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A systematic review of the tribes Hyphydrini Sharp and Pachydrini n. trib. (Coleoptera, Dytiscidae)

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Based on a phylogenetic study using adult morphology, the tribe Hyphydrini is redefined as including the following 12 genera: *Andex* Sharp, *Coelhydrus* Sharp, *Darwinhydrus* Sharp, *Hydropeplus* Sharp, *Primospes* Sharp, *Hyphovatus* Wewalka & Biström, *Agnoshydrus* n. gen. (contains two species: *A. laccophiloides* (Régimbart) and *A. densus* n. sp.), *Microdytes* J. Balfour-Browne, *Allopachria* Zimmermann, *Hyphydrus* Illiger, *Hovahydrus* Biström, and *Desmopachria* Babington. The two genera *Heterhydrus* Fairmaire and *Pachydrus* Sharp are transferred to Pachydrini n. trib. All genera in the two tribes are reviewed including descriptions and check lists. The phylogenetic analysis provided support for the monophyly of each of the genera *Allopachria* and *Desmopachria*, whereas that of *Microdytes*, *Hyphydrus* and *Hovahydrus* is considered doubtful. An identification key is provided for the genera and subgenera of both tribes. The following n. comb. are given: *Microdytes pasiricus* (Csiki, 1938) previously in *Hydrovatus* and *Agnoshydrus laccophiloides* (Régimbart, 1888) previously in *Microdytes*.

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1. Introduction

The classification of the large subfamily Hydroporinae Aubé is one of the more severe problems in current dytiscid systematics. Wolfe (1985, 1988) used cladistic methods to analyse the more basal clades of the subfamily, establishing Laccornini Wolfe & Rougley as the sister-group of all other tribes. He also provided arguments for recognizing Methlini Van den Branden + Hydrovatini Sharp as the sister-group of all other tribes except Laccornini. However, Biström (1997) argued for a monophyletic Hydrovatini including the two genera *Hydrovatus* Motschulsky and *Queda* Sharp, a grouping that contradicts Wolfe's (1988) synapomorphies used to group Hydrovatini with Methlini. The Bidessini Sharp was reviewed by Biström (1988), who established the segmented parameres as the chief synapomorphy of the tribe. As a consequence several genera were left with-

* Contribution to the study of Dytiscidae 66.

out tribal affiliation. Also the delimitation of the tribe Hydroporini Aubé is in a state of flux, and Nilsson and Holmen (1995) transferred *Hygrotus* Stephens and allied genera to the separate tribe Hygrotini Portevin. Nilsson and Angus (1992) established relationships within one clade of the Hydroporini, viz. the *Deronectes* group of genera.

The delimitation of the tribe Hyphydrini Sharp is especially problematic. Biström (1982a) gave the unequal length of the metatarsal claws as the unique synapomorphy of the tribe. However, the size reduction of the anterior metatarsal claw has occurred in many dytiscid lineages, and it is less pronounced in the two Oriental genera *Allopachria* Zimmermann and *Microdytes* J. Balfour-Browne than in other genera of the Hyphydrini. *Microdytes* was first described in Hyphydrini, later assigned to Hydrovatini (Nilsson *et al.* 1989), and more recently excluded from this tribe by Biström (1997). Moreover, Young (1980) suggested that the two New World genera *Desmopachria* Babington and *Pachydrus* Sharp should be excluded from Hyphydrini and placed in a tribe of their own.

In all species of Hyphydrini and Bidessini the metacoxal processes are adpressed to the same level as the base of the abdomen. Together with the reduction of the lateral lobes of the processes, this arrangement allows the greatest amount of rotating motion for the swimming legs. Moreover, Sharp (1882) noted after dissection that the metacoxae were soldered to the abdomen in all Bidessini, including also the genera *Heterhydrus*, *Pachydrus* and *Desmopachria* in this tribe. As noted by Zimmermann (1919: 131), this character state can only be observed through dissection as the metacoxal/abdominal suture is always present. Sharp (1882: 850) examined only a single badly preserved specimen of *Heterhydrus*, noting: "Whether the coxae be soldered with the ventral segments is not ascertained, but in my classification I have taken it for granted that such is the case." Our dissection of *Heterhydrus ghanensis* has proved Sharp correct on this point. However, Zimmermann (1919) thought that Sharp had made too much out of this character as it was more gradual and so far de facto observed in relatively few of the species involved. Finding the unequal length of the metatarsal claws more reliable, Zimmermann (1919) instead transferred these three genera to Hyphydrini. More recently, Young (1980) wanted to use Sharp's character for excluding *Desmopachria* and *Pachydrus* from this tribe. The different views of Sharp and Zimmermann reflects the traditional error of selecting one among many possible characters instead of the application of parsimony methods. Sharp (1882) thought that the metacoxal–abdominal fusion was the best character, whereas Zimmermann (1919) gave priority to the unequal metatarsal claws.

