is another apomorphic character state that suggests a close relationship between* Orectochilini *and* Andogyrus (+ Macrogyrus ?). Orectochilini *are characterized by distinctive synapomorphies, some of which are: opening between elytra and mesothoracic anepisternum narrow, anterior median ridge of the mesothoracic preepisternum present, lateral internal process of the mesocoxae trilobed, tendons of M. noto-coxalis (M 40) and M. coxa-subalaris (M 43) arise from the lateral internal process of the mesocoxa, basalar disc absent, loss of further flight muscles. A sister group relationship between* Orectogyrus *and* Orectochilus *is indicated by two apomorphic character states: anterior walls of mesocoxae*

attached to the ventral sclerite of the mesothorax, lateral internal process of the mesocoxae fused with the anepisternum. Whether Heterogyrus *is more closely related to the genera* Gyrinus, Metagyrinus *and* Aulonogyrus, *or to the enhydrine-orectochiline lineage remains open to question.*

Zusammenfassung

Sechs und dreizig Merkmale des Meso- und Metathorax von adulten Vertretern der Gyrinidae, insbesondere von Spanglerogyrus albiventris *Folkerts wurden untersucht und phylogenetisch ausgewertet. Die vorliegenden Daten legen den Schluß nahe, daß die* Spanglerogyrinae *den übrigen Gyrinidae als Schwestergruppe gegenüberstehen. Ruderartige Tibialfortsätze, gefiederte Schwimmhaare, und das Vorhandensein von nur einem Tibialsporn sind autapomorphe Merkmale von* Spanglerogyrus. *Die Gyrininae sind durch eine größere Anzahl von Synapomorphien gekenzeichnet. Einige dieser Merkmale werden im Folgenden aufgeführt: Öffnung zwischen dem mesothorakalen Anepisternum und der Elytrenbasis, Vertiefungen zum Anlegen der Vorderbeine in Ruhestellung, paddelartige Mittel- und Hinterbeine, Schwimmblättchen, Metanotum lateral verbreitert, Metapostnotum unter das Scutellum eingeschlagen, metasternale Transversalleiste völlig reduziert, Ursprung der Metafurca von den verwachsenen medialen Hinterhüftswänden, seitliche Metafurcalarme reduziert, mediale Hinterhüftswände verwachsen, Reduktion einiger Flugmuskeln, Mm. furca-coxalis anterior und lateralis (M 81 und 82) fehlen, M. furca-trochanteralis (M 84) ist vorhanden. Das Fehlen von M. sterno-episternalis (M 72) wird als mögliche Synapomorphie der Gattungen* Gyrinus *und* Aulonogyrus *(+* Metagyrinus, Heterogyrus?*) angesehen. Die* Orectochilini *scheinen zusammen mit den Gattungen der* Enhydrini *eine wohlbegründete monophyletischeEinheit zu bilden. Folgende Merkmale werden als Synapomorphien dieser Gruppierung interpretiert: die vorderen und hinteren Wände der Tibiae und der proximalen Tarsomeren sind durch kutikuläre Verstrebungen fest miteinander verbunden, die Glossula der Elytren ist stark ausgeprägt, das Metanotum ist median nur etwa halb so breit wie lateral, die mediane membranöse Zone fehlt. Die abgewandelte Form und Stellung der Metatarsomeren 4 + 5 wird als Synapomorphie der Gattungen* Dineutus, Porrorhynchus, Macrogyrus, Andogyrus *und der* Orectochilini *gedeutet. Daraus folgt, daß die* Enhydrini *nicht monophyletisch sind. Das verdeckte Schildchen des Mesoscutellum ist eine mögliche Synapomorphie der Gattungen* Dineutus *und* Porrorhynchus. *Die abgewandelte Form und Position der Mesotarsomeren 4 + 5 wird als Synapomorphie einer monophyletischen Gruppe gewertet, die die Gattungen* Macrogyrus, Andogyrus, *sowie die* Orectochilini *umfaßt. Die Verwachsung der vorderen Wand der Metacoxae mit dem Hinterrand des ventralen Sklerit des Metathorax ist ein weiteres apomorphes Merkmal, das eine nähere Verwandtschaft zwischen* Andogyrus *(+* Macrogyrus ?*) und den* Orectochilini *nahelegt. Die* Orectochilini *sind durch aussagekräftige Synapomorphien gekennzeichnet: die öffnung zwischen dem mesothorakalen Anepisternum und der Elytrenbasis ist verengt, das Praeepisternum des Mesothorax ist mit einer anteromedianen Leiste versehen, der laterale, innere Fortsatz der Mittelhüfte ist in drei Sektionen aufgefächert, die Sehnen von M. noto-coxalis (M 40) und M. coxa-subalaris (M 43) entspringen am lateralen Fortsatz der Mittelhüfte, die Basalarscheibe fehlt, weitere Flugmuskeln sind reduziert. Ein Schwestergruppenverhältnis zwischen* Orectochilus *und* Orectogyrus *wird durch zwei apomorphe Merkmale nahegelegt: die vordere Mittelhüftwände sind mit dem ventralen Sklerit des Mesothorax verwachsen, der lateralen Fortsatzes der Mittelhüfte ist mit dem Anepisternum verwachsen. Ob* Heterogyrus *näher mit den Gattungen* Gyrinus, Aulonogyrus *und* Metagyrinus, *oder näher mit den Gattungen der* Enhydrini *und* Orectochilini *verwandt ist bleibt ungeklärt.*

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INTRODUCTION

The purpose of this paper is to reconstruct the evolution of gyrinid meso- and metathoracic structures, and to use the acquired data to analyse the phylogenetic relationships within the family. Special emphasize is placed upon the study of *Spanglerogyrus albiventris* Folkerts, which was described by Folkerts in 1979, and placed in a newly erected subfamily Spanglerogyrinae Folkerts.

An outstanding and comprehensive study of the locomotor organs of Gyrinidae was made by Larsén (1966), and it should be emphasized that Larsén's work was an indispensable prerequisite for this study. However, *Spanglerogyrus*, which is substantially different from other gyrinids in many features (Folkerts, 1979; Steiner & Anderson, 1981; Beutel, in press, in prep.), was not known at that time. Moreover, Larsén's purpose was a comparative study of structure and function, and he did not subject his data to rigorous phylogenetic analysis. Larsén (1966) did not use cladistic methods (Hennig, 1966), and many of his phylogenetic statements remain vague.

Despite the great interest in Gyrinidae over a long period, and many brilliant taxonomic studies (*e.g.*, by Georg Ochs and Per Brinck), a stringent, cladistic analysis of Gyrinidae is lacking. This study proposes to reconstruct the evolutionary history of Gyrinidae through examination and phylogenetic interpretation of meso- and metathoracic characters of adult gyrinids. Emphasis is placed upon determination of the polarity of character states and on functional considerations.

MATERIAL AND METHODS

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

Representatives of the genera *Gyrinus* L., *Aulonogyrus* Motschulsky, *Orectochilus* Lac., *Orectogyrus* Rég., *Gyretes* Brullé, *Andogyrus* Ochs, *Dineutus* Macleay, *Enhydrus* Laporte were examined for external skeletal structures. Specimens of *Dineutus assimilis* Kirby, *Andogyrus colombicus* Rég., *Gyretes iricolor* Young, *Orectochilus villosus* Müll., *Aulonogyrus coccinus* Klug, and *Gyrinus marginellus* Fall were examined for both external and internal structures. Furthermore representatives of all the remaining adephagan groups, and specimens of *Priacma serrata* LeConte and *Tetraphalerus* (undescribed species) (Cupedidae) were examined.

Out-group comparison is used for the determination of the polarity of character states whenever possible. A flexible and comprehensive out-group, comprising terrestrial and aquatic families of Adephaga, and Cupedidae, was chosen, as recommended by Beutel (in press). The In-group or character-correlation criterion is used for structures of adults of Gyrinidae that either are not present or are radically different in the remaining Adephaga. As strong evidence is given for the monophyly of Gyrininae (*sensu* Folkerts) and a sistergroup relationship

Table I : Distribution of character states among genera of Gyrinidae. See text for explanations of character states.

Genera	Character and Character States[†]																	
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.
Spanglerogyrus	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Gyrinus	0	1	1	0	0	0	0	1	0	2*	0	0	1	1	1	1	1	1
Aulonogyrus	0	1	1	0	0	0	0	1	0	2*	0	0	1	1	1	1	1	1
Metagyrinus	0	?	1	?	?	?	?	1	0	2*	0	0	1	?	?	?	?	?
Heterogyrus	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Enhydrus	0	?	1	?	?	?	?	1	0	2*	0	1	1	?	?	?	2	1
Dineutes	1	1	1	0	0	0	1	1	0	2*	0	1	1	2	1	1	2	1
Porrorhynchus	1	?	1	?	?	?	?	1	0	2*	0	1	1	?	?	?	2	1
Macrogyrus	0	?	1	?	?	?	?	1	0	2*	0	1	2	?	?	?	?	?
Andogyrus	0	1	1	0	0	2	0	1	0	2*	0	1	2	2	1	1	2	1
Orectochilus	0	2	1	1	1	3b	1	1	0	2*	0	1	2	2	2	1	2	1
Orectogyrus	0	2	1	1	1	3b	1	1	0	2*	0	1	2	2	2	1	2	1
Gyretes	1*	2	1	1	0	3a	1	1	0	2*	0	1	2	2	2	1	2	1

[†] 0 = plesiomorphic;
  1 = apomorphic, step 1;
  2 , 3 = apomorphic, steps 2, 3;
  3a, 3b = substates of apomorphic character state 3;
  1*, 2* = apomorphic character states which have evolved independently from 0 or 1.

