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3. Monophyly of Hydrovatini and its genera

3.1. Character distribution and discussion

The systematic status of Hydrovatini, the composition of the tribe and the position of *Hydrovatus* in Hydroporinae, have been matters of discussion lately. The genus *Hydrovatus* has traditionally been associated with the genus *Queda*, together forming the tribe Hydrovatini (SHARP, 1882). This unification was generally accepted until WOLFE (1988) stressed the possible systematic significance of some morphological similarities between *Hydrovatus* and Methlini, excluding *Queda* as the sistergroup of *Hydrovatus*.

Below I present an analysis of how different morphological features are distributed in Hydradephaga, and by out-group comparison I try to determine the polarity of the characters. This survey provides information for a preliminary reconstruction of the phylogeny of the Hydrovatini.

For the comparison procedure I have used representants of the following Hydroporinae taxa: *Laccornis*, *Methles*, *Queda*, *Derovatelus*, *Herophydrus*, most genera of Bidessini, *Heterhydrus*, *Pachydrus*, *Microdytes* and *Hyphydrus*.

I have also made comparisons with other Dytiscidae taxa as well as with other water-living adephagans as follows: *Agabus*, *Platambus*, *Ilybius*, *Colymbetes*, *Graphoderes*, *Acilius*, *Eretes*, *Dytiscus*, *Copelatus*, Noteridae, Haliplidae, Gyrinidae, and Hygrobiidae.

To improve my knowledge of the anatomy of some Dytiscidae of special interest, e.g. the plesiotypic hydroporine lineages, I have used the works of Dr. William Wolfe in particular (WOLFE, 1985, WOLFE & SPANGLER, 1985, ROUGHLEY & WOLFE, 1987, WOLFE, 1988, and WOLFE & ROUGHLEY, 1990). Supplementing literature includes e.g. BRANCUCCI (1988), HOLMEN (1987), LARSON (1975), ROUGHLEY (1990), SATÔ (1981) and ZIMMERMANN (1924).

For this survey I have similarly monitored a large number of features exhibited by the different groups. Most of them proved useless, because I could not get any reliable picture of their occurrence and appearance; accordingly, their polarity remained unclear. Characters with determined polarity, which are important for the phylogeny of Hydrovatini (within Hydroporinae) I have listed in Table 1 (p. 583). Each character is provided with a number (1–19) to which I refer later in the text. Characters important for the phylogeny within *Hydrovatus* and accordingly for the new subdivision of the genus, here introduced, are treated in a separate chapter (p. 77) and listed in Table 2 (p. 584).

1. Shape of antenna: The male antenna of *Hydrovatus* exhibits much variation (see relevant illustrations). Many species have practically unmodified and slender antennae (all joints equally broad), but there are also many species with a variable number of enlarged and modified antennal joints. The female antenna is always slender and unmodified.

In Dytiscidae, the unmodified antenna is present almost throughout the family. Similar antennal modifications, as in *Hydrovatus*, are, however, also present in some *Queda* and *Laccornis* species (WOLFE & SPANGLER, 1985, WOLFE & ROUGHLEY, 1990). In *Hydrovatus* the modified antenna is not always restricted to certain recognized species groups but appears scattered among them.

The polarity of this character is difficult to determine and partly unclear, because regarding Hydradephaga the modified antenna is the derived state. On the other hand, the presence of modified antenna in three, probably quite close lineages in Hydroporinae supports the interpretation that this state could be assigned as a ground-plan for a lineage in Hydroporinae including Hydrovatini. Slender male antenna in Hydrovatini would then be a case of secondary loss of a former character.

The antenna is a part of the insect body probably highly significant for interaction between the insect and its environment. Accordingly, the antenna is also influenced by specialization toward different kinds of life-style, which can be seen as morphological adaptation. Modification of the male antenna is regarded as an unstable, adaptive character which has evolved independently in *Laccornis*, *Queda* and several times in *Hydrovatus*.

At least thus far, I consider the modified male antenna as the apomorphous state and the unmodified slender antenna as the plesiomorphous state.