The history of the species *Hydrovatus maculatus* Motschulsky illustrates well the confusion found among these tribes. Régimbart (1899) retained this species in *Hydrovatus*, but noted that it may belong to its own genus. Later Gschwendtner (1935) transferred it to the otherwise New World genus *Desmopachria* in the Hyphydrini. This was questioned by Balfour-Browne (1946) who suggested that Motschulsky's species belonged to his new genus *Microdytes* in the Hyphydrini. This suggestion was later confirmed by Vazirani (1969). The genus *Microdytes* was more recently listed under Hydrovatini by Nilsson *et al.* (1989). This example stresses the need for broad systematic studies analysing all available characters in all critical taxa.

The goal of this survey can be summarized into four points:

1. To present one or more synapomorphies for the recognition of the tribe Hyphydrini, and at the same time decide which species really belong to this tribe.
2. To provide a classification of the taxa excluded from Hyphydrini.
3. To recognize the main clades within Hyphydrini.
4. To give a generic classification of Hyphydrini including: an identification key to genera, generic diagnoses and brief descriptions, and species checklists.

2. Material and methods

2.1. Phylogeny reconstruction

Of the species previously placed in Hyphydrini, 58 were selected for a detailed examination in order to find qualitative characters to be used in the phylogenetic analysis. Species selection was designed to include representatives of all genera and subgenera in the tribe as well as the major spe-

cies groups of the speciose genus *Hyphydrus*. All characters found that displayed variation among the studied species, i.e. occurred in two or more different states, were scored. From this original matrix, the binary characters having one of their states, or the character states of multistate characters, restricted to one species were deleted. Two or more species having identical character distributions were lumped as one terminal taxon. The deletion of uninformative characters and lumping of identical taxa were made step-wise until no longer possible. This process resulted in a matrix with 23 terminal ingroup taxa (OTU's) and 26 characters (Table 1).

The terminal ingroup taxa (1–23) are here listed together with the examined species they include:

1. *Heterhydrus*
   H. sudanensis Zimmermann
   H. senegalensis (Aubé)
2. *Pachydrus*
   P. princeps (Blatchley)
   P. globosus (Aubé)
   P. cayenennsis (Laporte de Castelnau)
3. *Andex insignis* Sharp
4. *Coelhydrus brevicollis* Sharp
5. *Darwinhydrus solidus* Sharp
6. *Hydropeplus trimaculatus* (Laporte de Castelnau)
7. *Primospes suturalis* Sharp
8. *Microdytes* 1
   M. championi J. Balfour-Browne
   M. uenoi Satô
   M. belli J. Balfour-Browne
   M. pasiricus (Csiki)
   Four undescribed species
9. *Microdytes* 2
   Two undescribed species
10. *Allopachria* 1
    A. quadripustulata Zimmermann
    A. bimaculata (Satô)
11. *Allopachria* 2
    A. flavomaculata (Kamiya)
    A. wangi Nilsson & Wewalka
    One undescribed species
12. Allopachria 3
    Three undescribed species
13. *Agnoshydrus*
    A. laccophiloides (Régimbart)
    A. densus n.sp.
14. *Hyphovatus dismorphus* (Biström)
15. *Hovahydrus* 1
    H. minutissimus (Régimbart)

Table 1. Character matrix used in the parsimony analysis. See text for coding of characters and grouping of species into OTU's.

OTU	Character no.																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Laccornis oblongus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Methles cribratellus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Heterhydrus	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0
Pachydrus	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0
Andex insignis	0	0	0	0	0	0	1	0	0	0	0	1	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Coelhydrus brevicollis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	1	0	0	0	1	0	0	0
Darwinhydrus solidus	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Hydropeplus trimaculatus	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Primospes suturalis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Microdytes 1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0
Microdytes 2	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0
Allopachria 1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0	1	1	0	0	0	0	0	0	0	0
Allopachria 2	0	0	0	0	0	0	0	1	0	1	1	0	0	1	2	1	1	1	0	0	0	0	0	0	0	0
Allopachria 3	0	0	0	0	0	1	0	1	0	1	1	0	0	1	2	1	1	1	0	0	0	0	0	0	0	0
Agnoshydrus	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Hyphovatus dismorfus	0	0	0	0	0	1	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	1
Hovahydrus 1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Hovahydrus 2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Hyphydrus 1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	1	0
Hyphydrus 2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	1
Hyphydrus 3	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	1
Hyphydrus 4	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	0	0
Desmopachria 1	1	1	1	1	1	0	0	1	1	0	0	0	0	1	2	0	0	1	1	1	0	0	1	0	0	0
Desmopachria 2	1	1	1	1	1	0	0	1	1	0	0	0	0	1	2	0	0	1	1	1	1	0	1	0	0	0
Desmopachria 3	1	1	1	1	1	0	0	1	1	0	0	0	0	1	2	0	0	1	1	1	1	0	1	0	1	0