Table I (continued)

Genera	Character and Character States[†]																	
	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.
Spanglerogyrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyrinus	1	0	1	2	1	1	1	2	1	0	1	1	1	1	1	1	0	1
Aulonogyrus	1	0	1	2	1	1	1	2	1	0	1	1	1	1	1	1	0	1
Metagyrinus	?	?	?	2	1	?	?	2	?	?	1	?	?	?	?	?	?	?
Heterogyrus	?	?	?	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Enhydrus	1	?	?	1	1	?	?	1	?	?	1	1	?	?	?	?	?	?
Dineutes	1	0	1	1	1	1	1	1	2	0	2	1	1	0	1	1	0	1
Porrorhynchus	1	?	?	1	1	?	?	1	?	0	2	1	?	?	?	?	?	?
Macrogyrus	?	?	?	1	1	?	?	1	?	?	2	1	?	?	?	?	?	?
Andogyrus	1	0	1	1	1	1	1	1	2	1	2	1	1	0	1	1	0	1
Prectochilus	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1
Prectogyrus	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1
Gyretes	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1

[†] 0 = plesiomorphic;
1 = apomorphic, step 1;
2 , 3 = apomorphic, steps 2, 3;
3a, 3b = substates of apomorphic character state 3;
1*, 2* = apomorphic character states which have evolved independently from 0 or 1.

between Gyrininae and *Spanglerogyrus* (Beutel, in press, in prep.), character states that are shared by *Spanglerogyrus* and some members of Gyrininae are most likely primitive, whereas the corresponding character state is derived. *Spanglerogyrus* is used as an out-group for character evaluation within Gyrininae. Missing data for some characters resulted because no specimens of *Heterogyrus*, and no internal structures of members of the genera *Metagyrinus*, *Enhydrus*, *Porrorhynchus*, and *Macrogyrus* were examined. My analysis of these latter taxa is based on examination of dried specimens on loan from the British Museum (Natural History).

Some character states which are hypothesized as synapomorphies of Orectochilini in this study, may be found to be synapomorphies of a monophyletic group comprising Orectochilini and a part of the enhydrine set of genera. There is, however, little chance that future reevaluation of characters based on studies of internal structures of members of the genera listed above will affect the positions of the genera in the cladogram (Fig. 16).

Larsén's (1966) nomenclature is used for the muscles throughout the paper. The characters below are discussed from anterior to posterior on the body. The distribution of characters by taxon are shown in Table 1 and a cladogram of the relationships of the genera is given in Fig. 16.

Plesiomorphic character states are indicated as 0, apomorphic character states as 1, 2, 3 (transformation series). An asterisk designates an hypothesis of an independently derived apomorphic character state.

CHARACTERS

Mesoscutellar lobe of mesothorax (Character 1)

Character state 0.— The mesoscutellar lobe is triangular and visible externally. In members of *Spanglerogyrus* (Fig. 1, 2), *Heterogyrus* (Brinck, 1955), *Enhydrus*, *Andogyrus*, *Macrogyrus*, *Orectochilus*, *Orectogyrus*, *Metagyrinus*, *Gyrinus* and *Aulonogyrus* (Hatch, 1926).

Character state 1.— The mesoscutellar lobe is covered by the elytra at rest. In members of *Gyretes* and the enhydrine genera *Porrorhynchus* and *Dineutus* (Hatch, 1926).

Polarity rationale.— An exposed mesoscutellar lobe is characteristic of most adephagan adults and those of Cupedidae. The mesoscutellar lobe is concealed in members of Hydroporinae (Dytiscidae), Noteridae excl. *Phreatodytes* (Uéno, 1957), and Haliplidae.

Analysis.— It appears most plausible to interpret character state 1 as a possible synapomorphy of *Dineutus* and *Porrorhynchus* (char. 1. 1), and as independently derived in members of *Gyretes* (char. 1. 1*). As an exposed mesoscutellar lobe is present in members of *Orectochilus* and *Orectogyrus*, this condition has to be assigned to the groundplan of *Orectochilini*. The monophyly of Orectochilini is demonstrated by various synapomorphous character states in the following. This character should not be overvalued, as a concealed mesoscutellar lobe has evolved several times independently within Adephaga (see polarity rationale).

Opening between anepisternum and elytron of mesothorax (Character 2)

Character state 0.— No opening between basal elytral margin and anepisternum. In adults of *Spanglerogyrus* (Fig. 5).

Character state 1.— A conspicuous, fairly wide and triangular opening between basal margin of elytron and anepisternum (Larsén, 1966; Fig. 7). In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 2.— Opening between basal margin of elytron and anepisternum, narrowed by bulged dorsal parts of anepisternum (Larsén, 1966, Fig. 25). In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic, as an opening described above is found neither in members of Cupedidae, nor in members of any other adephagan group. Conspicuously bulged dorsal parts of the anepisternum are not found in *Spanglerogyrus*, and are not described for members of any other adephagan group. Therefore it appears plausible to consider character state 2 as derived from character state 1.

Analysis.— The opening between the basal elytral margin and the anepisternum allows compression of air into the subelytral space, as described by Larsén (1966). This uncommon feature is probably correlated with the highly efficient meso- and metathoracic locomotor system. Character state 1 is a derived groundplan feature of Gyrininae (char. 2.1). Character state 2 is a synapomorphy of Orectochilini (char. 2.2).

Excavations for reception of the prolegs in repose (Character 3)

Character state 0.— No excavations for reception of the forelegs in repose. In members of *Spanglerogyrus* (Fig. 5).

Character state 1.— A distinct concavity extended from hind margin of prothorax over lateral part of mesothoracic preepisternum, mesepimeron, metathoracic anepisternum, and elytral epipleuron. In members of *Gyrinus*, *Aulonogyrus*, *Metagyrinus*, in members of the enhydrine genera, and in members of Orectochilini (Hatch, 1927; Larsén, 1966; personal observation).

Polarity rationale.— A concavity for reception of the prolegs in repose as described above is not found in members of Cupedidae or members of other adephagan groups, and is thus plesiomorphic. Thus character state 1 is apomorphic.

Analysis.— These excavations improve the streamlining of the ventral body surface when the prolegs are drawn up against the body. Character state 1 is the result of a complex modification of the ventral body surface and a synapomorphy of Gyrininae (char. 3.1).

Anteromedian ridge of the mesothoracic preepisternum (Character 4)

Character state 0.— No internal median ridge in anterior region of preepisternum. In members of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, *Dineutus*, and *Andogyrus*.

Character state 1.— A high internal ridge, not marked by external suture, in anterior region of the preepisternum. In members of *Orectogyrus* (Larsén, 1966), *Orectochilus*, and *Gyretes* (pers. obs.).

Polarity rationale.— An internal ridge of anterior region of mesothoracic preepisternum is absent from members of Cupedidae (*Priacma serrata*; Baehr, 1975), and from members of other adephagan families. Thus character state 1 is apomorphic.

Analysis.— By means of this ridge the area of attachment of M. sterno-trochanteralis (M 51) is considerably enlarged. The ridge is a synapomorphy of Orectochilini (char. 4.1).

Flexibility of the mesocoxae (Character 5)

Character state 0.— Mesocoxal motility restricted to abduction and adduction. In members of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, *Dineutus*, *Andogyrus*, and *Gyretes*.

Character state 1.— Anterior walls of mesocoxae are solidly attached to hind margin of ventral sclerite of mesothorax. In members of *Orectochilus* and *Orectogyrus* (Larsén, 1966).

Polarity rationale.— Immobilized mesocoxae are not known from members of Cupedidae or members of any other adephagan group. Thus character state 1 is apomorphic.

Analysis.— Character state 1 is a synapomorphy of *Orectochilus* and *Orectogyrus* (char. 5.1).

Lateral process of the mesocoxae (Character 6)

Character state 0.— Internal, lateral process as attachment area of lateralmost part of M. coxo-trochanteralis (M 54). The process is slender in its basal section, and is extended distally. In members of *Spanglerogyrus* (Fig. 6), *Gyrinus*, and *Aulonogyrus*.

Character state 1.— The lateral process is short, fairly broad in the basal part and extended distally. In members of *Dineutus*.

Character state 2.— Lateral process of mesocoxae extensive, broad in the basal section, and extended distally. In members of *Andogyrus*.

Character state 3.— Lateral process trilobed, and strongly enlarged. In members of *Orectogyrus* (Larsén, 1966), *Orectochilus*, and *Gyretes* (Fig. 11).

Substate 3 a.—Anterolateral lobe of process not fused with the anepisternum. In members of *Gyretes*.

Substate 3 b.— Anterolateral lobe fused with anepisterum. In members of *Orectogyrus* and *Orectochilus* (Larsén, 1966)

Polarity rationale.— Following the in-group criterion, character state 0 has to be considered as plesiomorphic within Gyrinidae. Character states 1 and 2 represent similar conditions, although the difference in relative size of the process is distinct. It is quite likely that character states 1 and 2 are intermediate stages between character state 0 and character state 3. The latter character state is undoubtedly highly derived. Nothing comparable is known from any member of other adephagan groups. Substate 3 b is derived from 3 a in correlation with the immobilization of the mesocoxae (5.1).

Analysis.— The complex trilobed internal process of the mesocoxae is a synapomorphy of Orectochilini (6.3). Substate 3 b is a possible synapomorphy of *Orectochilus* and *Orectogyrus* (6.3 b). For a phylogenetic interpretation of character states 1 and 2, study of specimens of *Heterogyrus*, *Enhydrus*, *Porrorhynchus*, and *Macrogyrus* is needed.

Tendons of M. noto-coxalis (M 40) and M. coxa-subalaris (M 43) (Character 7)

Character state 0.— Tendons of both muscles arise from lateral region of posterior wall of mesocoxae. In members of *Spanglerogyrus* (Fig. 6), *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 1.— Tendons of M 40 and M 43 (if this muscle present) arise from median lobe of internal, mesocoxal process. In members of Orectochilini (Fig. 11) (Larsén, 1966; pers. obs.).