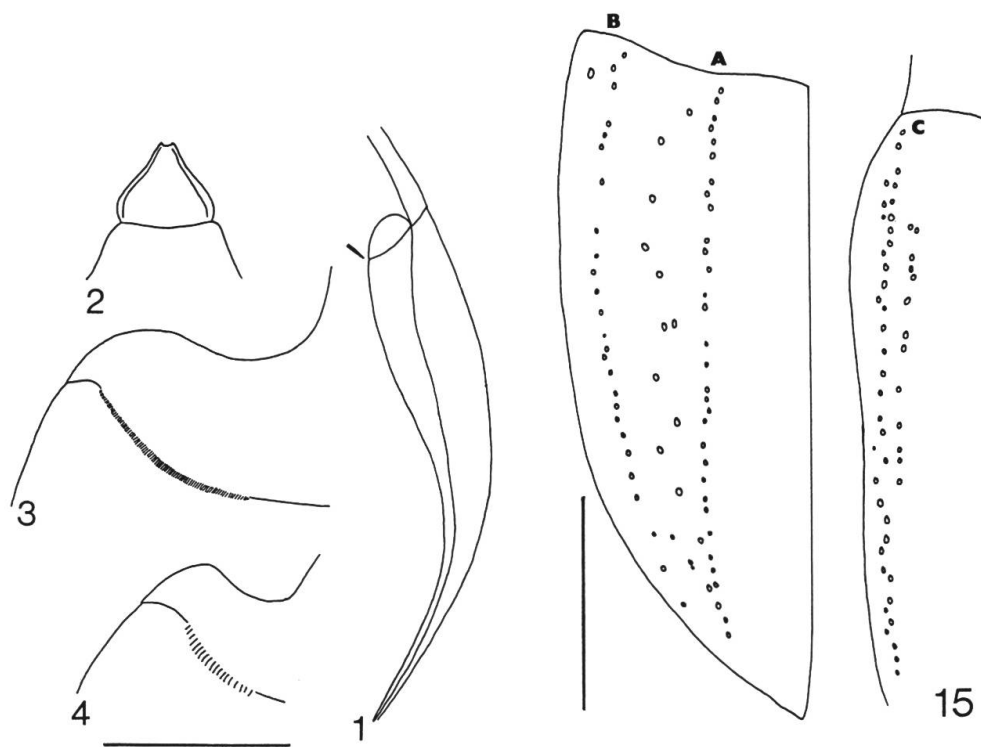
2. Appearance of frons: This region of the body is variable in *Hydrovatus*, but it is possible to recognize a ground-plan: Frons frontally edged between the eyes so that mouthparts are partly covered when the specimen is studied from above; outline of frons anteriorly rounded with a common medial straightening; with a narrow frontal margin between the eyes (e.g. Fig. 289).

Differentiation from this ground-plan are: Various reductions of the frontal margin and variation in the appearance of the outline of the frons (e.g. Fig. 498). An independent lineage in *Hydrovatus*

exhibits further modification: Frontal margin thickened and in one species the medial part of the margin hooked (Figs 30–31).

