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Comparative Studies on the Metathorax of Hydradephaga and Trachypachidae (Coleoptera)

by R. Beutel & T. Belkaceme

Abstract: Skeleton and musculature of the metathorax, especially the metacoxae of several Adephaga were studied. The immobility of the hind coxae is considered a synapomorphy of the Trachypachidae and the Hydradephaga. The fusion of the median walls of the metacoxae to an intercoxal septum in Trachypachidae and Hydradephaga excluding Haliplidae is synapomorphic for these groups. This data suggest that Haliplidae are the sister-group of Trachypachidae, Gyrinidae, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae. The reduction of the m. furca-coxalis anterior (M 81) and the metafurca arising from the intercoxal septum is synapomorphic for Hydradephaga exclusive of Haliplidae. Simplification of the metafurca and reduction of homologous muscles may point to a sister-group relationship between Gyrinidae and Noteridae.

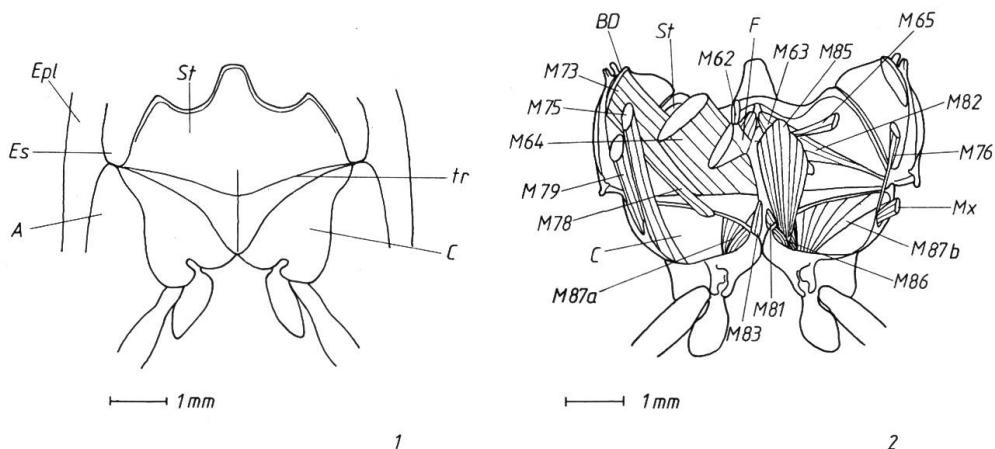
Key words: Coleoptera Hydradephaga, Trachypachidae – metathorax – comparative study – phylogeny.

The purpose of our work is to show some new aspects of adephagan phylogeny using characters of the metathorax, especially the metacoxae. According to the methods of HENNIG (1981) we suggest that only shared derived characters, synapomorphies, indicate phylogenetic relationships.

Our hypothesis is that Hydradephaga are not monophyletic, and the Haliplidae are the sister-group of Trachypachidae and all other Hydradephaga.

According to EVANS (1976), the ancestors of extant Adephaga were reasonably good runners, but also adapted to seeking their prey in subsurface habitats, which they enter by wedge-pushing. One of the adaptations to wedge-pushing is relative immobility of the metacoxae. The angle of swing of the hind coxae is reduced to about 5%. We consider the retention of this restricted mobility as being plesiomorphic, and the total immobilization of the hind coxae with the anterior coxal margin fused with the metasternum as a synapomorphy of Trachypachidae and Hydradephaga (Character 1).

Furthermore the hind coxae of these groups laterally contact the epipleurae, thus separating the abdominal sternites from the metepisterna (interrupted type sensu BELL, 1966; character 2). This situ-