Polarity rationale.— A condition similar to character state 1 is not described for any member of other adephagan groups or members of Cupedidae. Consequently, character state 1 is apomorphic.

Analysis.— Character state 1 is interpreted as a synapomorphy of Orectochilini (7.1).

Shape of femur and tibia (Character 8)

Character state 0.— Femora and tibiae not shortened, broadened, and only very slightly flattened. In adults of *Spanglerogyrus* (Fig. 12, 13).

Character state 1.— Femora and tibiae markedly shortened, broadened, and flattened. In members of Gyrininae examined (Bott, 1928; Larsén, 1966; Nachtigall, 1961; pers. obs.).

Polarity rationale.— Nothing similar to the highly specialized, paddle-like legs is found in any other group of Coleoptera. Character state 1 is thus apomorphic.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (8.1).

Insertion of the tarsus (Character 9)

Character state 0.— Mesotarsus inserted at distal end of tibia. In members of Gyrininae.

Character state 1.— Mesotarsus inserted close to base of tibia. Oar-like tibial projection extended almost parallel to tarsus. In adults of *Spanglerogyrus* (Fig. 12, 13).

Polarity rationale.— Character state 1 is apomorphic as a similar condition is not described for members of any other adephagan group or for members of Cupedidae.

Analysis.— Character state 1 is autapomorphic for *Spanglerogyrus* (9.1).

Swimming hairs (Character 10)

Character state 0.— Mesotibiae and mesotarsi with simple, unmodified swimming hairs. Not found among extant members of Gyrinidae.

Character state 1.— Mesotibiae and mesotarsi with ctenoid or feather like swimming-hairs, of stem with two rows of side branches. In members of *Spanglerogyrus* (Fig. 15).

Character state 2.— Mesotibiae and mesotarsi with swimming blades or lamellae. In members of Gyrininae (Bott, 1928; Nachtigall, 1962; Larsén, 1966; pers. observation).

Polarity rationale.— Character states 1 and 2 are apomorphic as nothing similar is known from members of any other adephagan group or from members of Cupedidae. It is very unlikely that one of both character states is derived from the other. Both structures are distinctly different in terms of structure and function. There is good reason to assume that they have evolved independently from simple, unmodified swimming hairs (character state 0).

Analysis.— The swimming blades or lamellae are an important part of the extremely efficient locomotor apparatus of members of Gyrininae, as pointed out by Nachtigall (1961). At the same time character state 2 is a significant synapomorphy of this group. Character state 1 is an autapomorphy of *Spanglerogyrus*.

Tibial spurs (Character 11)

Character state 0.— Two mesotibial spurs. In members of Gyrininae examined.

Character state 1.— Single large mesotibial spur with unusual fir-cone-like surface structure. In members of *Spanglerogyrus* (Fig. 13).

Polarity rationale.— Two mesotibial spurs are present in members of other adephagan families and members of Cupedidae. Consequently, character state 1 is apomorphic.

Analysis.— Character state 1 is autapomorphy of *Spanglerogyrus.*

Anterior and posterior wall of the tibiae and first tarsal segments connected by cuticular columnae (Character 12)

Character state 0.— Anterior and posterior walls of tibiae and first tarsal segments of middle (and hind) legs not connected by cuticular columnae. In members of *Gyrinus, Aulonogyrus* (Larsén, 1966), *Metagyrinus,* and *Spanglerogyrus.*

Character state 1.—Anterior and posterior walls of mesotibiae and first mesotarsomeres firmly connected by cuticular columnae. In members of Orectochilini, *Dineutus,* (Larsén, 1966), and remaining enhydrine genera (pers. obs.).

Polarity rationale.— Character state 1 is apomorphic because it is not described for any other member of Adephaga.

Analysis.— The firm connection of the anterior and posterior walls increases the rigidity of tibiae and proximal tarsomeres. Character state 1 is a synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera.

Arrangement and shape of mesotarsomeres (Character 13)

Character state 0.— Mesotarsomeres only very slightly flattened, and arranged in usual manner. In members of *Spanglerogyrus* (Fig. 13).

Character state 1.— Mesotarsomeres extremely flattened. Tarsomeres 1–4 together form a fan shaped structure; tarsomere 1 triangular; tarsomeres 2 and 3 very short, with long lobes; tarsomere 4 long whereas tarsomere 5 very short.; tarsomeres 4 + 5 semilunar in shape (Larsén, 1966); all tarsomeres connected in one plane. In members of *Gyrinus, Aulonogyrus, Dineutus* (Larsén, 1966), *Enhydrus,* and *Porrhorhynchus* (pers. obs.).

Character state 2.— Mesotarsomeres 1-3 arranged and shaped as above (character state 1); dorsal margin of tarsomeres 4 + 5 turned posteriorly, thus in form of shovel together with proximal tarsomeres; tarsomeres 4 + 5 nearly parallel sided. In members of *Andogyrus, Macrogyrus* (pers. obs.), and Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic because the same condition characterizes members of all remaining adephagan families and those of Cupedidae. Character state 2 is probably derived from 1. This interpretation would be in agreement with other derived features which indicate a closer relationship between the enhydrine genera and Orectochilini. The modified shape and position of tarsomeres 4 + 5 (character state 2) improves the backstroke of the leg according to Larsén (1966). It is quite likely that a more efficient structure has evolved from a less efficient preceding stage (character state 1).

Analysis.— Character state 1 is a derived groundplan feature and a synapomorphy of Gyrininae (13.1). Character state 2 is a synapomorphy of a monophyletic unit comprising *Andogyrus, Macrogyrus,* and Orectochilini (13.2). This implies that Enhydrini are not monophyletic.

Elytral glossula (Character 14)

Character state 0.— No elytral glossula. In members of *Spanglerogyrus* (Fig. 8).

Character state 1.— Elytral glossula slightly developed. In members of *Gyrinus*, and *Aulonogyrus* (Larsén, 1966).

Character state 2.— Elytral glossula markedly developed. In members of Orectochilini, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Polarity rationale.— Based on in-group comparison, character state 0 has to be considered as plesiomorphic. From this follows that character state 2 is derived from character state 1.

Analysis.— An elytral glossula, which acts as a locking device, is considered as a derived groundplan feature and synapomorphy of Gyrininae (14.1). The enlarged glossula (character state 2) represents a possible synapomorphy of Orectochilini and the enhydrine genera (14.2).

M. sterno-trochanteralis (M 51) (Character 15)

Character state 0.— M. sterno-trochanteralis (M 51) absent. In members of *Spanglerogyrus* (Fig. 6).

Character state 1.— M. sterno-trochanteralis present and originates from anterior margin of preepisternum. In members of *Gyrinus, Aulonogyrus, Dineutus* (Larsén, 1966), and *Macrogyrus.*

Character state 2.— M. sterno-trochanteralis present; originates from anterior wall of preepisternum, and from newly acquired median ridge in anterior region of ventral sclerite of mesothorax (see char. 4). In members of Orectochilini (Larsén, 1966; pers. obs.)

Polarity rationale.— M. sterno-trochanteralis (M 51) absent from members of *Priacma serrata* LeConte (Baehr, 1975) and from all members of Coleoptera examined by Larsén (1966) except for Gyrinidae. Therefore its presence is considered as an apomorphic character state. Anteromedian ridge is a derived feature (see char. 4). Consequently, the origin of M 51 from this structure is apomorphic.

Analysis.— M. sterno-trochanteralis has probably evolved by expansion of the origin of M. episterno-trochanteralis (M 48). Both muscles are inserted on the same trochanteral tendon. The efficiency of the hindstroke of the middle-leg is considerably improved by the action of M. sterno-trochanteralis. The newly developed muscle is a derived groundplan feature and a synapomorphy of Gyrininae (15.1). The expansion of the origin of M 51 (character state 2) is a possible synapomorphy of Orectochilini (15.2).

M. furca-coxalis anterior (M 44) (Character 16)

Character state 0.— M. furca-coxalis anterior (M 44) present. In members of *Spanglerogyrus* (Fig. 6).

Character state 1.— M. furca-coxalis anterior absent. In all members of Gyrininae examined by Larsén (1966), and those of *Andogyrus.*

Polarity rationale.— Character state 0 is plesiomorphic, as the muscle is present in all members of Coleoptera examined by Larsén (1966) except for Gyrininae.

Analysis.— The absence of M 44 is a possible synapomorphy of Gyrininae (16.1).

Shape of the metanotum, median membranous area (Character 17)

Character state 0.— Metanotum of normal adephagan shape and construction; medially about as long as laterally, with membranous area in front of alacristae; transverse suture separating attachment area of M. metanoti secundus (M 61) and M. noto-coxalis anterior (M 75) (Larsén, 1966) distinct, and extended to lateral margin of scutum. In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Metanotum distinctly broader laterally than in median region; membranous area present; transverse suture indistinct and totally obliterated in lateral scutal area. In members of *Gyrinus* and *Aulonogyrus*.

Character state 2.— Metanotum about twice as broad laterally as medially; median membranous area absent; transverse suture indistinct and totally obliterated in lateral scutal area. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Porrorhynchus* (Hatch, 1926; Brinck, 1980), *Enhydrus*, and *Andogyrus* (pers. obs.).

Polarity rationale.— Character state 0 plesiomorphic, as a metanotum of this type is generally found in members of other adephagan groups. Character state 2 is derived from character state 1.

Analysis.— Modifications of metanotum that lead from character 0 to 1, and from character state 1 to 2 are correlated with the profound changes in the flight musculature in members of Gyrininae. Character state 1 is a derived groundplan character state and synapomorphy of Gyrininae (17.1). Character state 2 is a synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera (17.2).

Metapostnotum (Character 18)

Character state 0.— Metapostnotum of normal adephagan size and shape (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986), and visible from above. In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Median postnotal area inflected below scutellum; actual posterior margin fused to the V-shaped ridge. In the members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 1 is apomorphic, as nothing similar is found in members of other adephagan families or members of Cupedidae.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (18.1).