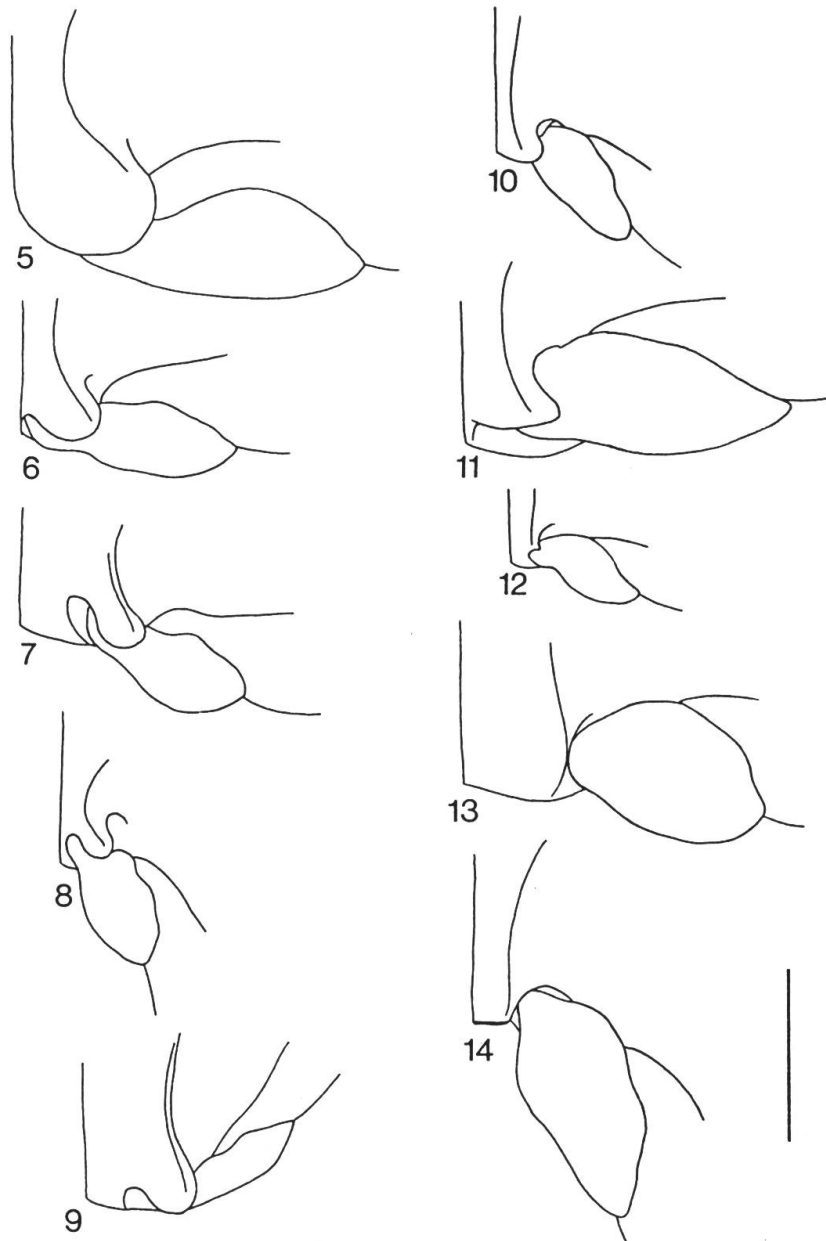
In Hydroporinae *Laccornis*, *Methles* and *Derovatellus* have non-margined frons. Hyphydrini (*Microdytes* has a non-margined frons), Bidessini and *Herophydrus* exhibit a similar condition to *Hydrovatus* but also the simpler state is represented. The ground-plan above coincides almost with the situation in *Queda*. In all but one of the non-hydroporinae dytiscids and the other adephagans, the simpler state is present. *Copelatus* specimens examined exhibit a very fine, partly fragmentary frontal rim.

An edged and margined frons is evidently the derived state. This feature is possibly also an unstable character, which has evolved several times independently in Hydroporinae. Any closer relationship between Hydrovatini and some Hyphydrini cannot, however, be excluded. The situation in *Copelatus* is morphologically different, and the rim may be ascribed as a case of convergence.



Figs 1–4, 15: 1, carinated (arrow) epipleuron of *Hydrovatus bonvouloiri*. – 2, prosternal process and anterior part of metasternum of *H. bonvouloiri*. – 3, stridulation apparatus of *H. vliersi*. – 4, stridulation apparatus of *H. confertus*. Scale 0.5 mm. 15, Location of discal (A), dorsolateral (B) and lateral (C) rows of punctures in *Hydrovatus parallelipennis*. Scale 1 mm.

3. Carination of epipleuron: The epipleuron is sometimes divided by a narrow carina into a small basal part (often cavity-shaped) and a long part, lying along the ventral part of the body, narrowing towards the body apex (Fig. 1).



Figs 5–14: Metacoxal process-metatrochanter and base of metafemur in different Dytiscidae taxa. – 5, *Agabus* sp. – 6, *Laccornis oblongus*. – 7, *Hydrovatus villiersi*. – 8, *Methles* sp. – 9, *Queda youngi*. – 10, *Derovatellus dagombae*. – 11, *Herophydrus* sp. – 12, *Hydroglyphus plagiatus*. – 13, *Heterhydrus sudanensis*. – 14, *Hyphydrus elegans*. Scale 0.5 mm.