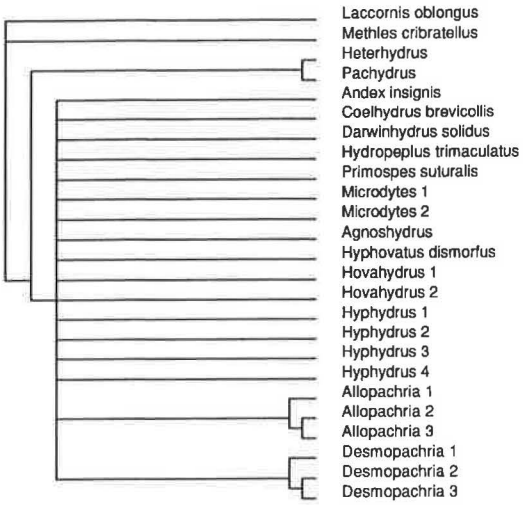
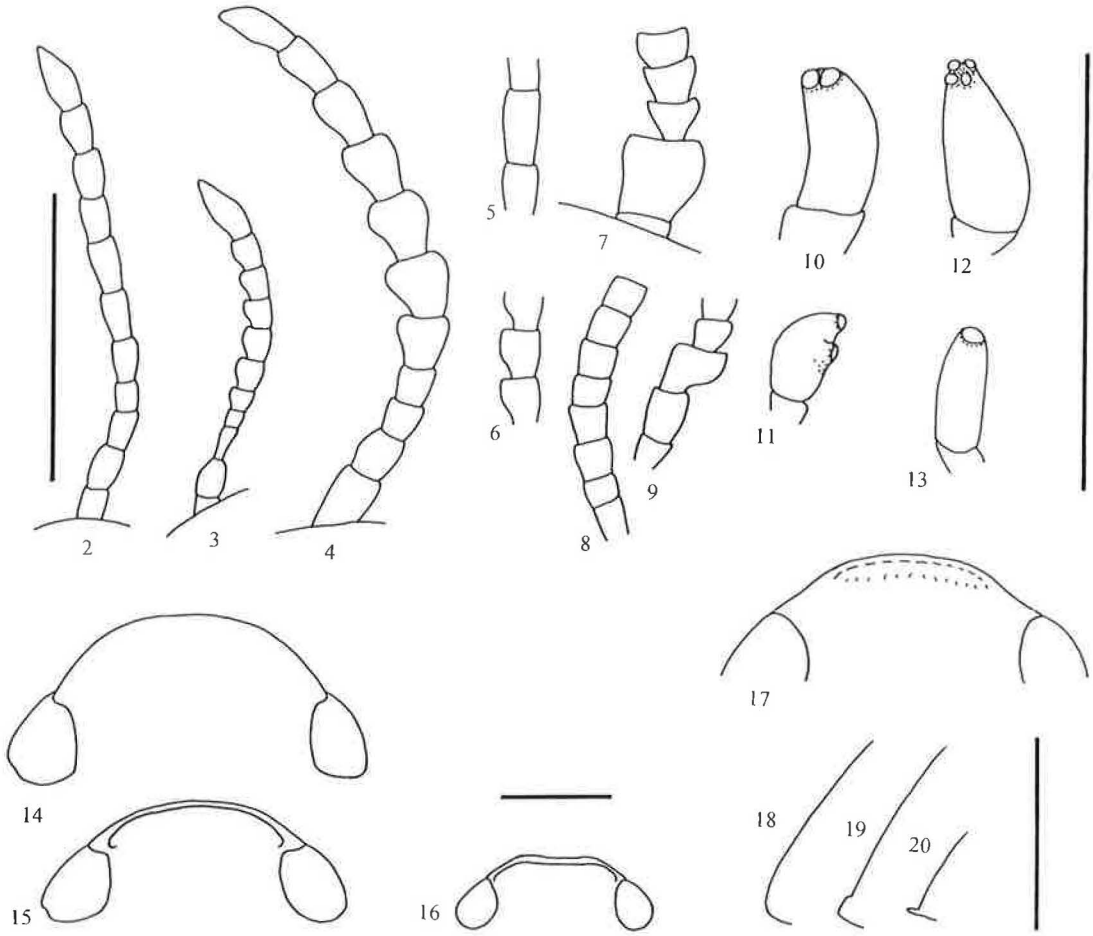


Fig. 1. Strict consensus tree based on 510 fundamental trees found by Hennig86 or on 624 shortest trees found by PAUP.

