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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 Antarctica 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.,

- faun.); DES GOZIS, 1913:88 (descr.); PESCHET, 1917:13 (descr., faun.); DORSSELAER, 1919:78, 79 (descr.); ZIMMERMANN, 1920a:31 (list.); BEDEL, 1925:333, 334 (descr., faun.); BRUCH, 1927:537 (list.); ZIMMERMANN, 1927:18 (descr.); BERTRAND, 1928:42 (juv. descr.); ZIMMERMANN, 1930:26 (descr., faun.); BALL, 1932:18 (faun.); FENG, 1932:20 (faun., list.); TAKIZAWA, 1933:165 (descr.); FENG, 1933a:324 (faun., list.); 1933b:91 (descr., faun.); GSCHWENDTNER, 1933:160 (faun.); IMMS, 1933:301 (descr., biol.); HOULBERT, 1934:41, 44 (descr.); GSCHWENDTNER, 1935:24 (descr., faun.); F. BALFOUR-BROWNE, 1936:28 (invalid type designation); FENG 1936:2 (incorr. spell. *Hydrotatus*); BERTRAND, 1936:199, 200, 204 (juv. descr., biol., faun.); WU, 1937:302 (faun.); KAMIYA, 1938:9 (descr.); F. BALFOUR-BROWNE, 1940a:186 (descr.); GUIGNOT, 1945a:296, 315 (faun., descr., disc.); 1946:114 (list.); CSIKI, 1946:587 (faun., descr.); GUIGNOT, 1947b:58 (descr., faun.); BERTRAND, 1947:396 (juv. faun., disc.); LEECH, 1948:385, 387, 388 (descr., disc., faun.); BERTRAND, 1948:10 (juv. disc., descr., faun.); 1951:115 (faun.); GUIGNOT, 1952a:520 (disc.); 1953a:234 (faun.); F. BALFOUR-BROWNE, 1953:11, 13 (descr.); PENNAK, 1953:596, 597 (descr., faun.); GUIGNOT, 1954c:376, 377 (disc., faun.); YOUNG, 1954:51 (descr., faun.); GUIGNOT, 1955a:36 (faun.); OMER-COOPER, 1956:22 (faun., biol.); GUIGNOT, 1956b:223 (disc.); 1956f:49 (descr.); 1956g:57 (descr.); OMER-COOPER, 1957:22 (descr., disc., faun.); GUIGNOT, 1959a:123 (descr., faun.); ARNETT, 1960:194, 197 (descr., faun.); SATÔ, 1961:7 (faun.); GUIGNOT, 1961b:927, 929 (faun.); ANDERSON, 1962:55 (descr.); FERREIRA, 1963:153 (faun., list.); BERTRAND, 1963:405, 451 (descr., disc., faun.); OMER-COOPER, 1963:159 (descr., disc.); WATTS, 1963:26 (juv. descr., faun.); OMER-COOPER, 1965:93 (descr., disc., faun.); GUÉORGUIEV, 1965a:114 (disc., faun.); 1965b:103, 117 (disc., faun.); FERREIRA, 1967:532 (faun., list); VAZIRANI, 1968:300 (descr.); 1970a:36 (descr.); 1970b:94 (descr., disc., faun.); BERTRAND, 1970:16 (descr.); GALEWSKI, 1971:59 (descr.); SCHAEFLEIN, 1971:25 (descr., faun.); ZAITZEV, 1972:115 (descr., faun.); LARSON & PRITCHARD, 1974:57 (descr.); BILARDO, 1976:190 (faun.); VAZIRANI, 1977a:25 (faun., list.); WATTS, 1978:16 (descr.); FRANCISCOLO, 1979:272, 690 (imago & juv. descr., disc., faun.); MEDLER, 1980:155 (faun., list.); FORGE, 1981:497 (descr., faun.); SATÔ, 1981:68 (disc.); PEDERZANI & ROCCHI, 1982:70 (faun.); NIEUKERKEN, 1982:13 (disc.); MATTA, 1983:207 (juv. descr.); ROCCHI, 1984a:446 (faun.); Aiken, 1985:182 (disc.); BURMEISTER, 1985:41 (faun.); WOLFE, 1985:152 (phylog. disc.); GALEWSKI, 1985:46, 47, 48 (descr., disc.); BISTRÖM, 1985:198 (faun.); WEWALKA, 1986:277 (faun., biol.); GUÉORGUIEV, 1987:43 (descr., faun.); LAWRENCE & al., 1987:332 (faun., list.); PEDERZANI, 1988:106, 115 (disc., biol.); NILSSON, 1988:2285, 2291 (juv. descr., disc.); NAKANE, 1988a:21 (faun.); WOLFE, 1988:237-3 44 (phylog. disc.); NILSSON, 1989:114 (disc.); NILSSON & al., 1989:298, 313 (disc.); LAFER, 1989:231 (descr.); BISTRÖM, 1990:211 (disc.); ALARIE & al., (juv. descr., disc.); ALARIE & HARPER, 1990:373 (juv. disc.); ALI & ABDUL-KARIM, 1990:10 (descr., faun.); BILARDO & ROCCHI, 1990:178 (disc.); WOLFE & ROUGHLEY, 1990:323 (phylog. disc.); KLAUSNITZER, 1991:163 (larva descr.); BISTRÖM, 1992:20 (disc.).
- Oxynoptilus* SCHAUM, 1868:28 (orig. descr.); CROTCH, 1873:387 (list.); SHARP, 1882b:14 (list.); RÉGIMBART, 1895b:99 (list.); GANGLBAUER, 1892:446 (list.); ZIMMERMANN, 1920a:31 (list.); BEDEL, 1925:334 list.); PORTEVIN, 1929:180 (list.); TAKIZAWA, 1933:165 (list.); F. BALFOUR-BROWNE, 1936:28 (disc.); WU, 1937:203 (list.); F. BALFOUR-BROWNE, 1940a:186 (list.); KAMIYA, 1938:9 (list.); CSIKI, 1946:587