All *Hydrovatus* species have a carinated epipleuron. Hydroporinae genera that I compared have similar carina, except *Laccornis*, *Methles*, *Derovatellus* and some Bidessini genera. Other dytiscids and adepagans lack epipleural carina.

The polarity of this character is quite clear. A carinated epipleuron is the apomorphous state. Also as in character 1 and 2, I suspect frequent independent evolution of this character in different lineages of Hydroporinae.

4. Incision of metacoxal process: The region of the metacoxal processes exhibits much variation among the groups compared (Figs 5–14). A distinct medial incision of the metacoxal process is exhibited solely by *Methles*, *Hydrovatus*, *Queda* (Figs 7–9) and Hygrobiidae. In non-hydroporine dytiscids a minute and narrow furrow is often present, but because of its clear difference in appearance and position it is not be regarded as homologous with the incision of some hydroporines.

The polarity of this character is quite clear, although the derived state is also exhibited by a relatively distant group outside Dytiscidae in Hydradephaga. An incised metacoxal process is a probable apomorphous character combining *Methles* with *Hydrovatus* and *Queda*. The appearance of this character in the derived state in Hygrobiidae is assigned as convergence but requires attention in future studies. (See also character 6.)

5. Shape of prosternal process: *Hydrovatus* and *Queda* have an almost similar prosternal process: Posteriorly broad, its shape triangular and laterally edged, with mesocoxal cavities broadly separated (Fig. 2).

In almost all other taxa compared, the process is narrower, often lancet-shaped; with mesocoxal cavities not broadly separated. A similar shaped process to that of *Hydrovatus* is exhibited by *Heterhydrus* and *Pachydrus*, but the process is not equally triangular and differs laterally (not edged). (These two genera are true Hyphydrini characterized by metatarsal claws of unequal length). In noterid and haliplid species examined, the prosternal process is also quite broad, but on the other hand so different that this similarity is regarded as superficial and caused by convergent development.

The posteriorly broad, triangular and laterally edged prosternal process is considered the apomorphous state.

6. Shape of metacoxal incision: The incision is deep in *Hydrovatus*, *Methles* and the Hygrobiidae examined, while it is reduced and less deep in *Queda* (Fig. 9) (in *Q. hydrovatooides* the reduction is less distinct than in the two other recognized *Queda* species).

The reduced incision, being a further modification of character 4 above, is with some hesitation regarded as the apomorphous state. The possibility that a moderately deep incision, as in *Queda*, represents an intermediate state between absence of incision and deep incision cannot be excluded. The first alternative, however, is in my opinion supported by possible functional difference combined with a different location of the metatrochanter, resulting in a distinct gap between the metacoxal process and and metafemur and a reduced incision. See also character 8 below.

7. Base of metatrochanter concealed/exposed: As characters 4–5 this case exhibits considerable variation in the groups compared (Figs 5–14). Most taxa monitored have the base of the metatrochanter partly concealed by the metacoxal process. In Bidessini, “*Hydrovatus pasiricus*”, *Microdytes*, *Heterhydrus*, *Pachydrus* and *Hyphydrus*, the base of the metatrochanter is exposed and clearly visible (Figs 12–14). (*Allopachria* and probably also *Nipponhydrus* have the base of the metatrochanter exposed (ZIMMERMANN, 1924, SATÔ, 1981).)

I consider the polarity of this character quite clear - the exposed base of the metatrochanter is the apomorphous state. This character may allow us to combine Bidessini and Hyphydrini including *Microdytes* and probably also *Allopachria* and *Nipponhydrus*. The removal of the taxon “*Hydrovatus pasiricus*” from *Hydrovatus* in this work is partly based on the presence of the exposed base of the metatrochanters and the absence of a metacoxal incision. Its location in Hydroporinae is somewhat unclear, but possibly to be attributed somewhere close to Hyphydrini.