Anterior notal process (Character 19)

Character state 0.— Anterior notal process of normal size and position; clearly visible from above as in other members of Adephaga (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986). In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Anterior notal process distinctly smaller and hardly visible from above. In all members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic because such a condition is found in most members of other adephagan groups, and in members of Cupedidae.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (19.1).

Basalar disc (Character 20)

Character state 0.— Basalar disc present. In members of *Spanglerogyrus* (Fig. 7), in members of *Gyrinus*, *Aulonogyrus* (considerably smaller; Larsén, 1966), *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 1.— Basalar disc absent.; basalare solidly attached to anepisternum and pleural wing process. In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic because a well developed basalar disc is found in members of most adephagan groups (Larsén, 1966).

Analysis.— Character state 1 is a synapomorphy of Orectochilini, and correlated with loss of coxo-basalar muscle (M 42).

Subalare (Character 21)

Character state 0.— Subalare well developed. In members of *Spanglerogyrus* (Fig. 4).

Character state 1.— Subalare minute. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic, because a well developed subalare is found in most members of other adephagan families with developed flight organs (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986).

Analysis.—Reduction in size of subalare is correlated with loss of M. coxa-subalaris (M 79) in members of Gyrininae (Larsén, 1966). Character state 1 is a synapomorphy of Gyrininae (21.1).

Size of the ventral sclerite of the metathorax (Character 22)

Character state 0.— Ventral sclerite of metathorax, largely represented by preepisternum (Matsuda, 1970), only slightly constricted between posteromedial margin of mesocoxae and anterior metacoxal margin; broad in lateral parts. In members of *Spanglerogyrus* (Fig. 5, 12).

Character state 1.— The ventral sclerite is reduced to a narrow strip between the posteromedial margin of mesocoxa and anterior margin of metacoxa, but fairly broad and triangular in lateral parts. In members of *Heterogyrus* (Brinck, 1955), and in members of enhydrine genera (Hatch, 1926; pers. obs.).

Character state 2.— Ventral sclerite reduced to narrow strip except small central area between medial walls of mesocoxae and anterior walls of metacoxae. In members of Orectochilini, *Gyrinus*, *Aulonogyrus*, and *Metagyrinus*.

Polarity rationale.— Character state 0 is closest to characteristic of terrestrial members of Adephaga excl. Trachypachidae, and in members of Cupedidae. Therefore this character state is plesiomorphic, and a groundplan feature of Gyrinidae. Character state 1 is an intermediate stage, and is closer to groundplan than character state 2.

Analysis.— As a gradual modification, the reduction of the ventral sclerite should not be overvalued. Character state 1 is probably a derived groundplan feature and a synapomorphy of Gyrininae (22.1). As a working hypothesis, character state 2 is interpreted as a synapomorphy of Orectochilini (22.2*) on one hand, and as a synapomorphy of a monophyletic unit comprising *Metagyrinus*, *Gyrinus*, and *Aulonogyrus* on the other (22.2). This interpretation is suggested by several characters which indicate a closer relationship between Orectochilini and the enhydrine genera.

Metasternal transverse ridge (Character 23)

Character state 0.— Complete transverse ridge, dividing metathoracic preepisternum from katepisternum (Matsuda, 1970). In members of *Spanglerogyrus* (Fig. 5).

Character state 1.— Transverse ridge completely reduced. In members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic because a complete metasternal transverse ridge is present in members of Cupedidae (Baehr, 1975, pers. obs.), Haliplidae (Belkaceme, 1986), and in the vast majority of terrestrial members of Adephaga.

Analysis.— Character state 1 is a possible synapomorphy of Gyrininae (23.1). This character should not be overvalued, as the metasternal transverse ridge is also reduced in members of Noteridae and Dytiscidae.

Metafurcal origin (Character 24)

Character state 0.— Metafurca origin from katepisternum and attached to medial metacoxal walls by posteriorly directed process. In members of *Spanglerogyrus* (Beutel & Roughley, 1988).

Character state 1.— Metafurca origin from fused medial metacoxal walls. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Metafurca arises from the katepisternum in terrestrial members of Adephaga, in members of Haliplidae (Beutel & Belkaceme, 1986), and in adults of *P. serrata* (Baehr, 1975). Therefore character state 0 is considered plesiomorphic.

Analysis.— The origin of the metafurca from the fused medial metacoxal walls is considered as a synapomorphy of Gyrininae (24.1). A similar condition is found in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae (Beutel & Roughley, 1986). This is certainly a result of parallel evolution, and interpreted as a synapomorphy of these adephagan families by Beutel & Roughley (1988).

Lateral projections of the metafurca (Character 25)

Character state 0.— Metafurca with extensive lateral projections. In members of *Spanglerogyrus* (Fig. 7).

Character state 1.— Lateral metafurcal projections absent. In members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Well developed lateral metafurcal projections are generally characteristic of members of other adephagan families (Crowson, 1938; 1942). These projections are markedly reduced in members of *Rhysodes* (Crowson, 1938) and *Omoglymmius* (pers. obs.), but well developed in members of *Clinidium* (pers. obs.). The lateral metafurcal projections of members of Cupedidae are hardly developed (Crowson, 1938; Baehr, 1975). It appears more plausible to interpret absence of lateral projections as a secondary condition for Gyrininae, rather than as plesiomorphic. There are significant differences between the gyrinine and the cupedid metafurca in terms of shape and muscle attachment (Larsén, 1966; Baehr, 1975).

Analysis.— As a working hypothesis, character state 1 is considered a synapomorphy of Gyrininae (25.1).

Shape of metacoxae (Character 26)

Character state 0.— Metacoxae triangular, elongate in medial parts, and markedly tapered laterally. In members of *Spanglerogyrus* (Fig. 5, 12, 14).

Character state 1.— Metacoxae trapezoidal; fairly broad laterally, but not expanded anterolaterally. In members of *Heterogyrus* (Brinck, 1955) and the enhydrine genera.

Character state 2.— Metacoxae parallelogram-shaped, and markedly expanded anterolaterally. In members of *Gyrinus, Aulonogyrus, Metagyrinus*, and Orectochilini.

Polarity rationale.— Out-group comparison suggests that character state 0 is plesiomorphic; metacoxae of a similar type are found in members of Cupedidae (Baehr, 1975; pers. obs.) and in terrestrial members of Adephaga excluding Trachypachidae (Beutel & Belkaceme, 1986). Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— It is apparent that this character is closely correlated with reduction of ventral sclerite of metathorax (char. 22), and with fusion of metacoxae. Enlargement of metacoxae results in an expansion of attachment areas of coxo-trochanteral muscles. Character state 1 is an apomorphic groundplan feature of Gyrininae (26.1). Character state 2 is a possible synapomorphy of Orectochilini (26.2*) on one hand, and a possible synapomorphy of a monophyletic unit comprising *Gyrinus*, *Aulonogyrus*, and *Metagyrinus* on the other (26.2; see char. 22). Distinctly expanded metacoxae are found also in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae. Metacoxae of members of Trachypachidae are slightly expanded.

Medial metacoxal walls (Character 27)

Character state 0.— Medial metacoxal walls not fused to each other but only attached to posterior process of metafurca on either side. In members of *Spanglerogyrus* (Beutel & Roughley, 1988).

Character state 1.— Medial metacoxal walls fused along their anterior margin. In members of *Gyrinus* and *Aulonogyrus* (Larsén, 1966).

Character state 2.— Medial metacoxal walls completely fused. In members of Orectochilini, *Dineutus* (Larsén, 1966), and *Macrogyrus* (pers. obs.).

Polarity rationale.— Medial metacoxal walls not fused in members of Cupedidae (Baehr, 1975; pers. obs.), Haliplidae (Beutel & Belkaceme, 1986), and in terrestrial members of Adephaga excluding Trachypachidae. Character state 0 is thus plesiomorphic. Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is a derived groundplan feature and a synapomorphy of Gyrininae (27.1). Character state 2 is a possible synapomorphy of Orectochilini and the enhydrine genera (27.2).

Anterior metacoxal wall (Character 28)

Character state 0.— Anterior metacoxal wall and ventral sclerite linked by a membrane. In adults of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, and *Dineutus* (Larsén, 1966; pers. obs.).

Character state 1.— Medial parts of anterior metacoxal walls fused with ventral sclerite. In adults of *Andogyrus*.

Character state 2.— Medial parts of anterior metacoxal walls fused with ventral sclerite. Anterolateral metacoxal wall in form of high ridge, expanded over triangular part of ventral sclerite, and fused to margin of preepisternal pouch (Larsén, 1966). In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Anterior metacoxal wall is not fused to ventral sclerite in members of Cupedidae (Baehr, 1975; pers. obs.), and terrestrial members of Adephaga excluding Trachypachidae. Therefore character state 0 is plesiomorphic. Character state 1 is probably an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is an apomorphic feature which suggests a closer relationship between *Andogyrus* (*Macrogyrus*?) and Orectochilini. Character state 2 is a synapomorphy of Orectochilini. This character should not be overvalued as fusions of the anterior metacoxal wall and the ventral sclerite are characteristic of

members of Trachypachidae, Haliplidae, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae.

Position of metatarsomeres 4 + 5 (Character 29)

Character state 0.— Metatarsomeres slightly flattened, arranged in usual manner (see char. 13., mesotarsomeres). In members of *Spanglerogyrus* (Fig. 14).

Character state 1.— Metatarsomeres modified in same manner as mesotarsomeres (character state 13.1). Tarsomeres 4 + 5 of semilunar shape.; all tarsomeres connected in one plane. In adults of *Gyrinus, Aulonogyrus, Metagyrinus,* and *Enhydrus.*

Character state 2.— Tarsomeres 4 + 5 almost parallel-sided and turned posteriorly, in form of kind of shovel together with proximal tarsomeres. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Porrorhynchus, Macrogyrus,* and *Andogyrus.*

Polarity rationale.— see character 13.