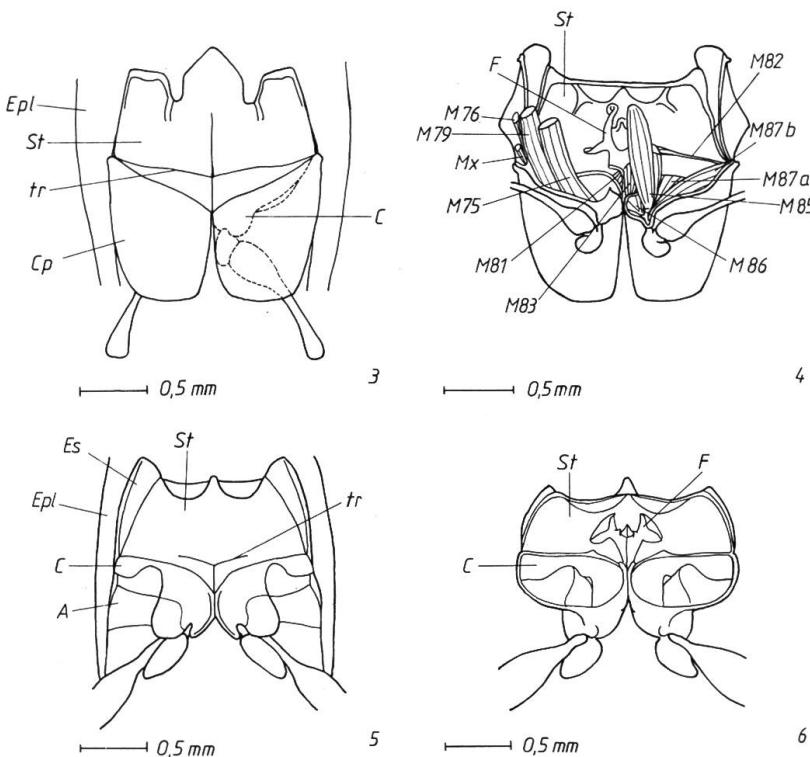
Figs 1–2: 1. *Nebria brevicollis*, ventral view. 2. *Nebria brevicollis*, dorsal view, notum and dorsal flight muscles removed.

ation is supposed to be derived, as compared with that of (nearly) all carabids and the Cicindelidae, where the metepisterna contact with the abdominal sternites (non-interrupted type, Fig. 1). Hind coxae of the interrupted type occur also in Gehringiini, Rhysodidae and Cupedidae but we suggest that this feature has developed independently in these groups. In Gehringiini and Rhysodidae, metacoxal-epipleural contact is evidently due to the wide separation of the metacoxae.

In Haliplidae, the immobilization of the metacoxae is achieved only by attachment of the anterior coxal walls to the metasternum. The medial coxal walls lie closely together, but are not fused (Figs 4, 11), and can be easily separated from each other¹. In contrast to all other Adephaga (e. g. *Nebria*, Fig. 2), the medial coxal walls of Trachypachidae and Hydradephaga excluding Haliplidae are fused to an intercoxal septum (Figs 6, 7, 10, 12, 13). We interpret this character as synapomorphic for Trachypachidae, Gyrinidae, Noteridae, Amphizoidae, Hygrobiidae and Dytiscidae (Character 3).

Another synapomorphy of these groups may be the partly (Trachypachidae, Fig. 5, Amphizoidae, Hygrobiidae) or totally (Noteridae, Fig. 8, Gyrinidae except *Spanglerogyrus*, Dytiscidae) reduced metasternal transverse ridge (Character 4). In Haliplidae, the transverse ridge is complete as it is in Cupedidae (CAMPAU, 1940), Cicin-

¹ Treatment by KOH or boiling diethylenetriamine often results in a ventral cleft between the fused medial coxal walls, but their dorsal parts never separate from each other. The full size of coxal fusion is deceived by allowing the musculature to rot in water.



Figs 3–6: 3. *Haliplus lineatocollis*, ventral view. 4. *Haliplus lineatocollis*, dorsal view, notum, dorsal flight muscles and M 65 removed. 5. *Trachypachus zetterstedti*, ventral view. 6. *Trachypachus zetterstedti*, dorsal view.