8. Connection of metacoxal process and metafemur: In all non-hydroporine dytiscids compared, in Noteridae and Hygrobiidae and in the hydroporine genus *Laccornis*, the metacoxal process and metafemur are in contact. The condition of this character in Haliplidae and Gyrinidae is unclear. In the rest of the hydroporines compared, there is a gap between the metacoxal process and metafemur except in *Hydrovatus*, in which both states are present (Figs 7, 318).

It seems quite clear that the formation of a gap is a result of modification (often reduction) of the metacoxal process. Accordingly having a gap between the metacoxal process and metafemur is the apomorphous state. The occurrence of both states in *Hydrovatus* is problematic because it provides different but equally probable alternatives when the relationships of Methlini, *Queda* and *Hydrovatus* are studied. It remains unresolved whether the formation of a gap is a unique event in Hydroporinae or whether it has taken place at different times in separate lineages. Without any definite evidence, at least at present I consider the latter alternative to be the correct interpretation.

9. Shape of body apex: Except for *Hydrovatus* and *Methles*, all groups compared exhibit an unmodified, posteriorly unexpanded body apex.

A modified and posteriorly expanded apex of the body is an apomorphous state. According to WOLFE (1988), similarity in this character indicates monophyly of Methlini and *Hydrovatus*, excluding *Queda*.

There are considerable differences in this character between the two taxa in question, which on the other hand supports separate development. The differences were observed by Wolfe, who distinguished three morphotypes: 1. The original plesiomorphous state generally distributed in Dytiscidae, 2. An intermediate state present in *Hydrovatus* and 3. The most derived, apomorphous state in Methlini. The difference between morphotype 2 and 3 is in the modification of terga (only the apical tergum modified in morphotype 2; the seventh and eighth terga modified in morphotype 3). Additionally Wolfe stressed at least a partly different function in different morphotypes. (Regarding detailed description of structures, see WOLFE (1988).)

Separate development, which I think in this case is more probable, is supported by two considerations:

1. Different function of similar structure in the two taxa.

As WOLFE (1988) stated, ovipositional function in Methlini is ruled out because modifications are identical in both sexes. In *Hydrovatus* both sexes have a modified apical part of the body but internal anatomy differs between female and male. In the female modification, is probably associated with oviposition. One strategy in oviposition of Dytiscidae is to make incisions in plant tissues in which eggs are deposited (SPANGLER, 1981). Without any conclusive

field-evidence, *Hydrovatus* is suggested to belong with dytiscids who exhibit this kind of egg-laying, alternatively, they may deposit eggs in other kinds of sheltered places. In Methlini the abdominal modification may be a device for obtaining trapped air from plant tissues. It is not known whether or not adult Methlini have this ability, but this kind of behaviour has been postulated for the larvae of at least one species of the genus *Celina* belonging to Methlini (SPANGLER, 1973), and it is well known among larvae of noterids (HOLMEN, 1987).

2. Considerable morphological difference in structure between the two taxa.

Similar devices for penetration into plant tissues have evolved in many separate lineages of Hydradeephaga. Adults of some noterids have internal abdominal structures quite similar to those of *Hydrovatus* (homology of bodyparts unclear). BURMEISTER (1976) reports knife-like ovipositors for cutting plant tissue in *Dytiscus* and *Cybister* and saw-shaped gonocoxae in *Ilybius* and *Hydrovatus*. The genera *Laccophilus* and *Agabetes* are reported to have saw-shaped genital appendages.

Although the argumentation above does not prove separate development, I at present consider the similarity between Methlini and *Hydrovatus* in this case to be superficial and a result of separate development.

10. Head punctate/non-punctate at eyes: Almost all *Hydrovatus* species, except those with strongly developed reticulation, have close to the eyes a narrow area with dense punctation. In hydroporines used for comparison, both states are present. *Methles* is non-punctate at the eyes, while *Queda* is provided with a punctate area at the eye. In hydroporines with widely distributed punctures on the head, the state of this character remains unclear. All non-hydroporine dytiscids exhibit the same state as *Hydrovatus*. In non-dytiscide adephagans both states are exhibited.

