

Zeitschrift: Entomologica Basiliensia
Herausgeber: Naturhistorisches Museum Basel, Entomologische Sammlungen
Band: 19 (1996)

Artikel: Taxonomic revision of the genus *Hydrovatus* Motschulsky (Coleoptera, Dytiscidae)
Autor: Biström, O.
Kapitel: 4: Subdivision of *Hydrovatus*
DOI: <https://doi.org/10.5169/seals-980453>

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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).

OMER-COOPER (1957), who also worked with the African fauna, stated that no satisfactory subgrouping of the genus had thus far been proposed. Her subgrouping, however, was partly based on the same characteristics as her predecessors' (body size, colour pattern) and additionally the shape of male antenna, but not the appearance of the frontal part of the head.

A few years later GUIGNOT (1959a), who distinguished two subgenera in *Hydrovatus*, made further subdivisions in the genus. In subgenus *Vathydrus* he separated seven further subgroups on the basis of body size, colour pattern of body, elytral microsculpture, elytral punctation and enlarged male antennal segments. In *Hydrovatus* s. str. he distinguished two subgroups depending on appearance of elytral microsculpture.

OMER-COOPER (1963, 1965) rejected Guignot's division into two subgenera as unsatisfactory. She simply divided the genus into two main groups on the basis of body length, and in the two main groups she further distinguished four and two subgroups respectively. In the later work she does not, however, divide the second main group into two separate groups.

No subdivision taking into consideration all recognized species has thus ever been worked out. Neither are the characters used in previous subdivisions now regarded as reliable for systematic purposes, because of their inexactness when polarity of characters is determined. *Hydrovatus* is most probably a monophyletic genus but lacks a subdivision based on all species, which is needed for practical reasons as well as a basis for more profound systematic examination in future.

4.2. An attempt at subdivision and reconstruction of the phylogeny

This subdivision is to be regarded as preliminary, although the polarity of a number of characters is quite clear. Monophyly of many subgroups seems to be evident, but my knowledge of the branching into the different lineages is still poor. The existence of two species-rich paraphyletic subgroups (species groups 4 and 11) demonstrates the difficulties met with in this respect. The characters indicating monophyly are listed in Table 2 (p. 584) and briefly discussed below. As an outgroup for *Hydrovatus* I have used *Queda*. The within-genus characters of *Hydrovatus* are provided with letters in alphabetical order (A–P). Later in the text I shall simply refer to these letters.

A. Penis lacks dorsal spines/with spines: The soft tissue dorsally on the penis is in a few species provided with backwards-projecting pointed processes (Figs 25, 33). *Queda* lacks similar structures, possibly with the exception of *Q. hydrovatooides*, in which a similar feature is exhibited. Probably a case of convergence.

Possession of dorsal spines is regarded as the apomorphous state.

B. Male head frontally unmodified/modified: The frontal margin of the male head is in a few species modified; angular (Fig. 23) and thickened (Fig. 30). *Queda* lacks modifications frontally on the head.

Modifications on male frons is considered as an apomorphous structure.

C. Male mesotarsal claws unmodified/modified: One species of *Hydrovatus* exhibits a peculiar modification of mesotarsal claws; claws asymmetric, one of the claws in a pair distinctly prolonged (Fig. 46). This feature is unique in *Hydrovatus*. Some *Hydrovatus* species have modified mesotarsal claws, but modifications appear differently. *Queda* does not exhibit modifications of the mesotarsal claws.

The peculiarly modified mesotarsal claws is an apomorphous structure.

D. Penis short, broad/elongated: A number of *Hydrovatus* species (e.g. Fig. 25) and *Queda* have a broad and short penis. Most *Hydrovatus* species have a distinctly elongated and narrower penis.

The elongated, narrower penis is regarded as the apomorphous state.

E. Penis apex short/prolonged: A number of species have a distinctly prolonged and slender apex of the penis (e.g. Fig. 107). *Queda* species have a short and broad penis, which is quite different from this kind of penis. One additional species of *Hydrovatus* also has a long penis apex, but it is also provided with a stridulation apparatus which clearly indicates separate development.