(list.); GUIGNOT, 1959a:123 (list.); FERREIRA, 1967:532 (list.); VAZIRANI, 1977a:25 (list.); FRANCISCOLO, 1979:273 (list., incorr. spell. *Oxynoptylus*); GUÉORGUIEV, 1987:43 (list.); NILSSON & al., 1989:303 (list.).

Hydatonychus KOLBE, 1883:402 (orig. descr.); PESCHET, 1917:13 (list.); ZIMMERMANN, 1920a:31 (list.); TAKIZAWA, 1933:165 (list.); WU, 1937:203 (list.); CSIKI, 1946:587 (list.); KAMIYA, 1938:9 (list.); GUIGNOT, 1959a:123 (list.); FERREIRA, 1967:532 (list.); VAZIRANI, 1977a:25 (list.); FRANCISCOLO, 1979:273 (list.); NILSSON & al., 1989:297 (list.).

Vathydrus GUIGNOT, 1954e:197 (orig. descr. n. subg.); 1956f:49 (descr.); 1956g:57 (descr.); 1959a:124 (descr.); FERREIRA, 1963:153 (list.); OMER-COOPER, 1963:161 (descr.); FERREIRA, 1967:532 (list.); NILSSON & al., 1989:309, 313 (disc., list.).

Type species of *Hydrovatus* (valid name): *Hyphydrus cuspidatus* Kunze, 1818, by monotypy. – *Oxynoptilus* (junior objective synonym): *Hyphydrus cuspidatus* Kunze, 1818, by monotypy. – *Hydatonychus* (junior subjective synonym): *Hydatonychus crassicornis* Kolbe, 1883, by monotypy. – *Vathydrus* (junior subjective synonym): *Hydrovatus sordidus* Sharp, 1882, by original designation.