Analysis.— Character state 1 is a derived groundplan feature, and a synapomorphy of Gyrininae (29.1). Character state 2 is a possible synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera excluding *Enhydrus* (29.2).

Further characters of the hind-legs are not treated here, as the characters of the middle-legs described above also apply to the hind-legs.

Cubital angle of the hind wing (Character 30)

Character state 0.— No cubital angle. In members of *Spanglerogyrus* (Figs. 9, 10).

Character state 1.— Slightly expressed cubital angle. In members of *Gyrinus, Aulonogyrus, Enhydrus, Porrorhynchus, Andogyrus* (Hatch, 1926), and in adults of *Dineutus melhyi* Rég. (Ward, 1979).

Character state 2.— Cubital angle is markedly pronounced. In members of Orectochilini (Hatch, 1926).

Polarity rationale.— No cubital angle is present in members of *Hygrobia, Amphizoa,* Dytiscidae, and most members of Carabidae examined by Ward (1979). Therefore character state 0 is plesiomorphic. Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is a derived groundplan feature and a possible synapomorphy of Gyrininae (30.1). Character state 2 is a synapomorphy of Orectochilini (30.2).

Flight muscles (Character 31)

Character state 0.— Full complement of flight muscles. Flight muscles were reduced in all specimens of *Spanglerogyrus* examined for this study (Fig. 7). However, flight is reported by Steiner & Anderson (1981), and skeletal structures clearly suggest that a full complement of flight muscles is present in a certain percentage of populations of *Spanglerogyrus,* especially during early imaginal life.

Character state 1.— M. metanoti primus and secundus (M 60 and 61), M. dorsoventralis primus and secundus (M 64 and 65), M. sterno-basalaris (M 73), M. noto-coxalis anterior (M 75), and M. coxa-subalaris (M 79) absent. In members of *Gyrinus, Aulonogyrus, Dineutus* (Larsén, 1966), and *Andogyrus.*

Character state 2.— M 60, M 61, M 64, M 65, M 73, M 75, M 79, M. noto-basalaris (M 69), and M. coxa-basalaris (M 78) absent. In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Full set of flight muscles is a groundplan feature of Coleoptera and Adephaga (Larsén, 1966; Baehr, 1975). Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Loss of flight muscles in members of Gyrininae is not correlated with loss of flying capabilities. Reduced muscles are functionally replaced by M. noto-trochanteralis (M 84). Character state 1 is a derived groundplan feature and synapomorphy of Gyrininae (31.1). Character state 2 is a synapomorphy of Orectochilini (31.2).

M. sterno-episternalis (M 72) (Character 32)

Character state 0.— M. sterno-episternalis (M 72) present. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Andogyrus*, and *Spanglerogyrus*.

Character state 1.— M 72 absent. In members of *Gyrinus* and *Aulonogyrus* (Larsén, 1966).

Polarity rationale.— The presence of M 72 is plesiomorphic. This muscle is found in *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966).

Analysis.— Character state 1 is a common derived feature of *Gyrinus* and *Aulonogyrus* (32.1). Whether M 72 is also absent from members of *Heterogyrus* and *Metagyrinus* is not known at present. As a muscle reduction which has certainly occurred several times independently within Adephaga (Larsén, 1966), this character should not be overvalued.

M. furca-coxalis anterior (M 81) (Character 33)

Character state 0.— M. furca-coxalis present. In members of *Spanglerogyrus* (Fig. 7).

Character state 1.— M 81 absent. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic, as M 81 is present in *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966).

Analysis.— Loss of M 81 is probably correlated with the origin of the metafurca from the fused medial metacoxal walls. Character state 1 is a synapomorphy of Gyrininae (33.1). The muscle is reduced also in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae (Beutel & Roughley, 1988). Absence of the muscle in members of these families is interpreted as a result of parallel evolution.

M. furca-coxalis lateralis (M 82) (Character 34)

Character state 0.— M. furca-coxalis lateralis (M 82) present. In adults of *Spanglerogyrus* (Fig. 7).

Character state 1.— M 82 absent. In the members of Gyrininae examined (Larsén, 1966; pers. obs.)

Polarity rationale.— M 82 is present in members of *Priacma serrata* (Baehr, 1975), and most members of Coleoptera examined by Larsén (1966). Character state 1 is apomorphic.

Analysis.— Absence of M 82 from members of Gyrininae is probably correlated with loss of lateral metafurcal projections, and presence of M. noto-trochanteralis (M 84). Character state 1 is a synapomorphy of Gyrininae (34.1). Reduction of M 82 in members of Noteridae (*Notomicrus, Phreatodytes* ?) is correlated with fusion of lateral metafurcal projections with posterior metacoxal wall.

M. furca-coxalis posterior (M 83) (Character 35)

Character state 0.— M. furca-coxalis posterior (M 83) present. In members of *Gyrinus, Aulonogyrus, Dineutus* (Larsén, 1966), *Andogyrus*, and *Spanglerogyrus* (pers. obs.).

Character state 1.— M 83 absent. In members of Orectochilini.

Polarity rationale.— M 83 is present in adults of *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966). Character state 0 is plesiomorphic.

Analysis.— Character state 1 is a synapomorphy of Orectochilini (35.1). Parallel loss of M 83 has occurred in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae according to Beutel & Roughley (1988).

M. noto-trochanteralis (Character 36)

Character state 0.— M. noto-trochanteralis (M 84) absent. The muscle is absent from members of *Spanglerogyrus*. A modestly sized M 84 in specimens with well developed flight muscles cannot be fully excluded, but is unlikely, as suggested by skeletal features, such as shape of the metanotum (char. 17), and presence of extensive lateral metafurcal projections (char. 25).

Character state 1.— M 84 is markedly developed. In members of Gyrininae examined.

Polarity rationale.— M 84 is present in adults of *Priacma serrata* (Baehr, 1975), but absent from all members of Coleoptera examined by Larsén (1966) except *Sphaeridium scarabaeoides* L.. The muscle is also absent from members of *Amphizoa lecontei* (Beutel, 1988) and *Noterus laevis* Sturm (Belkaceme, pers. comm.). Determination of the polarity is difficult in this case, if Gyrinidae are considered as the sistergroup of the remaining Adephaga, as suggested by Beutel & Roughley (1988). Skeletal structures, which are obviously correlated with presence of M 84, such as shape of metanotum (char. 17), and complete absence of lateral metafurcal projections (char. 25) are almost certainly apomorphic. Therefore it appears more plausible to interpret presence of M 84 as a secondary condition in case of Gyrininae.

Analysis.— M 84 is the dominant flight muscle in members of Gyrininae. The muscle has replaced functionally several flight muscles which are reduced (char. 31), and is the main depressor muscle of the hind leg when the beetles swim. M 84 is probably derived from lateral parts of M. furca-trochanteralis (M 85) which is extremely weak in members of Gyrininae (Larsén, 1966), but powerful in adults of *Spanglerogyrus* and members of other adephagan families (Larsén, 1966; Beutel, 1986, 1988; Belkaceme 1986). As a working hypothesis, character state 1 is considered as a synapomorphy of Gyrininae (36.1).

NOTES ABOUT THE EVOLUTIONARY HISTORY OF GYRINIDAE AND PHYLOGENETIC CONCLUSIONS (Table 1, Fig. 16)