A narrow area of punctures most probably represents the ancestral state, and accordingly absence of punctures may be regarded as an apomorphic structure.

11. Elytron provided with rows of punctures/rows absent: Almost all non-hydroporine dytiscids: *Hydrovatus*, *Queda*, *Heterhydrus*, *Pachydrus*, *Hyphydrus* and Noteridae have longitudinal rows of punctures on the elytron (Fig. 15, p. 67). In a number of

hydroporine taxa these rows are absent. The situation in Haliplidae, Gyrinidae and Hygrobiidae is unclear.

The polarity of this character is quite clear. Absence of elytral rows of punctures is the apomorphous state.

12. Shape of male protarsal claws: In *Hydrovatus* males, the protarsal claws often exhibit modifications: length, thickness and shape of claws are unequal. Similar modifications are present in *Laccornis* and *Methles*. All other groups examined have simple, almost symmetric protarsal claws.

Modified, asymmetric male protarsal claws are regarded as the apomorphous state. A distinction between modifications in male protarsus of Dytiscidae is well known. Large-sized species often have flattened tarsal joints with suckers, while smaller species may have modifications predominantly in the claws. Both kinds of modifications are probably used when gripping females while mating in water. In my opinion this indicates strongly that this character is unstable and may have evolved separately several times in Dytiscidae.

13. Shape of metatarsal claws: Metatarsal claws may be of two different kinds: Both claws equal in length or one claw reduced and distinctly to slightly shorter than its partner. Both states appear scattered in the dytiscide groups examined. All examined non-dytiscide groups have equally long metatarsal claws. *Methles* exhibits slight asymmetry, while *Hydrovatus* and *Queda* have claws of equal length.

The equally long metatarsal claws, which are widely distributed in Coleoptera, is the plesiomorphous state while asymmetry of claws is a case of apomorphy. This character, too, is to be regarded as unstable, which explain its occurrence in clearly distant lineages in Dytiscidae.

14. Paramere haired/nude: The apical half of the paramere is nude in almost all *Hydrovatus* species. Most groups examined have a hairtuft, which sometimes is reduced but still clearly discernible. Exceptions are *Derovatellus* and *Methles*, which have nude parameres. Among Bidessini genera there is variation between nude and haired parameres. The condition in *Acilius*, *Eretes* and *Graphoderes* is regarded as unclear (hairs seem to be absent or are very indistinct). Non-dytiscide adephagans have a haired paramere, except Hygrobiidae.

Most probably the nude paramere represents the apomorphous state.

15. Paramere with/without external membranous lobe: In most *Hydrovatus* species the paramere is externally provided with a membranous lobe, which generally covers the apical hook of the paramere (e.g. Fig. 680). In a few, predominantly American species, this character seems to be absent. Instead, many of these have a small, softer, membranous part apically on the paramere (Fig. 74) (cf. point F below on p. 78). The homology of these features is unclear. A small number of *Hydrovatus* species cannot be placed in either group. Two of three *Queda* species have the basal part of the paramere partly membranous. Three *Laccornis* species are provided with a subapical, weakly sclerotized, membranous lobe. The paramere of a few *Heterhydrus* species has a comparatively large, softer part. Other groups examined lack a membranous part of their paramere. Moreover, it is known that some species of *Nebrioporus* have a sac-like feature on the paramere (NILSSON, 1982).

This lobe is rather difficult to recognize, as is homology between the features. The presence of a membranous lobe is, however, quite clearly an apomorphous state. It is not known whether the softer part of the paramere indicates synapomorphy or separate development of similar characters in different lineages.

16. Paramere without/with long apical extension (narrow also at its base): Among dytiscids examined only *Methles* and *Queda* have parameres provided with a long apical extension. A small apical extension is present in *Copelatus* (cf. character 17). Among non-dytiscids a long apical extension is present in some haliplids and in hygrobiiids studied.

This is also a difficult case, because the apical extension, which seems to be the apomorphous state, occurs also among the non-dytiscide adephagans. This character could unite *Queda* and *Methles*, but in my opinion separate development is more or at least equally probable because of existence of the character in the apomorphous state in out-groups. Incorrect polarity determination cannot be excluded.