16. *Hovahydrus* 2
    H. praetextus (Guignot)
    H. perrieri (Fairmaire)
    H. sinapi (Guignot)
17. *Hyphydrus* 1
    H. ovatus (Linnaeus)
    H. aubei Ganglbauer
18. *Hyphydrus* 2
    H. separandus Régimbart
19. *Hyphydrus* 3
    H. parvicollis Sharp
    H. grandis Laporte de Castelnau
20. *Hyphydrus* 4
    H. elegans (Montrouzier)
21. *Desmopachria* 1
    D. (D.) attenuata Régimbart
    D. (D.) convexa (Aubé)
    D. (D.) nitida Babington
    D. (Pachirdis) iridis Young
    D. (Pachriostrix) grouvellei Régimbart
    D. (Portmannia) basicollis Guignot
    D. (P.) laevis Sharp
    D. (P.) portmanni Clark
22. *Desmopachria* 2
    D. (Portmannia) dispar Sharp
    D. (Pachriodesma) brevicollis Régimbart
    D. (P.) sanfilippoi Guignot
    D. (P.) mexicana Sharp
    One undescribed species
23. *Desmopachria* 3
    D. (Nectoserrula) concolor Sharp
    D. (N.) mendozana (Steinheil)
    D. (N.) punctatissima Zimmermann
    D. (N.) vicina Sharp

The following 26 characters were used in the parsimony analysis (cf. Fig. 1):

1. Antennomeres 1–2: (0) of about same width as following segments (Fig. 2); (1) wider than following segments (Fig. 3).
2. Antennomeres 5–10: (0) cylindrical and of varying length (Fig. 5); (1) short and slightly expanded in apical half (Fig. 6).
3. Labial palpus: (0) apical pair of sensilla placed close together (Fig. 10); (1) apical pair of sensilla widely separated (Fig. 11).
4. Maxillary palpus: (0) with two or more sensilla (Fig. 12); (1) with one apical sensillum (Fig. 13).
5. Head, anterior margin: (0) unbeaded and straight (Fig. 14); (1) beaded and straight or bent upwards (Figs. 15 and 16).
6. Head, mediofrontal depression: (0) absent (Figs. 14–16); (1) present (Fig. 17).
7. Body, lateral outline: (0) continuous (Fig. 21); (1) broken at level of base of pronotum (Fig. 22).
8. Body, outline: (0) elongate; (1) more or less globular (Fig. 32).
9. Pronotum, posterior angle: (0) not produced posteriorad (Figs. 22 and 23); (1) produced posteriorad (Fig. 24).
10. Pronotum, lateral bead: (0) of even width (Fig. 24); (1) with posterior dilation (Fig. 26).
11. Prosternal process: (0) with "neck" delimited by ridge (denticulate in lateral view) (Fig. 38); (1) with "neck" not delimited by ridge (smooth in ventral view) (Fig. 37).
12. Prosternal process, apex: (0) reaching metasternum (Figs. 33 and 34); (1) not reaching metasternum (Fig. 35).
13. Prosternal process and mesocoxae: (0) process lanceolate and mesocoxae narrowly separated (Figs. 33 and 35); (1) process dilated, triangular and mesocoxae widely separated (Fig. 34).
14. Elytron, ventrolateral carina: (0) in posterior two thirds (Fig. 57); (1) in posterior half (Fig. 58).
15. Elytron, apical portion of ventrolateral carina: (0) thickened and undulate (Fig. 57); (1) not strongly modified; (2) ligulate (Fig. 58).
16. Elytron, anterolateral angle: (0) not extended anteriorad (Figs. 21–25); (1) extended anteriorad (Fig. 26).
17. Elytron, humeral yellow macula: (0) absent (Fig. 32); (1) present (Fig. 29).
18. Metasternal wing: (0) medially broad (Fig. 39); (1) medially narrow (Fig. 40).
19. Metacoxal process, lateral lobe: (0) covering base of trochanter (Fig. 42); (1) reduced, not covering base of trochanter (Figs. 41 and 43).
20. Metacoxae: (0) not soldered to base of abdomen; (1) soldered to base of abdomen.
21. Metacoxal processes, posterior margin of ventral lamina: (0) visible (Fig. 41); (1) reduced (Fig. 43).
22. Metatibia, longitudinal row of punctures on disc: (0) present (Fig. 44); (1) reduced (Fig. 45).
23. Metatibia, apical transverse row of spines: (0) continuous (Figs. 44–46); (1) broken medially (Fig. 47).
24. Metatibia, apical transverse row of spines: (0) medium



Figs. 2–20. — 2–4. Antenna. 2: *Agnoshydrus laccophiloides*; 3: *Desmopachria punctatissima*; 4: *Allopachria flavomaculata*. — 5–6. Antennal segments 6–8. 5: *Agnoshydrus laccophiloides*; 6: *Desmopachria dispersa*. — 7. *Microdytes* sp., Antenna, segments 1–5. — 8–9. Antenna, middle segments. 8: *Microdytes* sp.; 9: *Allopachria* sp. — 10–11. Labial palpus. 10: *Andex insignis*; 11: *Desmopachria sanfilippoi*. — 12–13. Maxillary palpus. 12: *Heterhydrus senegalensis*; 13: *Desmopachria mendozana*. — 14–17. Head, frontal aspect. 14: *Hydropeplus trimaculatus*; 15: *Hyphydrus elegans*; 16: *Desmopachria portmanni*; 17: *Allopachria sausai*. — 18–20. Head, frontal aspect, lateral view. 18: *Hydropeplus trimaculatus*; 19: *Hyphydrus elegans*; 20: *Desmopachria mexicana*. — Different scale bars (0.5 mm) for Figs. 2–4 (left), 5–13 (top right), 14–17 (bottom middle), and 18–20 (bottom right).