The crucial step in evolution of Gyrinidae, after having acquired surface swimming habits with various adaptive characters, *e.g.,* highly specialized antennae, divided eyes, and others, was the splitting event, resulting in the two extant subfamilies Spanglerogyrinae and Gyrininae (Folkerts, 1979). In addition to the many newly acquired characters of the head and prothorax of Gyrininae, such as widely separated eyes, and the loss of the ventral procoxal joint (Beutel, in press, in prep.), dramatic changes in the skeleto-muscular system of the meso- and metathorax must have taken place.
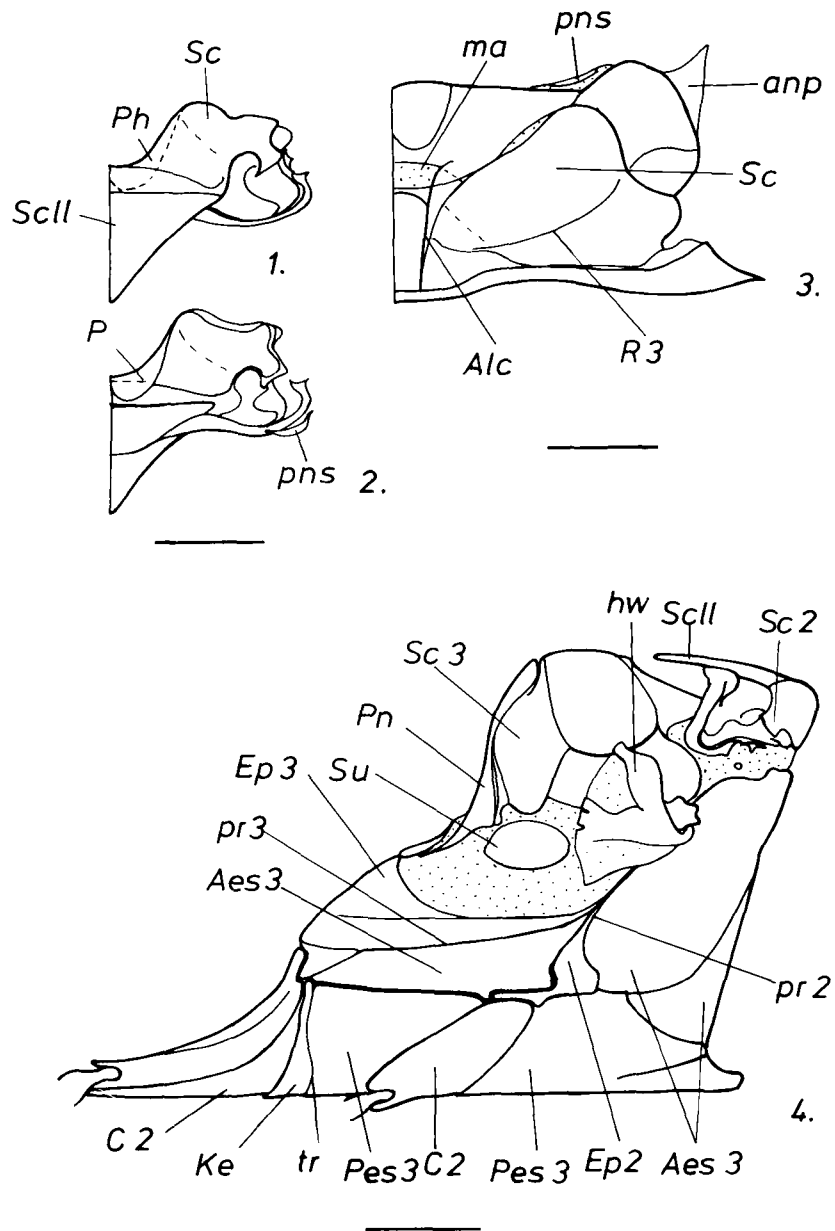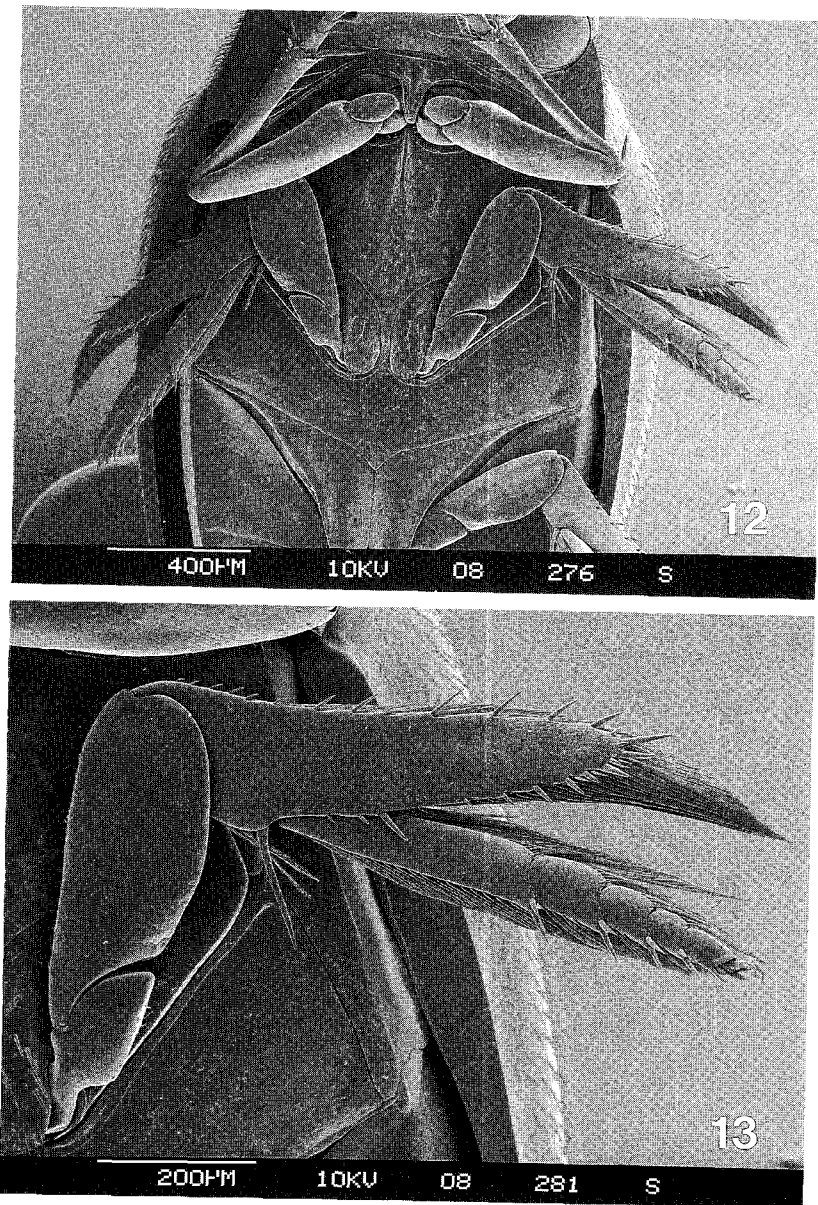
Figs. 1–4. *Spanglerogyrus albiventris* Folkerts. 1, Mesonotum, dorsal view. 2, Mesonotum, ventral view. 3, Metanotum, dorsal view. 4, Meso- and metathorax, lateral view. Legend: Aes, anepisternum; Alc, alacrista; anp, anterior notal process; C, coxa; Ep, epimeron; hw, hind wing; Ke, katepisternum; ma, membranous area; Pes, preepisternum; Ph, phragma; Pn, postnotum; pns, prenotal sclerite; pr, pleural ridge; R 3, posterior scutal ridge; Sc, scutum Scll, scutellar lobe; Su, subalare; tr, transverse ridge. Scale bars = 0.25 mm.
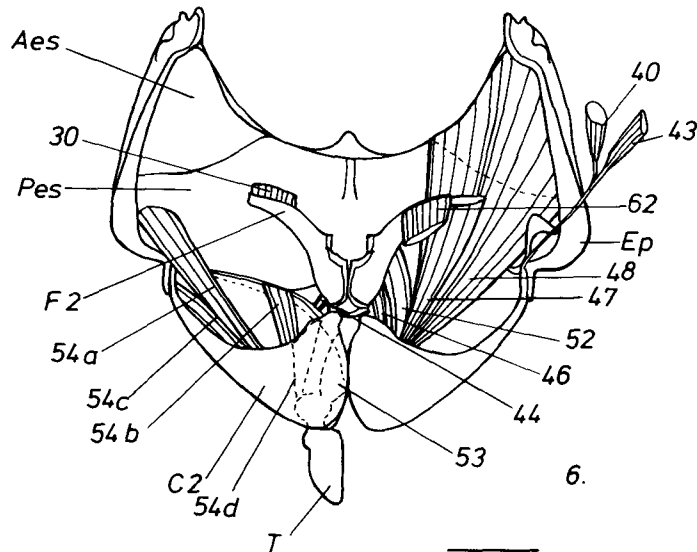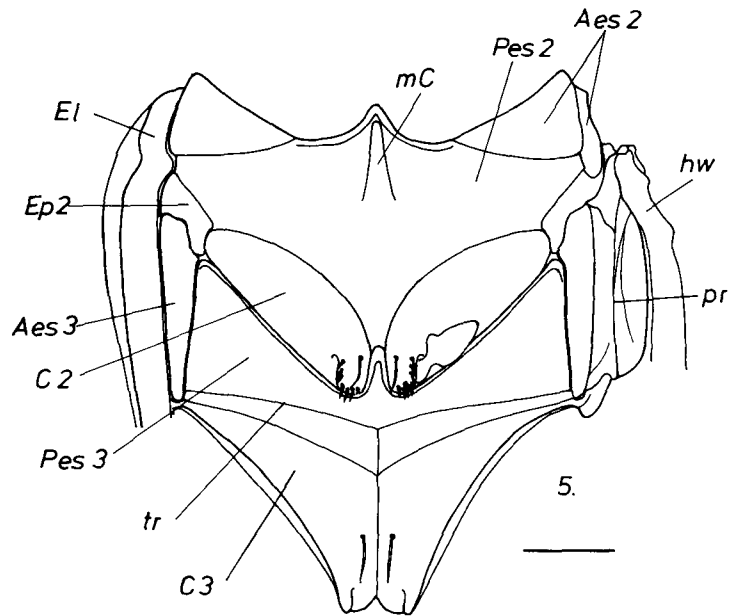
Figs. 5–6. *Spanglerogyrus albiventris* Folkerts. 5, Meso- and metathorax, ventral view, right elytron removed. 6, Mesothorax, dorsal view, notum removed. Legend: Aes, anepisternum; Bas, basalare; Bd, basalar disc; C, coxa; El. elytra; Ep, epimeron; F. furca; hw, hind wing; lp, lateral process of mesocoxa; mC, median carina; Pes, preepisternum; pr, pleural ridge; T, trochanter; tr, transverse ridge. Mesothoracic muscles: 30, M. mesosterni primus; 43, M. coxa-subalaris; 44, M. furca-coxalis anterior; 46, M. furca-coxalis posterior; 47, M. noto-trochanteralis; 48, M. episterno-trochanteralis; 52, M. furca-trochanteralis; 53, M. coxa-trochanteralis medialis; 54, M. coxa-trochanteralis lateralis. Scale bars = 0.25 mm.
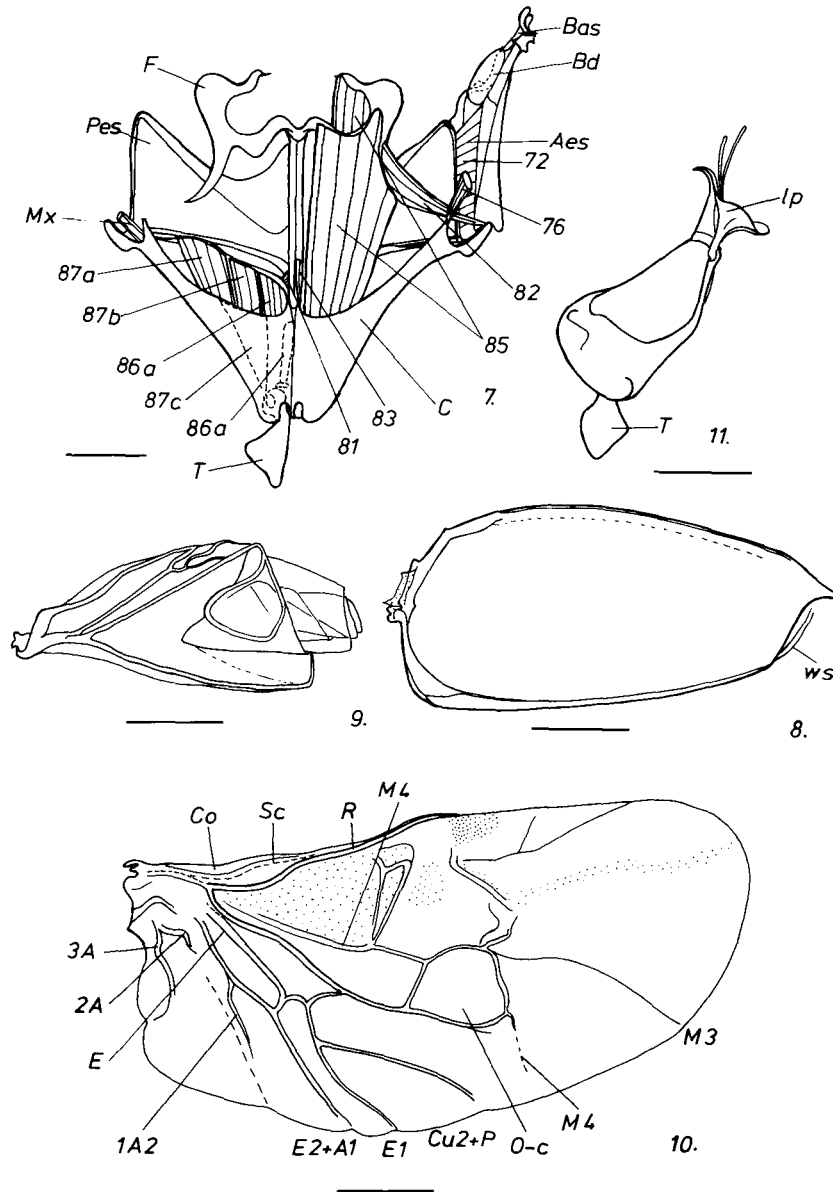
Figs. 7–11. Figs. 7–10. *Spanglerogyrus albiventris* Folkerts. 7, Metathorax, dorsal view, notum removed. 8, Elytron, ventral view. 9, Hind wing, completely folded. 10, Hind wing, unfolded. 11, *Gyretes iricolor* Young, mesocoxa, dorsal view. Legend: A, anal vein; aes, anepisternum; C, coxa; Co, costa; Cu, cubitus; E, empusal vein; Ep, epimeron; F, furca; lp, lateral process of mesocoxa; M, media; O-c, oblongum cell; P, plical vein; Pes, preepisternum; T, trochanter; ws, whip-like setae. Metathoracic muscles: 72, M. sterno-episternalis; 76, M. noto-coxalis posterior; 81, M. furca-coxalis anterior; 82, M. furca-coxalis lateralis; 83, M. furca-coxalis posterior; 85, M. furca-trochanteralis; 86, M. coxa-trochanteralis medialis; 87, M. coxa-trochanteralis lateralis. Scale bars = 0.50 mm.