The subsequent designation by Balfour-Browne (1936), of *Hydrovatus castaneus* Motschulsky as type of *Hydrovatus* is invalid (NILSSON & al., 1989).

Diagnosis of the genus: The possession of the character combination (adults: deeply incised metacoxal processes - body apex extended - prosternal process triangular; apex broad), distinguishes the genus *Hydrovatus* from all other recognized Dytiscidae genera.

Description (includes derivation)

Length of body: 1.62–5.28 mm, breadth: 0.92–3.56 mm. Body shape varies between elongated, parallel-sided and globular (Figs 769, 990). Dorsoventrally somewhat flattened. Colour pattern of body variable: Unicoloured, black to pale brown or body with colour pattern on pronotum and elytra (vague to distinct) (Figs 36, 50, 130).

Head: Punctate. Punctuation varies between very sparse, indistinct and quite dense and clearly discernible. Often reduced so that punctures only visible close to eyes and in shallow frontal depressions. Microsculptured. Meshes of microsculpture vary between strongly developed, dense to very indistinct and partly reduced. Regarding shape of frontal aspect, antenna and maxillary palpi, see below, under the different species groups.

Pronotum: Sides of pronotum finely margined, rounded to straight. Punctate. Discal punctuation generally finer, sparser, sometimes rather indistinct or even absent. Punctures coarser and denser at

pronotal margins. Generally microsculptured. Meshes of microsculpture variable, sometimes strongly developed, very distinct, sometimes reduced, hardly visible. Submat to shiny.

Elytra: Punctuation variable. Almost obliterated to coarse and dense. Three longitudinal rows of punctures may be seen in many species. In the text they are called discal, dorsolateral and lateral row of punctures (Fig. 15, p. 67). Rows of punctures often more or less reduced. Lateral row of punctures medially divided into two almost parallel separate rows. Microsculpture variable. Sometimes very distinct, sometimes almost obliterated. Mat to shiny. Apex of elytra extended but shape of extension variable, sometimes even truncate (Figs 138, 932, 630). Epipleura basally carinated.

Ventral side: Punctuation generally distinct on metathorax and metacoxal plates and basally on abdomen. Abdominal punctuation otherwise finer and sparser, often indistinct or even absent. Microsculptured, but meshes particularly on metacoxal plates and metathorax often much finer, quite rarely even absent. Prosternal process laterally always margined, but sometimes margins rather indistinct. Metacoxal process deeply incised (Fig. 7).