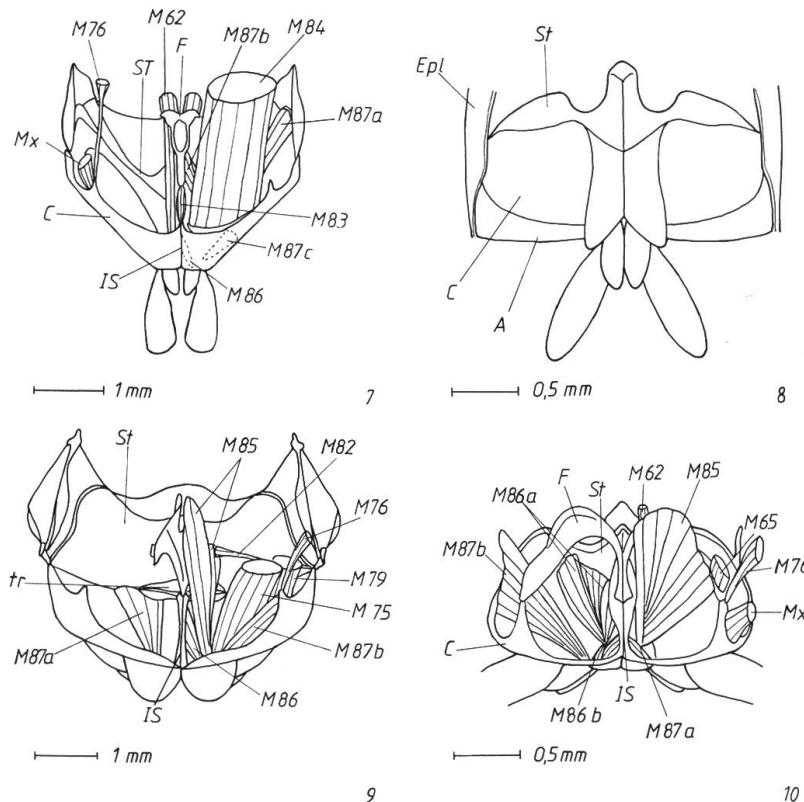
delidae and Carabidae with few exceptions.

In contrast to Haliplidae (Fig. 3) and all other Adephaga (e. g. *Nebria*, Fig. 1), the hind coxae of Trachypachidae, Gyrinidae, Noteridae, Amphizoidae, Hygrotiidae and Dytiscidae more or less (least in *Trachypachus*) broadly meet the epipleurae (Figs 5, 8); this we regard as another shared-derived character of these groups (Character 5).

Reduction of m. furca-coxalis anterior, M 81 (nomenclature of LARSÉN, 1966) is a synapomorphy which indicates that Gyrinidae, Noteridae, Amphizoidae, Hygrotiidae and Dytiscidae together form the sister-group of Trachypachidae (Figs 7, 9, 10, character 6). This muscle is retained in *Trachypachus* (EVANS, 1976) and in contradiction to the results of LARSÉN (1966), also in *Haliplus* (Figs 4, 11).

Another synapomorphy of Hydradephaga exclusive of Haliplidae may be the furca arising from the intercoxal septum (Character 7).