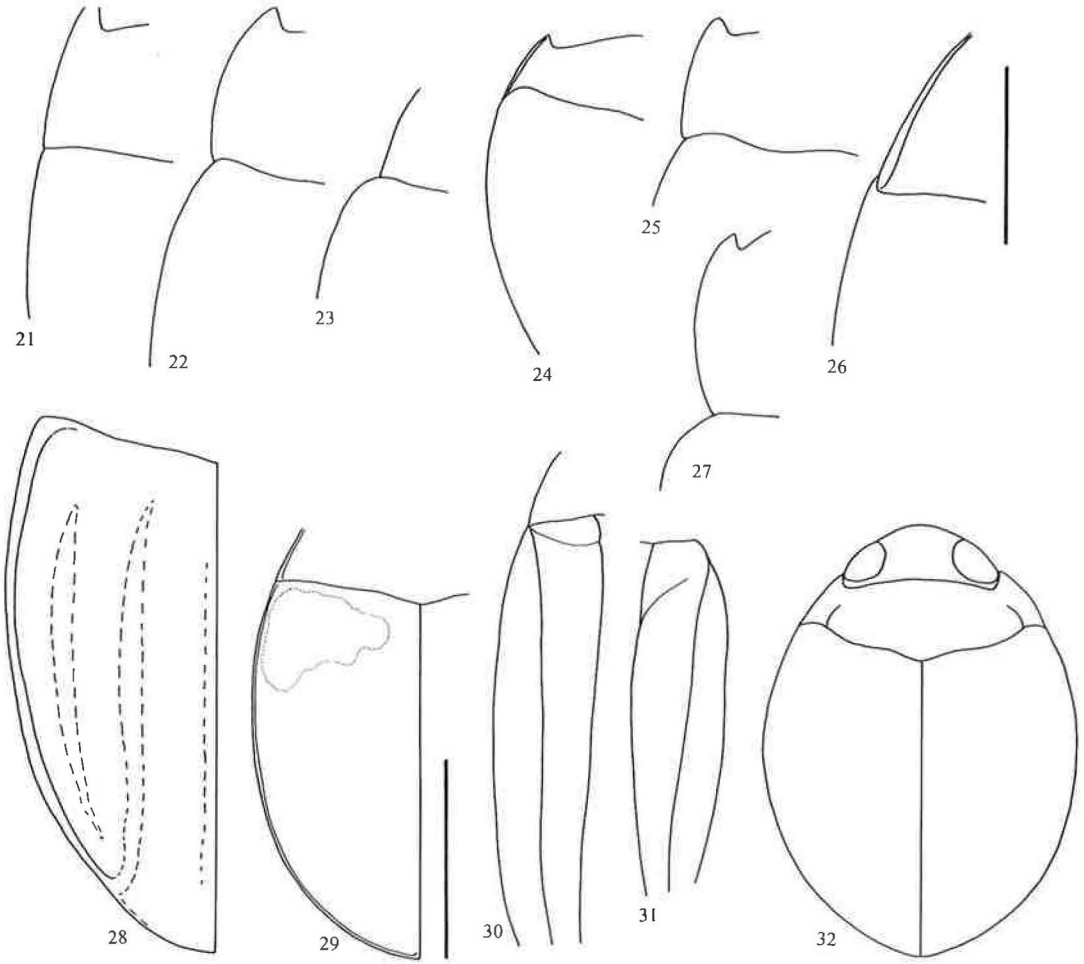
to long (Figs. 44, 46 and 47); (1) short and scale-like (Fig. 45).

25. Metatibia, longer spur: (0) smooth (Fig. 54); (1) serrate (Figs. 55 and 56).
26. Metatibia, shape: (0) club-shaped (Figs. 44 and 45); (1) cylindrical (Fig. 46).

In most Dytiscidae, the posterior part of the metacoxal processes is formed by two laminae; one more ventral that is fully exposed, and one more dorsal that is more or less exposed only in its posterior end. We here refer to the two laminae as dorsal and ventral (cf. Zimmerman 1982: 414). In Bidessini and Hyphydrini the ventral lamina is adpressed to the body, to the same plane as the dorsal lamina and the base of the abdomen. The posterior margin of the ventral lamina is retained as a distinct suture in most Hyphydrini, whereas it is reduced in *Heterhydrus*, *Pachydrus*, and many species of *Desmopachria* (character no. 21).

The matrix was tested for a phylogenetic signal with the Random Permutation Program 1.91 (J. S. Farris 1993, Stockholm). The parsimony analysis used Hennig86 version 1.5 (by J. S. Farris) and PAUP 3.1.1 (= Phylogenetic Analysis Using Parsimony; by D. L. Swofford).

