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

Artikel: Taxonomic revision of the genus Hydrovatus Motschulsky (Coleoptera, Dytiscidae)
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Kapitel: 5: Zoogeographical considerations
DOI: https://doi.org/10.5169/seals-980453

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.

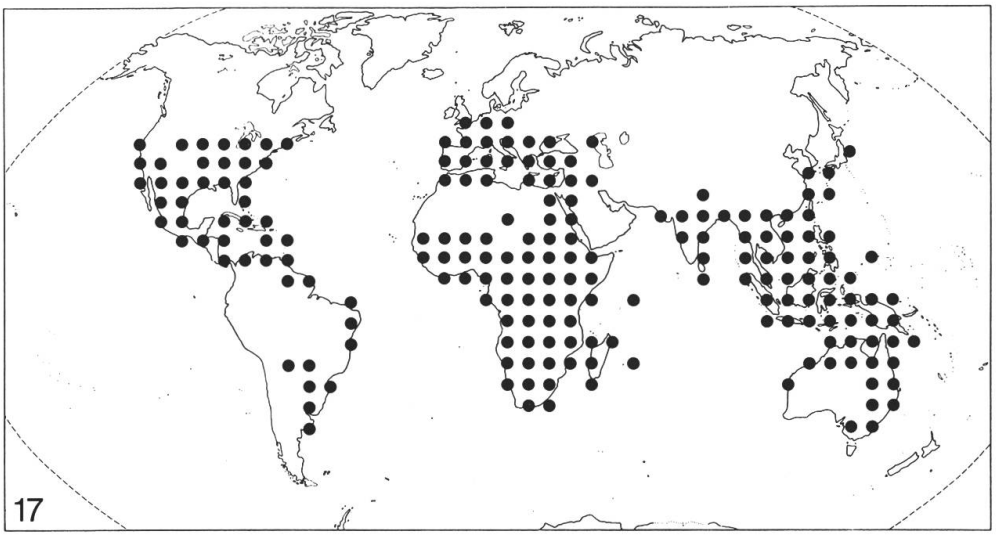

Fig. 17: Distribution of *Hydrovatus* on the basis of specimens examined in this study.

The separation of the two genera *Queda* and *Hydrovatus* also took place before the splitting of Gondwanaland. *Queda,* which today is restricted to South and Central America, probably originated in a region which today belongs to South America or then it has become extinct in other parts of the world. The third possibility, which cannot be totally excluded, is that it represents a later derivative from South American *Hydrovatus*. If the third possibility holds true, the genus *Hydrovatus* would be a paraphyletic group. At present I find the first alternative the most probable, because of morphologically greater similarity between American *Hydrovatus* and those of the Old World, than between American *Hydrovatus* and *Queda.*

Hydrovatus, which probably had a wide distribution in Gondwanaland, was separated by the splitting of this continent into two main areas of distribution: Neotropis and Ethiopian region. The species groups which today occur in both main areas of distribution (America versus the Ethiopian-Palearctic-Oriental-Australian region) are probably the most ancestral ones (species groups 1 and 3). The species groups occurring only in one main region may represent later branches. It cannot be denied that such groups may have gone extinct in one of the main areas; they therefore need not be derived groups. Nevertheless, later lineages are characterized by morphological features (apomorphies) exhibited only by species in a certain main area. Such characters, which have evolved after the opening of the South Atlantic, are, for instance, the stridulation apparatus in the male and the apical hook of the paramere. The *Hydrovatus* species

distributed today over Europe and Asia have predecessors in the Ethiopian region. The species occurring in Australia are also of the Ethiopian-Oriental type, and it is most probable that they came to Australia by migration from the North. They are clearly different from the American representatives of *Hydrovatus,* which makes a migration from South America via Antarctis to Australia improbable. The migration from the north is supported not only by morphological similarities between the fauna elements of Australia and Oriental region, but also by present-day distribution in Australia; *Hydrovatus* occurs predominantly in its northern areas. The North American members of *Hydrovatus* are definitely of the South American type, and it seems clear that they evolved from South American predecessors after the formation of a land-bridge between South and North America in the end of the Miocene epoch about six m.y. ago.

The discussion above is of course hypothetical. If it does coincide with the real evolutive history of Hydrovatini, we can calculate the approximate age of Hydrovatini and *Hydrovatus.*

The oldest fossils so far known and attributed to Coleoptera are from the early Permian period. They are estimated to be about 280 million years old (LAWRENCE & NEWTON, 1982). CROWSON (1981) reports fossil records from the early Jurassic period (about 200 m.y. old), which may be regarded as ancestors of Dytiscidae. The oldest fossils known of true Dytiscidae are from the late Cretaceous period (about 80 m.y. old); and the known fossils of Dytiscidae from the Tertiary period (about 65–2 m.y. old) seem to be Dytiscidae of the modern type. A rough estimation of the age of origin of Hydrovatini suggests over 100 m.y. The splitting of the South Atlantic rift started about 100 m.y. ago, so based on the above hypothesis, the age of *Hydrovatus* would also be at least a little more than 100 m.y. Taking into consideration the known fossils, this can be a correct calculation. The present-day distribution and the great specific diversity of *Hydrovatus* also support the suggestion that the genus represents an old lineage in Dytiscidae.

6. Classification and descriptions

6.1. Genus Hydrovatus Motschulsky

Hydrovatus MOTSCHULSKY, 1853:4 (orig. descr.); 1855:82 (descr.); CROTCH, 1873:386 (descr.); SHARP, 1882a:321, 848 (descr., disc., faun.); 1882b:14 (faun.); KOLBE, 1883:403 (faun.); GANGLBAUER, 1892:446 (descr., faun.); RÉGIMBART, 1895b:99 (descr., disc., faun.); REITTER, 1908:207 (descr.); BLATCHLEY, 1910:211 (descr.,