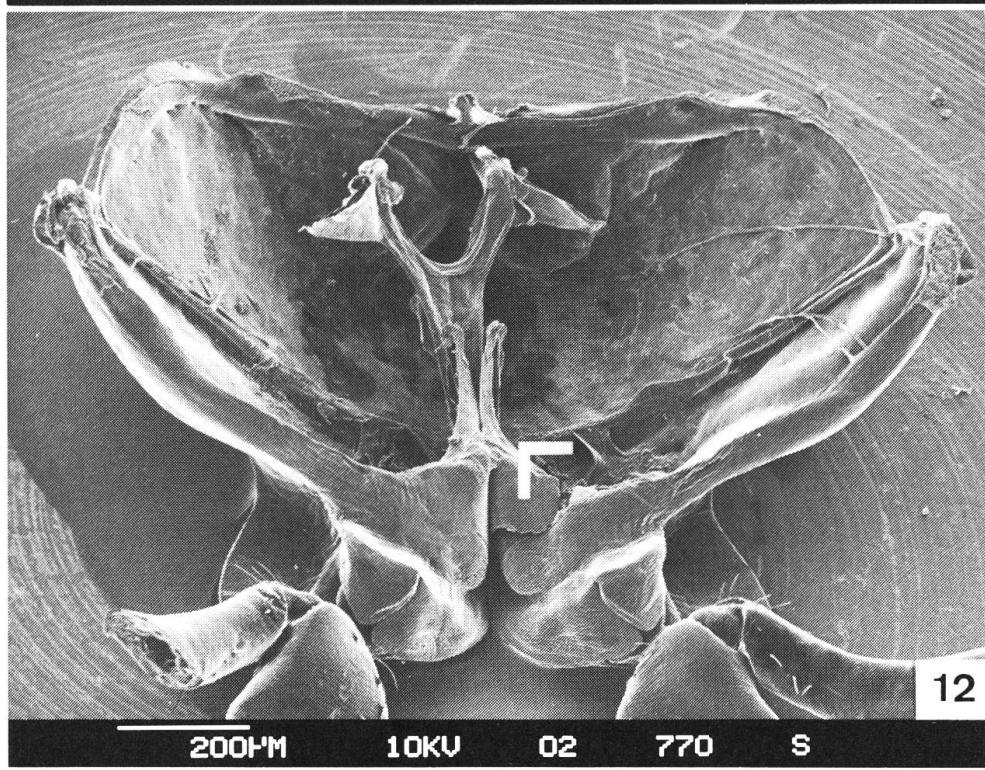
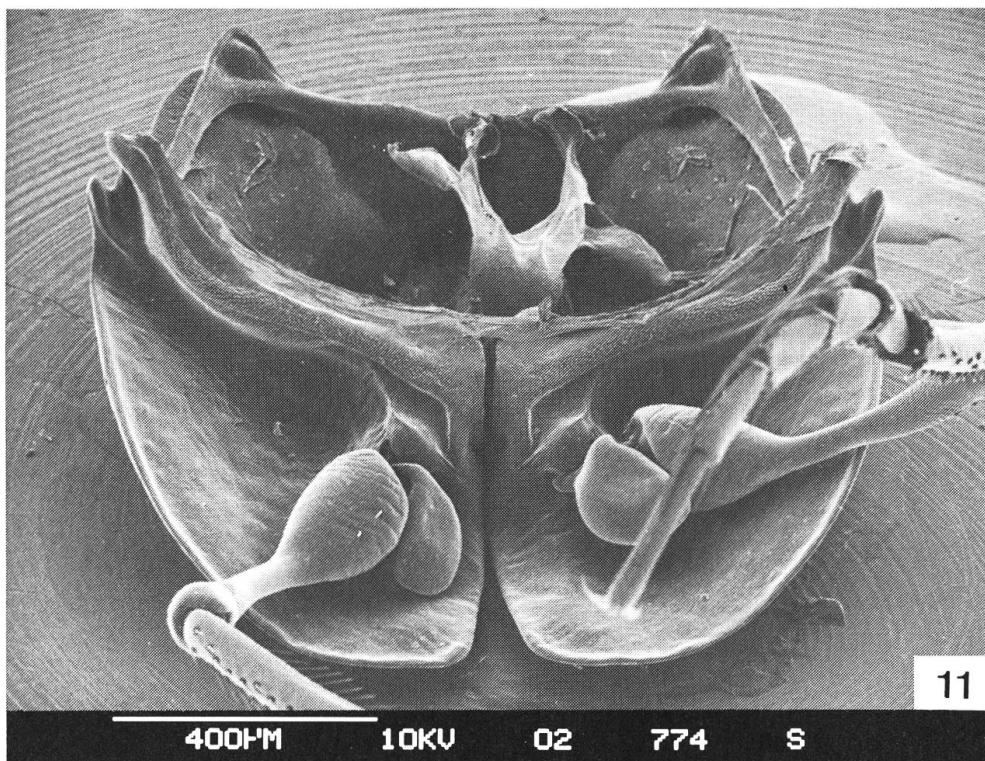
In the following, we discuss some characters which may indicate that Noteridae and Gyrinidae are sister-groups. In all gyrinid genera examined by LARSÉN (1966) the indirect flight muscles M 60, M 61, M 64, M 73, and M 75 are absent. M 78 is absent in the Orectochilinae and



Figs 7–10: 7. *Gyrinus substriatus*, notum removed. 8. *Noterus clavicornis*, ventral view. 9. *Hygrobia tarda*, dorsal view, notum, dorsal flight muscles and M 65 removed. 10. *Noterus clavicornis*, dorsal view, notum removed.

M 79 in all genera except *Dineutes* where it is rudimentary (LARSÉN, 1966). In Orectochilinae, only M 84 (m. tergo-trochanteralis) mediates the high-frequency movements of the wings. M 84 is known only from Gyrinidae, *Sphaeridium* and related hydrophilid genera (LARSÉN, 1966) and *Priacma* (BAEHR, 1975). In all noterid species we examined (*Noterus clavicornis* (Deg.), *Noterus crassicornis* (Müller), *Noterus laevis* Sturm, *Hydrocanthus cf. iricolor* Say) M 60, M 61, M 64, M 73, M 75, M 78 and M 79 were absent. JACKSON (1973) however found three specimens of *Noterus clavicornis* (Deg.) among 180 with normal (?) flight muscles. Unfortunately it is not clear which (or all) of the indirect flight muscles are present.