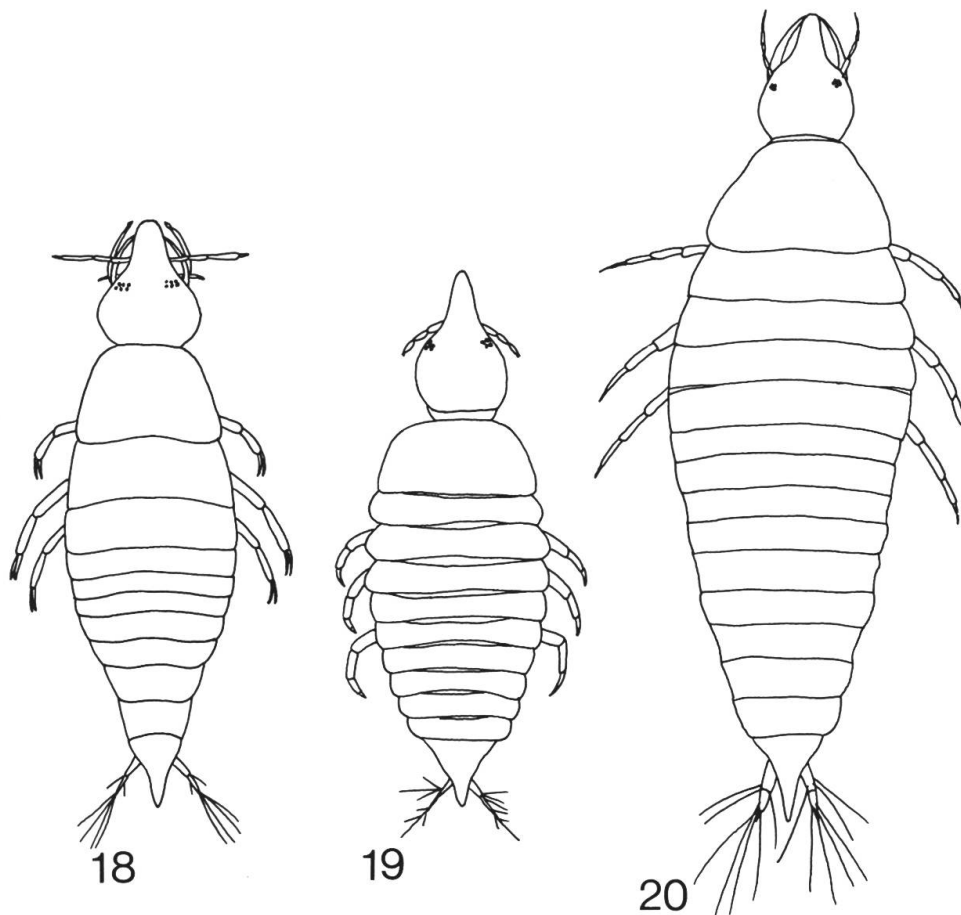
Legs: Pro- and mesotarsi with fourth segment (discernible at base of fifth segment) reduced so that these tarsi appear four-segmented. Claws of metatarsi equally long, not modified. Pro- and mesotarsal claws often modified.

Sexes: Male exhibits in many species modifications in the shape of antenna, maxillary palpus, shape of frontal aspect of head, claws of pro- and mesotarsi. Pro- and mesotarsi often broader in males than in females. At border region of metasternum and metacoxal plates of male, often with a stridulatory apparatus, the appearance of which is somewhat variable (Figs 3, 4, 1031–1032). Female quite rarely dimorphous: General appearance of body as in male or duller, often more strongly microsculptured. Concerning shape of male genitalia, see the different species groups.

Juvenile stages: Thus far, quite a few papers have been published dealing with the juvenile stages of *Hydrovatus*. Up to now the larva of only a small number of species have thus been described. Below I present a review based on available publications.

Larva (Figs 18-20).

Head with frontal projection (nasale) and body lacking fringes of swimming hairs. Nasale rounded, not expanded at tip. Ventral abdo-



Figs 18–20: Larvae of *Hydrovatus*. – 18, *H. pustulatus* (after SPANGLER, 1962). – 19, *H. clypealis* (after FRANCISCOLO 1979). – 20, *H. cuspidatus* (after GALEWSKI, 1974). Sizes of different illustrations are incompatible.

minal segments 2–8 with a sclerotized plate. Ocelli all separate, distinct. Pleural suture extending through segment four. Pro- and mesotarsal claws $2/3$ length of tarsus (Matta, 1983). Legs comparatively short, lacking swimming hairs. Terminal abdominal segment provided with short urogomphi with seven primary setae.

Habitus illustration of an American representant (*H. pustulatus*) of the genus accompanied by many detail-figures, is given by SPANGLER (1962). Body of third instar spindle-shaped, anteriorly slightly narrowed, posteriorly more strongly so, with length of body 3.5 mm. *H. clypealis* occurring in western Palearctis is described and illustrated in different works (eg. BERTRAND, 1928, GUIGNOT, 1933, ZAITZEV, 1972, FRANCISCOLO, 1979). On the basis of illustrations, *H. clypealis* differs morphologically very much, eg. anterior segment of thorax is remarkably broad and short in *H. clypealis* in compari-

son with that of *H. pustulatus*. The third instar larva of the Palearctic species *H. cuspidatus* is described in GALEWSKI (1974). It resembles very much *H. pustulatus*, but the head for instance, seems to be proportionally smaller in comparison with the body. The length of the body of the third instar of *H. cuspidatus* is reported to be 4.0 mm. The apical body segment is short and conical (cf. also KLAUSNITZER, 1991).