Figs. 12–13. *Spanglerogyrus albiventris* Folkerts. 12, Meso- and metathorax, ventral view. 13, Middle leg.
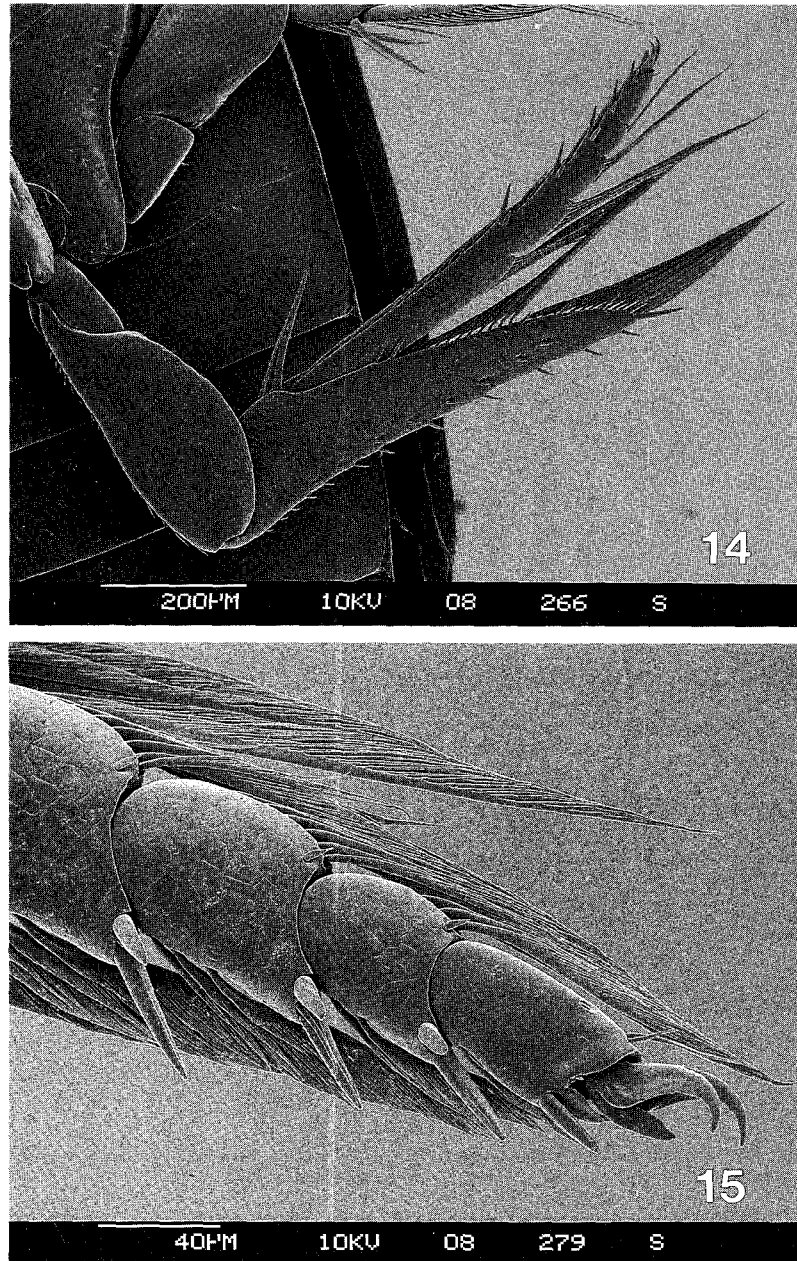
Figs. 14–15. *Spanglerogyrus albiventris* Folkerts. 14. Hind leg. 15. Distal mesotarsomeres, swimming hairs.
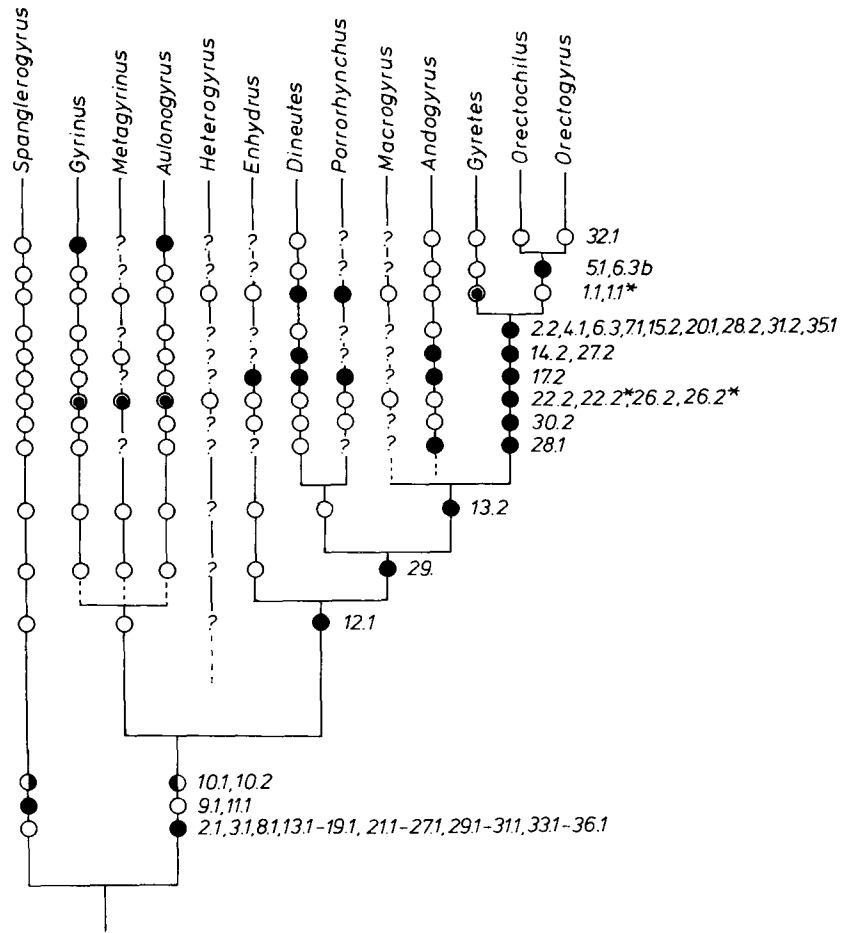
Fig. 16. Reconstructed phylogeny of gyrinid genera. Apomorphic character states are indicated
by full circles (char. state 1) or spots within circles (independently acquired; 1*).