In any case we observe very strong tendencies towards reduction of indirect flight muscles in both Gyrinidae and Noteridae (Character 8). Parallel reduction of flight muscles occur in carabids with reduced flight apparatus (*Carabus*, *Cyclus*) and the dytiscid *Platambus* (LARSÉN, 1966).



Figs 11–12: 11. *Haliplus lineatocollis*, dorsal view. 12. *Trachypachus zetterstedti*, dorsal view.

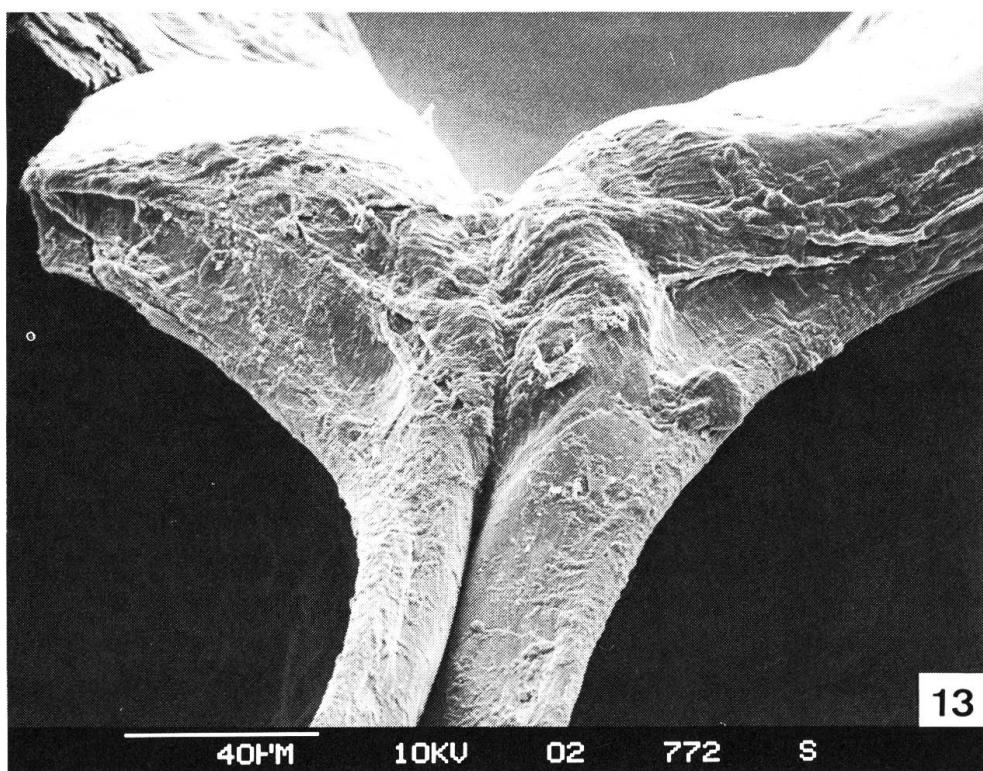
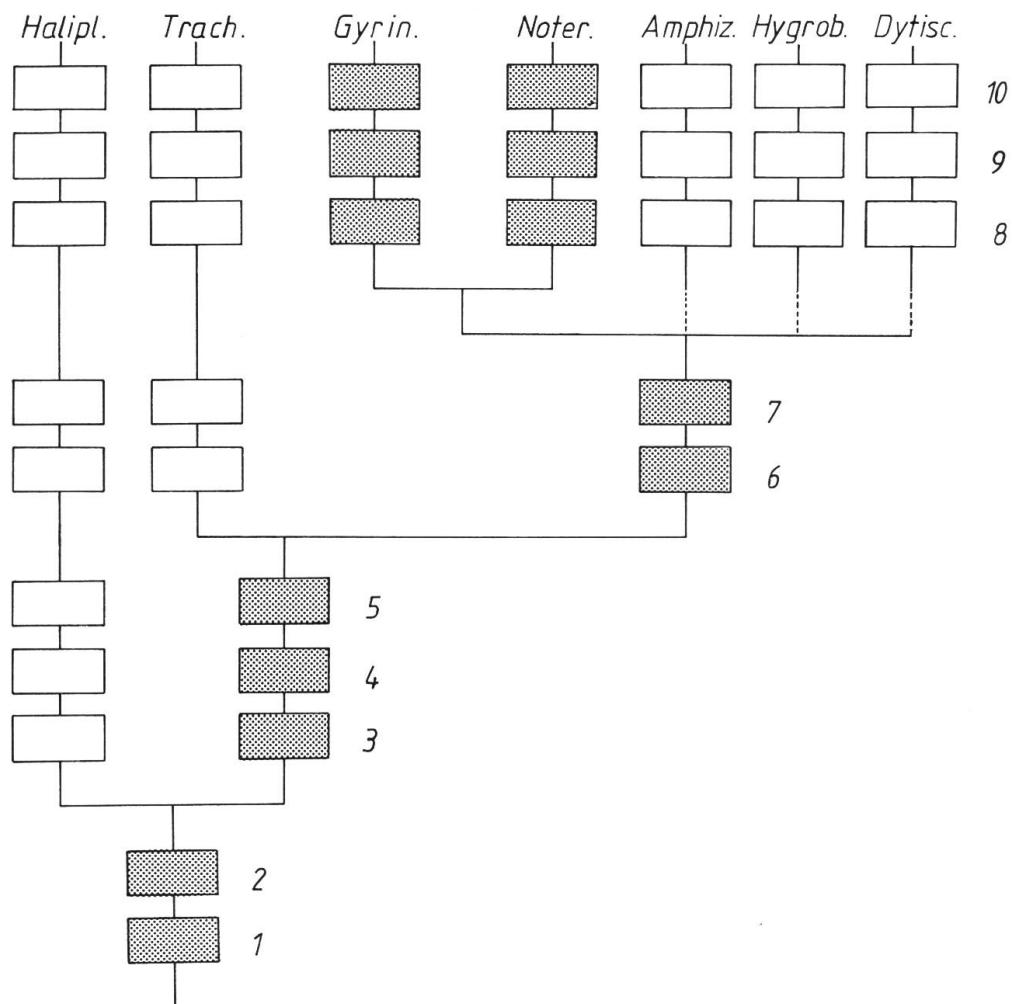