In the parsimony analysis, we used an outgroup consisting of *Laccornis oblongus* (Stephens) and *Methles cribratellus* Fairmaire. The genus *Laccornis* is seemingly the



Figs. 21–32. — 21–27. Pronotum and base of left elytron, lateral portion, dorsal view. 21: *Heterhydrus sudanensis*; 22: *Hydropeplus trimaculatus*; 23: *Hyphydrus parvicollis*; 24: *Desmopachria mendozana*; 25: *Primospes suturalis*; 26: *Allopachria wangi*; 27: *Andex insignis*. — 28–29. Left elytron, dorsal view. 28: *Darwinhydrus solidus*; 29: *Allopachria bimaculata*. — 30–31: Epipleuron, anterior portion, lateral view. 30: *Heterhydrus senegalensis*; 31: *Andex insignis*. — 32. *Desmopachria dispersa*, habitus. — Different scale bars for Fig. 26 (top, 0.5 mm), and others (bottom, 1 mm).

sister-group of all other Hydroporinae and *Methles* represents another basal clade of this subfamily (Wolfe 1985, 1988). In PAUP's rooting options, *Laccornis oblongus* was entered as the sister-taxon of *Methles* plus the ingroup, and the ingroup was kept monophyletic.

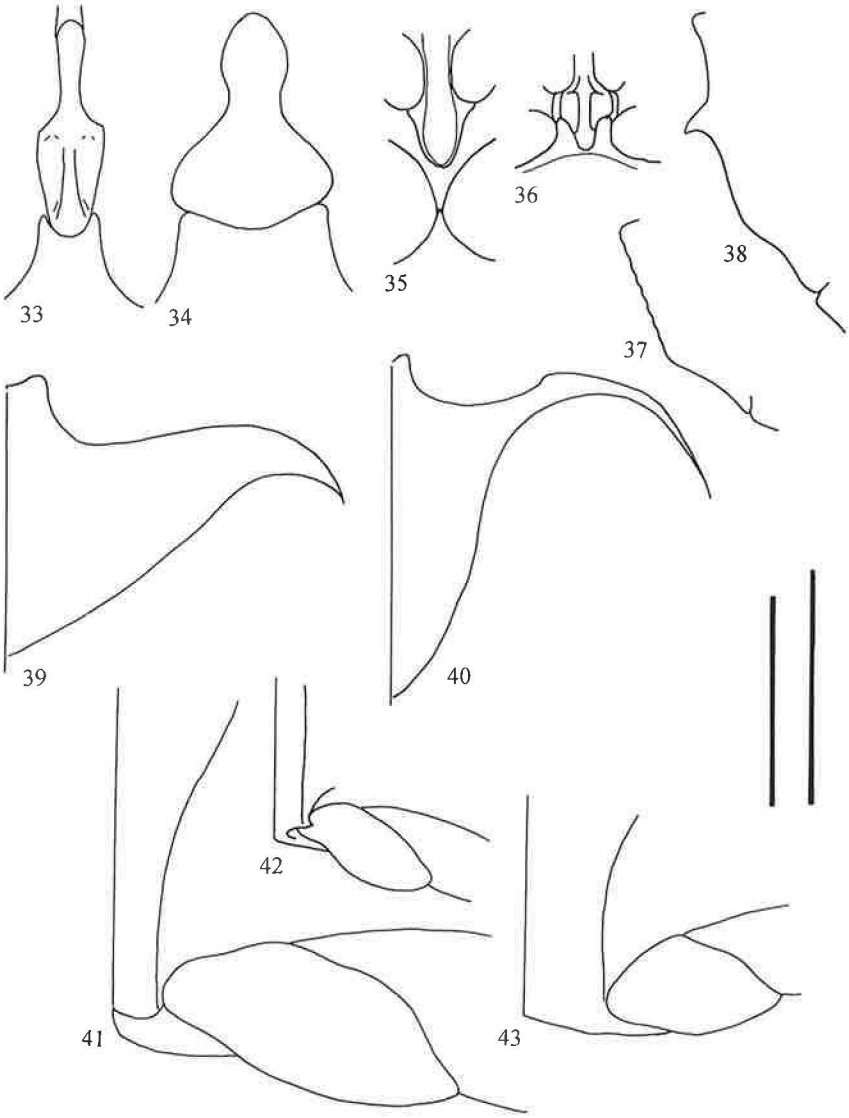
2.2. Abbreviations

Collections: (MAC) Musée Royal de l'Afrique Centrale, Tervuren, Belgium; (MCG) Museo Civico di Storia Naturalia "Giacomo Doria", Genoa, Italy; (MNHN) Museum National d'Histoire Naturelle, Paris, France; (MZH) Museum Zoologicum, Helsingfors, Finland; (NMW) Naturhistorisches Museum Wien, Austria; (RNHL) Rijksmuseum van Natuurlijke Histoire, Leiden, the Netherlands; (TMP) Transvaal Museum, Pretoria, South Africa; (CYB) coll. F. Young, Bloomington, Indiana, USA; (CWV) coll. Wewalka, Vienna, Austria.