The prolonged, slender penis apex is an apomorphous structure.

F. Paramere lacks a small membrane/with a small membrane: Some species of *Hydrovatus* have a paramere which is api-

cally provided with a small, soft and weakly sclerotized area (e.g. Fig. 109). The paramere of *Queda* lacks corresponding membraneous area.

Possession of a small membraneous area is considered the apomorphic state.

G. Paramere lacks apical hook/with apical hook: Most *Hydrovatus* species have a paramere which apically is provided with a distinctly sclerotized hook-like structure (e.g. Fig. 185). *Queda* and some *Hydrovatus* species lack a hook on the paramere.

A paramere with a hook is the apomorphic state of this character.

H. Elytral punctation coarsest basally at suture/apically on disc: Two *Hydrovatus* species have elytral punctation, which is coarsest apically on the disc. *Queda* and most *Hydrovatus* species have evenly distributed punctation or punctures coarsest basally at the suture of elytra.

The apically coarse punctures of the elytra are regarded as an apomorphic structure.

I. Body, medium- to large-sized/small: Most *Hydrovatus* species and *Queda* are medium- to large-sized. A small number of species with similarly shaped male genitalia all also have a small body.

The small body is regarded with some hesitation as an apomorphic structure. The status of this character as an apomorphy is to be considered uncertain. Its acceptance is supported by the similarly shaped male genitalia.

J. Apical segment of maxillary palpus simple/modified: A small number of *Hydrovatus* species have distinctly modified male maxillary palpi: Apical segment distinctly enlarged (e.g. Fig. 676). Two *Queda* species also have modified palpi, but their structure are different in comparison with *Hydrovatus* species provided with modified palpi.

Modified maxillary palpus is the apomorphic state. Occurrence of a similar character in *Queda* is ascribed as convergence.

K. Penis lacks strengthening lobes/with strengthening lobes: Very many *Hydrovatus* species with a large body size have

a penis which is laterally provided with strongly sclerotized, rounded lobes (e.g. Fig. 942). This feature is not present in *Queda*.

Occurrence of the strengthening lobes is probably a case of apomorphy.

L. Penis tip rounded to pointed/narrowly obtuse: Quite a small number of *Hydrovatus* species have an almost similar extreme tip of the penis: the apical part is quite long and somewhat curved downwards, the tip narrow and obtuse (e.g. Fig. 781). The penis of *Queda* is totally different.

The narrow and obtuse penis tip may be an apomorphous structure. The apomorphy of this character is rather weakly supported.

M. Without/with stridulation apparatus: A considerable number of *Hydrovatus* species have morphological structures which probably have a stridulatory function. Males exclusively have on each bodyhalf in the border-region of the metasternum and metacoxalplates a narrow file of densely placed, minute (often hardly visible) striae. Deviations from this ground-plan are recognized: the original state of the file with 50–60 minute striae (Fig. 3); a reduced number of clearly visible tubercles (10–15)(Fig. 4); a further modified state with 2–3 tooth-shaped tubercles (Fig. 1032). A few species show a total disappearance of this apparatus. Existence of the final state is supported by male genital characters which link deviating, file-lacking species with file-provided species. Additionally, there are a few species provided with a glabrous area instead of a file. I regard this also as a modification of the original state of the file. *Queda* lacks stridulatory files.

Possession of stridulatory files is the apomorphous state.

N. Penis apex without lateral flaps/with lateral flaps: A small number of *Hydrovatus* species have a penis, apically provided with distinct, lateral flaps (e.g. Fig. 1109). Similar structures are lacking in other *Hydrovatus* species and in *Queda*.

Possession of lateral flaps on the penis apex is considered an apomorphous state.

O. Penis apex straight or bent downwards/apex curved upwards before downwards curved tip: A rather small number of species exhibit a peculiar shape on the penis apex; the

apex is curved upwards anterior to the downwards curved tip of the penis (e.g. Fig. 1240). Similar modification is lacking in *Queda* and most *Hydrovatus* species.