The locomotor organs of Gyrininae are the most efficient rowing apparatus of the animal kingdom according to Nachtigall (1961). Frequencies of 50-60 strokes per second result in a maximum speed of 100 cm/s. The total efficiency factor exceeds that of comparable technical machines (Nachtigall, 1961). As described above, the middle and hind legs of members of Gyrininae are broadened, shortened, and markedly flattened. The tarsomeres are arranged in a fan-like manner and are able to rotate posteriorly and to be partly withdrawn into an excavation of the distal end of the tibia. The swimming lamellae contribute 52% of the whole propulsion force, but result in a minimum of counterthrust, when they reflex toward the rigid parts of the legs during the upward stroke (Nachtigall, 1961). The counterthrust during the upward stroke is only about 1/40 of the thrust resulting from the backward stroke (Nachtigall, 1961). The decrease of propulsion force as a result of the comparatively short axis of rotation is certainly overcompensated by the high frequency of strokes, which is correlated with the decrease in length of the middle- and hind-legs.

The middle- and hind-legs of *Spanglerogyrus*, which are almost identical in size and shape (Figs. 13, 14), may be very efficient during the backward stroke due to the arrangement of the tibia and tarsus described above (9.1), and the feather-like swimming hairs (10.1), which increase the area creating the propulsion force even more than in members of Gyrininae. However, the minimization of the counterthrust during the upward stroke is not as efficient as it is in members of Gyrininae. The tarsus as a whole is rigidly constructed, the segments of the legs are only slightly flattened, and the swimming hairs may cause considerable counterdrive when the leg is drawn forward.

The disadvantages of the swimming apparatus of *Spanglerogyrus* may be largely compensated for by the small size of the beetle. This view is supported by investigations of Nachtigall (1960) on the locomotion of dytiscids of different sizes. It is probably not by accident that the only extant representative of Spanglerogyrinae is distinctly smaller than any other member of Gyrinidae. The specialized niche occupied by *Spanglerogyrus*, which is certainly correlated with small size, may exclude direct competition by larger members of the gyrinine genera *Gyrinus*, *Dineutus* and *Gyretes*, which occur in the same habitat.

The muscular system of members of Gyrininae is adapted to the perfect locomotor system of the middle and hind-legs. The newly evolved mesothoracic M. sterno-trochanteralis results in a considerable improvement of the propulsion forces of the middle leg. The most important change however, is the acquisition of the metathoracic M. noto-trochanteralis, which is probably derived from lateral parts of M. furca-trochanteralis. M. furca-trochanteralis is a feeble muscle in members of Gyrininae, but powerful in *Spanglerogyrus* and members of other adephagan groups, especially in the aquatic families (Larsén, 1966; Beutel, 1986; Belkaceme, 1986). Lateral parts of the metafurca (and M. furca-trochanteralis lateralis) are reduced in Gyrininae, but well developed in *Spanglerogyrus*, and in members of other adephagan families (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986). It appears plausible, that lateral parts of M. furca-trochanteralis have shifted their area of attachment from the metafurca to the metanotum. M. noto-trochanteralis acts as a dominant flight muscle and as a powerful swimming muscle, which is able to perform high-frequency movements as do other indirect flight muscles. The hind legs are interlocked by antagonistic muscles during flight. Most of the regular flight muscles are absent from Gyrininae (see 31.1), and functionally are replaced by M. noto-trochanteralis. These changes of metathoracic structures are not known from any other group of Coleoptera, and represent a masterpiece of economy and efficiency. The double function of M. noto-trochanteralis results in superb

swimming abilities with high frequency movements, and capacity of flight, which is not affected by the loss of several flight muscles, and decrease in size of the metafurca and M. furca-trochanteralis.

Structural changes of the metanotum in members of Gyrininae (17.1, 2) are doubtlessly a result of the muscular changes described above. Flight muscles were reduced in all specimens of *Spanglerogyrus* dissected for this study, but well developed aleae are present. Attempts at flight are reported by Steiner & Anderson (1981), and the metanotal structures suggest, that the arrangement of flight muscles in specimens with the abilities to fly is the same as in members of other adephagan families. It appears plausible that flight muscles are reduced in a high percentage of specimens of *Spanglerogyrus* during early imaginal life. A similar phenomenon is known from members of *Noterus* (Jackson, 1956), *Platambus* (Larsén, 1966), and *Amphizoa* (Beutel, 1988). This is probably a matter of economy, especially when flight as a matter of dispersal appears risky, as the chance of finding a new suitable habitat is low. Specialized running water habitats are characteristic for *Spanglerogyrus, Amphizoa* and *Platambus*. The limited geographic range of *Spanglerogyrus* may be correlated with the loss of flying abilities in a high percentage of specimens.

The opening between the elytral base and the mesothoracic anepisternum of members of Gyrininae allows to press air into the subelytral space, and is certainly correlated with the highly efficient locomotor apparatus. The excavations for reception of the prolegs in repose improve the streamlining of the ventral body surface, thus resulting in a further improvement of swimming abilities of members of Gyrininae.

A much less dramatic step in the evolutionary history of Gyrinidae than the separation of the spanglerogyrine and the gyrinine lineage, was the splitting event, separating the *Gyrinus-Aulonogyrus-Metagyrinus* lineage from the orectochiline-enhydrine lineage. The apomorphic characters acquired by members of *Gyrinus* and *Aulonogyrus, e.g.,* anterolateral expansion of metacoxae, and loss of M. sterno-episternalis, are of a relatively minor, functional importance.

Some more important adaptive changes mark the start of the orectochiline-enhydrine lineage. As described above, the metanotum is highly derived (17.2), the elytral glossula is markedly developed (14.2), the medial metacoxal walls are fused to each other over their whole length (27.2), and the anterior and posterior walls of the tibia and proximal tarsomeres of the middle and hind-legs are connected by cuticular columnae and provided with air sacs (12.1). The latter two features may increase the capacity of the locomotor apparatus by stabilization of the metacoxae, which are not involved in movement of the hind legs, and an increase of the rigidity of the distal segments of the legs.

The loss of the dorsal pubescence, increase in size and a broadly oval, flat appearance are characteristic for most members of the enhydrine lineage, and are considered as groundplan conditions of the orectochiline-enhydrine lineage.

The hypothesized sister-group relationship between *Enhydrus* and the remaining orectochiline-enhydrine lineage is based on one derived character. Tarsomeres 4 + 5 of the hind legs are nearly parallel-sided, and are turned posteriorly, thus forming a kind of shovel with respect to the proximal tarsomeres in members of Orectochilini, *Dineutus, Porrorhynchus, Macrogyrus* and *Andogyrus*. This arrangement results certainly in a considerable increase of swimming abilities. Reversal of this character state in the stream-dwelling *Enhydrus* is quite unlikely.

The monophyly of *Dineutus + Porrorhynchus* is supported by the concealed mesoscutellar lobe, a character state which is quite common among Adephaga, and of little adaptive significance. The monophyly of *Dineutus* is doubtful, as no

synapomorphic characters are available at present. *Porrorhynchus* seems to be more closely related to certain members of *Dineutus*, and is considered as a subgenus of *Dineutus* by Ochs (1926).

The modification of both the middle and hind tarsi in the manner described above (13.2, 29.2), causing a further improvement of swimming abilities, may indicate that the genera *Macrogyrus* and *Andogyrus* form a monophyletic unit together with Orectochilini. As pointed out by Brinck (1977), no reliable characters for generic separation of species of *Andogyrus* and *Macrogyrus* are available at present. A close relationship between both taxa is quite likely, even though no common derived feature is presented within this study. The body shape of *Macrogyrus* and *Andogyrus*, which is more parallel-sided and more convex than in other members of enhydrine genera, may be supportive of the hypothesized closer relationship between these genera and Orectochilini.

A substantial advance in the evolutionary history of Gyrinidae was appearance of the orectochiline lineage. The comparatively young age of this group is indicated by its absence from Australia. Orectochilini represent a very well characterized monophyletic group of fairly small, stream-dwelling forms, with markedly convex body and lateral pubescence. A median row of setae on the abdominal sternites VII and VIII (strongly prolonged) (Hatch, 1925) acts as a steering organ.

Members of Orectochilini show the highest degree of efficiency of the locomotor organs within Gyrinidae. This is achieved by enlargement of the attachment area of M. sterno-trochanteralis (M 51, 4.1, 15.2), and conspicuous modifications of middle and hind coxae which are described above (6.3, 6.3 b, 7.1, 26.2, 28.2). Another feature of Orectochilini is the tendency toward reduction of flying organs. The basalar disc and several flight muscles, which are present in other gyrinids (20.1, 31.2), are absent from all members of Orectochilini.

A sister group relationship of the genera *Orectochilus* and *Orectogyrus* is suggested by rigid fusion of mesocoxae with the preepisternum (5.1), and fusion of the anterolateral metacoxal process with the preepisternal pouch (6.3 b). This is in agreement with biogeographic data. The distribution of *Orectochilus* is mainly Oriental, with one species in Europe and North Africa, and one species in Central Africa (Ochs, 1969). *Orectogyrus* is confined to the Ethiopian region (Ochs, 1969). *Gyretes* represents the orectochiline lineage in America, ranging from Patagonia to California, Texas and Alabama (Hatch, 1925; Ochs, 1969; personal observation).

It appears as a kind of ironic fate of evolution that Orectochilini as the most highly developed members of Gyrinidae, and *Spanglerogyrus* as the most primitive representative are very similar in their appearance. The comparatively small body size, markedly convex dorsal surface, and lateral pubescence are characters shared by the first and the latest offshoot of the gyrinid lineage. However, despite Oscar Wilde's statement, that "it is only shallow people who do not judge by appearances", it is a well known fact that superficial similarities are misleading in phylogenetic analysis. This view is confirmed by the results of this study.

ACKNOWLEDGEMENTS

Hearty thanks are conveyed to I. Askevold, Dept of Entomology, University of Manitoba for generous gift of well preserved specimens of *Andogyrus colombicus*. It is gratefully acknowledged, that SEM facilities were provided by the Lehrstuhl für spez. Zoologie, Inst. für Biologie III, Universität Tübingen.

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