Regions: (Austr) Australian Region; (Carib) Caribbean-Antilles; (Eth) Ethiopian Region; (Mad) Madagascar; (Mex) Mexico; (Nearc) Nearctis; (Neotr) Neotropis; (Or) Oriental Region; (Pal) Palaearctis.

3. Phylogeny

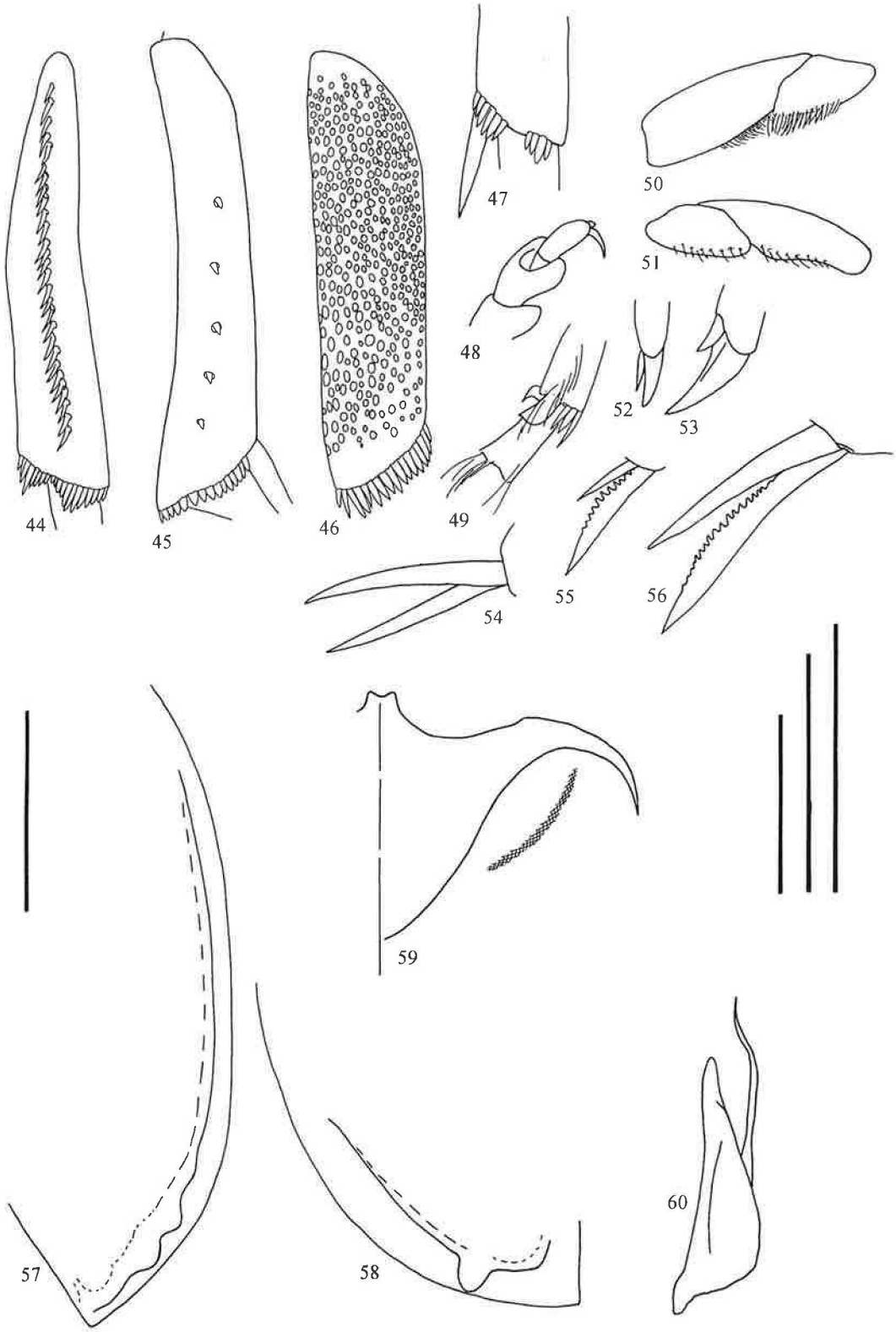
The permutation test showed that our matrix had a strong phylogenetic signal (maximum and total



Figs. 33–43. — 33–36. Prosternal process and anteromedian part of metasternum, ventral view. 33: *Hyphydrus parvicollis*; 34: *Heterhydrus senegalensis*; 35: *Andex insignis*; 36: *Desmopachria portmanni*. — 37–38. Prosternal process, ventral outline in lateral view. 37: *Allopachria wangi*; 38: *Hyphydrus parvicollis*. — 39–40. Metasternal wing. 39: *Heterhydrus sudanensis*; 40: *Hyphydrus parvicollis*. — 41–43. Left metacoxal process and metatrochanter, ventral view. 41: *Hyphydrus elegans*; 42: *Hydroglyphus angularis*; 43: *Heterhydrus senegalensis*. — Different scale bars for Figs. 33–42 (left, 0.5 mm) and 43 (right, 1 mm).

support a = 0.001). Still it produced 510 shortest trees in the Hennig86 search (mhennig*bb*: length 38, consistency index 0.71, rescaled dito 0.83), and 624 trees in PAUP (heuristic search using the default options). The strict consensus tree from each of these sets of fundamental trees had only six resolved clades in the ingroup (Fig. 1). Treating our single multistate characters as ordered or unordered did not change this result.