Fig. 13: *Trachypachus zetterstedti*, fusion of the median coxal walls.

Furthermore Noteridae and Gyrinidae agree in the loss of M 82 (m. furca-coxalis lateralis) (Character 9), in contrast to its constant presence in all other beetles examined (LARSEN, 1966, BALFOUR-BROWNE, 1969, BAEHR 1975).

Another argument for a sister-group relationship between Noteridae and Gyrinidae might be the simplified metafurca in both groups. In the groundplan of Adephaga, the metafurca is provided with well developed anterior arms, lateral arms and a ventral median process as in Carabidae, Haliplidae, Amphizoidae, Hygrobiidae and Dytiscidae with exception of very small forms like Bidessini (RIHA, 1952). Noteridae and Gyrinidae coincide in the same simplification of their metafurca, having retained only one pair of arms, presumably the anterior ones (Character 10). These arms are strongly prolonged laterally in the Noteridae, where they are fused with a laminar extension of the hind wall of the metacoxae. We consider this fusion of furca and coxa as an autapomorphy of the Noteridae. The weak development of the furca in Gyrinidae is probably correlated with the presence of M 84 (M 84 acts as depressor of the hind legs as well as flight muscle) and the exceptional reduction in strength of M 85 (m. furca-trochanteralis).



1: *Coxae immovable*

2: *Coxal-epipleural contact*

3: *Medial coxal walls fused to the intercoxal septum*

4: *Coxal-epipleural contact extended*

5: *Transverse-ridge more or less reduced*

6: *M81 reduced*

7: *Furca arising from intercoxal septum*

8: *Tendency towards reduction of indirect flight muscles*

9: *M82 reduced*

10: *Furca simplified*

A final decision concerning the phylogenetic relationship of Noteridae and Gyrinidae based on these arguments would be risky. In any case further studies are required.

M 83 (m. furca-coxalis posterior has been lost, as we consider independently in the specialized gyrinid subfamily Orectochilinae, in the Noteridae and in Amphizoidae, Hygrotiidae and Dytiscidae (the latter groups form a monophyletic unit as shown by RUHNAU (1986) with several larval and pupal characters).

The results of our work have been summarized with a cladogram.

Abbreviations of the figures

A:	Abdomen	Es:	Episternum
BD:	Basalar disc	F:	Furca
C:	Coxa	IS:	Intercoxal septum
Cp:	Coxal plates	St:	Sternum
Epl:	Epipleura	tr:	transverse ridge

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