17. Paramere segmented/not segmented: Only genera associated with Bidessini have a clearly segmented paramere. All other

groups examined have a unisegmented paramere, possibly with the exception of *Ilybius* and *Copelatus*, that have parameral features which can be interpreted as segmentation.

The segmented paramere is regarded as a clear apomorphy.

18. Penis nude/haired: The haired penis has quite a scattered distribution in hydradephagans examined (some *Laccornis* species, *Methles*, many *Hydrovatus* and *Hyphydrus* species, monobasic *Huxelhydrus* in Bidessini, *Dytiscus*). Because of their different appearance, homology of character is unclear.

A penis provided with hairs is regarded as the apomorphous state. Most probably this character in its apomorphous state has evolved separately in different lineages in Dytiscidae.

19. Penis straight/curved: Almost all groups examined have a principally straight penis. Exceptions are some *Laccornis* species and many *Hydrovatus* species, which have an apically strongly bent penis.

An apically strongly bent penis is with some hesitation regarded as the apomorphous state.

3.2. Conclusions

When the phylogeny of Hydrovatini is discussed, characters in Table 1 (p. 583) may be classified in accordance with their information-value. Some of these characters may be of importance at subfamily and tribus level indicating relationship: for instance between Hyphydrini and Bidessini or Hydrovatini and Hyphydrini. Their information-value is, however, still quite restricted, not allowing for far-reaching conclusions in this respect.

Characters which are in their plesiomorphous state in *Hydrovatus* and *Queda* are: 7, 10, 11, 13 and 17. Of these characters 10, 11 and 13 are exhibited in their derived state in *Methles*. At least character 13 is regarded as unstable, occurring scattered among different lineages in groups examined.

Unstable, possibly adaptive external characters and some genital characters (homology uncertain), which probably have evolved separately in different lineages are 1, 2, 3, 12, 13, 14, 15, 16, 18 and 19. With some hesitation, character 8 is also placed here. Character 9, which is important for the independence of both *Hydrovatus* and *Methlini*, is also regarded as an unstable character.

This study thus supports the following hypotheses:

1. Monophyly of Hydrovatini and *Methles* is indicated by character 4.
2. Monophyly of Hydrovatini, consisting of the genera *Hydrovatus* and *Queda*, is indicated by character 5. If this hypothesis is correct, the traditional separation of the tribe as a separate lineage in Hydroporinae is maintained.
3. Monophyly of *Queda* is indicated by character 6, supported by apomorphy in character 16.
4. Monophyly of *Hydrovatus* is indicated by character 9, which has evolved separately. Thus *Methles*, which also exhibits modifications (apomorphy) in the same body region, does not belong to the same lineage as *Hydrovatus*, when *Queda* is excluded.

4. Subdivision of *Hydrovatus*

4.1. Historical review

Although *Hydrovatus* is a diverse and widely distributed genus, occurring in all continents but Antarctica, there are quite a few papers where subgrouping is introduced or discussed.

The genus was introduced by MOTSCHULSKY (1853), who recognized only one species (*H. cuspidatus*). A few years later MOTSCHULSKY (1855) added two species: *H. castaneus* and *H. obtusus*. During the years new species have accumulated and up to now approximately 260 names of the species group are associated with *Hydrovatus*.

SHARP (1882a) counted 43 species of *Hydrovatus* in his monography of Dytiscidae of the world. He did not, however, propose any subdivisions of the genus.

The first subdivision of *Hydrovatus* was introduced by RÉGIMBART (1895b) in his work on the Dytiscidae of Africa and Madagascar. Three subgroups were recognized on the basis of body size and colour pattern of body.

The subdivision into four subgroups, introduced by GUIGNOT (1945a) for the African species, was also based on size and colour pattern characteristics.

Almost ten years later the genus was divided into two subgenera, *Hydrovatus* s. str. and *Vathydrus*, depending on the appearance of the frontal part of the head: Margined, non-margined or frontal margin reduced (GUGINOT 1954e, cf. also GUIGNOT 1956f).