The upwards curved penis apex anterior to the downwards curved tip is regarded as a probable apomorphy.

P. Paramere simple, often hooked/not hooked, provided with minute tubercles: One *Hydrovatus* species has small tubercles apically on the paramere (Fig. 1323). This feature is unique in *Hydrovatus* and *Queda*.

Small tubercles apically on the paramere is an apomorphous structure.

Possible monophyly of *Methles* and Hydrovatini has been discussed above under conclusions (p. 75).

This examination supports a subdivision of *Hydrovatus* into three basal units: Species groups 1, 2 and a diverse subgroup containing species groups 3–15. Apomorphous characters are demonstrated for the lineages of this basal trichotomy. Species group 1 is characterized by apomorphies A and B, species group 2 is characterized by apomorphy C, and the diverse group – including the rest of the recognized species groups – by apomorphy D. This big subgroup can be further divided into two groups: Species group 3 characterized by apomorphy E, and possibly also apomorphy F (recognized in only some of the species in this group). The other group contains the species groups 4–15 and is characterized by apomorphy G. The latter group is divided into a paraphyletic group, including species groups 4–10, and a monophyletic group (species groups 11–15) characterized by apomorphy M.

In the paraphyletic group (species groups 4–10) I distinguish seven species groups out of which species group 4 is undoubtedly paraphyletic, species group 9 is possibly paraphyletic, and species group 8 is monobasic and forms an intermediate group between species groups 7 and 9, whereas species groups 5–7 and 10 are probably monophyletic lineages characterized by probable apomorphies (5–H; 6–I; 7–J; 10–L). The relationships between these lineages are still mostly unknown.

In the monophyletic group, including five species groups (11–15), at least species group 11 is paraphyletic. The phylogenetic status of species group 13 is unclear, while species groups 12 and probably