WILLIAMS (1936) gives an illustration of the first instar of *H. confertus* (determination not controlled) from Hawaii. In many respects it resembles the illustrations of the third instars of the species mentioned above. Legs and cerci are, however, proportionally longer in the first instar.

The egg of *H. confertus* is described in WILLIAMS (1936): Shape oval, slightly curved and about 0.6 mm long.

I have seen no descriptions of *Hydrovatus* pupae.

Distribution: Southern half of Europe, Africa including Madagascar, southern parts of Asia (Turkey, Iraq, India–China–Japan and Malaysia, Indonesia, Philippines, Papua New Guinea), Australia, N–S America (Fig. 17).

Biology: Living-habits of *Hydrovatus* are still rather fragmentarily known. Scattered records are, however, available in the literature. Below I present a brief review based on information from some literature considered important, as well as facts that may be of interest, from label-texts of the specimens studied.

Based on the shape of the apical body segment, GALEWSKI (1974) suggests that living habits of *Hydrovatus* larvae may partly coincide with what is known of the burrowing larvae of *Noterus*. Both larvae seem to be of the creeping type. The short cerci indicate limited function, and the pointed body apex suggests that the larvae hide among vegetation and for respiration only stick out their respiratory “tubes”. Galewski adds, however, that alternatively the apical body segment may also be used for oxygen intake from bubbles in water. Long sickle-shaped mandibles may be regarded as effective in food-catching and small crustaceans are possibly an important food source for the larvae.

Thus, it is possible that many species prefer shallow bodies of water with dense vegetation. For instance, GALEWSKI (1974) reports that *H. cuspidatus* is found along calm lake shores overgrown with vegetation (cf. also OMER–COOPER, 1956). The species seeks feebly eutrophized sites with a sandy or sandy-muddy bottom.

KLAUSNITZER (1991) adds that *H. cuspidatus* occurs in standing water and also in brackish water.

H. cuspidatus is a “red-list” species in the Berlin area of Germany (BALKE & HEDRICH, 1991). It is regarded as a stenotope species (iliophilous and acidophilous) preferring warm and sunny bodies of water. Changes in the quality of the water, e.g. increase in nutrientcontent, is suggested as a major reason for threats to the species. In northern Germany the species obviously overwinters as larva and imago. In the same region the species was sampled only in woodland fens and mosses among peat-moss (HENDRICH & BALKE, 1991b). (See also under the section Biology, p. 376).

SPANGLER (1962) reports that numerous larvae of *H. pustulatus* together with adults were sampled from a small *Potamogethon* choked farm pond in Missouri, USA.

From Hawaii, WILLIAMS (1936) gives some behavioural and ecological notations on *H. confertus* (determination not controlled), predominantly based on observations of specimens kept in a glass jars. Thus the conditions for the specimens are different from those in the field, and accordingly the results must be examined, taking this into consideration.

H. confertus is recorded from weedy lowland swamps, abandoned rice fields, hoof prints of cattle and other small water-bodies. When swimming along the bottom it pauses at intervals. Adults live for many months in laboratory dishes, to which filamentous green algae, debris and occasional food such as dead insects are added. Dissection revealed some food remains: Head-portions of larvae of the fly family Psychodidae, fragments of tiny crustaceans, and bristles of a nereid worm. One egg was found weakly glued to algae in the jar. The newly hatched larva runs lightly over the flocculent bottom or keeps to vegetation – it does not swim. For air it creeps to the surface (cf. also above).

The male of many species is most probably capable of sound-production by use of its stridulation apparatus.

6.2. Special taxonomic cases

Here I have listed different problematic cases as unexamined specific taxa, exclusion of species from *Hydrovatus*, unsolved confusion of names, use of nomen nudum etc.