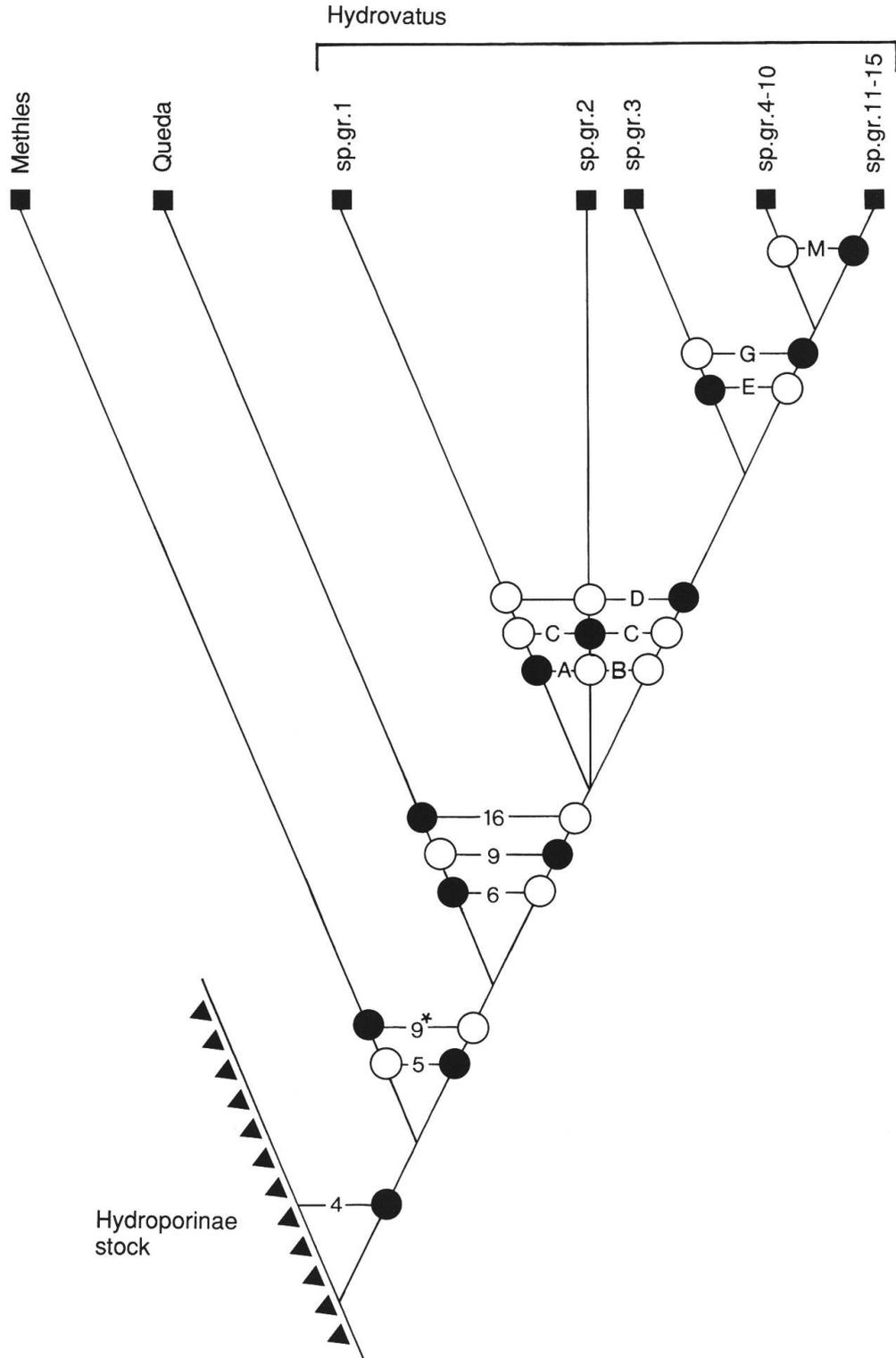


Fig. 16: Preliminary argumentation scheme for Hydrovatini and *Methles* and subdivision of *Hydrovatus*. Numbers and letters refer to corresponding symbols in the text. Dot = apomorphy; circle = plesiomorphy. Character 9 has evolved separately twice.

also species groups 14–15 are monophyletic lineages with probable apomorphies (12–N; 14–O; 15–P). The sequence of branching is also in this case still mainly unknown.

The proposed phylogeny of Hydrovatini is presented in Fig. 16. Only the most well-supported and clear apomorphies are included in the dendrogram. Characters such as number 2 and 3 are excluded, because they are considered highly unstable with limited information-value when their status is determined (apomorphy-synapomorphy ?).

More light will probably be focussed on these problems when juvenile stages have been examined and described more thoroughly. The knowledge of living habits of *Hydrovatus* and especially of the juveniles is still very scanty. Also the stridulation behaviour and the “song” produced may be of interest when the relationships among different species and species groups are studied. Moreover, methods such as electrophoresis, examination of chromosomes etc. could be useful in the reconstruction of the phylogeny of Hydrovatini-Methlini.

5. Zoogeographical considerations

Present-day distribution and knowledge of the phylogeny in combination with the drifting of continents may sometimes explain distributional patterns of a taxon, particularly if the taxon is distributed over many continents. Occurrence of different recognized groups in certain regions and their absence in others may indicate that a certain group evolved after the separation of land masses or when contact between land masses was established. In most cases, we have no fossil evidence, and thus it should be remembered that it is then a question of a hypothesis and not of scientifically reliable examination. The widely distributed Hydrovatini with known phylogeny on a generic level is a case allowing for such a zoogeographical analysis.

The distribution of the tribe Hydrovatini is pantropical, with some species also occurring in the subtropics and the temperate regions. The greatest diversity seems, however, to be at the Equator. The genus *Queda* is restricted to South and Central America, while *Hydrovatus* has a much wider distribution (Fig. 17).

The place of origin of the Hydrovatini is most probably Gondwanaland. This hypothesis is supported by the present-day occurrence of Hydrovatini in regions which earlier belonged to the Gondwanian continent.