The basal dichotomy is between (*Heterhydrus* + *Pachydrus*) and all other taxa. Our interpretation of this result is that Hyphydrini in previous usage is polyphyletic. We think that this problem is best solved by placing the two genera *Heterhy-*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drus and *Pachydrus* in their own tribe, the Pachydrini, whereas the other genera remain in Hyphydrini. It is here important to note that we have not included any representatives of other tribes above the Methlini in our analysis. Consequently we have not adressed and cannot solve the problem of recognising relationships among tribes of Hydroporinae. The only character uniting Hyphydrini and Pachydrini is the reduced length of the anterior metatarsal claw. Other characters suggest other groupings, e.g. the soldering of the metacoxae to the abdomen found in Pachydrini and Bidessini.

Pachydrini is supported by six synapomorphies (character nos. 13, 15, 20–22 and 24). The fusion of the metacoxae with the abdomen, and the reduced suture separating the dorsal and ventral laminae of the metacoxal processes have both evolved independently within Hyphydrini in the genus *Desmopachria*. The four synapomorphies unique to Pachydrini are: (1) prosternal process dilated and mesocoxae widely separated, (2) elytron with ventrolateral carina apically thickened and undulate, (3) metatibia with longitudinal row of punctures on disc reduced, and (4) metatibia with apical row of spines short and scale-like.

Hyphydrini is now supported by three synapomorphies (character nos. 14, 15 and 18): (1) elytron with ventrolateral carina reduced in length, (2) the same carina apically ligulate, and (3) metasternal wing medially narrow.

Within the Hyphydrini we have found evidence for monophyly of each of the relatively heterogeneus genera *Allopachria* and *Desmopachria*. Synapomorphies of *Allopachria* are: (1) prosternal process smooth (shared with *Agnoshydrus*), and (2) elytron with humeral yellow macula. Two of our three *Allopachria* OTU's share a posteriorly dilated lateral bead on pronotum and an anterolateral elytral angle that is extended anteriorly.

Seven synapomorphies support a monophyletic *Desmopachria* (character nos. 1–4, 9, 20 and 23). The medially broken apical row of spines on the metatibia is shared with *Coelhydrus* and the two characters found also in Pachydrini were mentioned above. Unique synapomorphies are found in modifications of the antennae and palpi, and the posterolateral pronotal angle being produced backwards. Within *Desmopachria* two of our OTU's share the complete fusion of the dorsal and ventral laminae of the metacoxal processes.

The other genera entered in multiples into our analysis (*Microdytes*, *Hovahydrus* and *Hyphydrus*) remain without unambiguous evidence of monophyly. Future studies will show if the large genus *Hyphydrus* should be split into a predominantly Palearctic lineage (species group *H. ovatus*), an Ethiopian–Oriental lineage including many species groups and an Australian lineage (species group *H. lyratus*) (for species groups, cf. Biström 1982a).

4. Classification and descriptions

4.1. Key to genera and subgenera of Pachydrini and Hyphydrini

Pachydrini and Hyphydrini are distinguished from all other Hydroporinae by the reduced anterior metatarsal claw that is distinctly shorter than the posterior claw (Figs. 52 and 53). Additionally, all Pachydrini and many genera of Hyphydrini have the base of the metatrochanter totally exposed and not covered by the lateral lobes of the metacoxal processes — this character is absent in other Hydroporinae. The key to subgenera of *Desmopachria* is modified from Young (1980), and it is to be considered tentative.

1. Metasternal wing medially broad (Fig. 39). Prosternal process with apex enlarged and in broad contact with metasternum (Fig. 34). Ventrolateral elytral carina long and apically undulate (Fig. 57) (Pachydrini) 2

Figs. 44–60 (Left). — 44–46. Metatibia, ventral view. 44: *Hydropeplus trimaculatus*; 45: *Heterhydrus senegalensis*; 46: *Hyphydrus grandis*. — 47. *Desmopachria sanfilippoi*, apex of metatibia, ventral view. — 48. *Heterhydrus senegalensis*, protarsus. — 49. *Agnoshydrus laccophiloides*, apex of metatibia. — 50–51. Metatrochanter and -femur, ventral view. 50: *A. densus*; 51: *A. laccophiloides*. — 52–53. Metatarsal claws. 52: *Allopachria wangi*; 53: *Heterhydrus senegalensis*. — 54–56. Metatibial spurs. 54: *Hyphydrus elegans*; 55: *Desmopachria mendozana*; 56: *Hyphydrus aubei*. — 57–58. Elytron, laterodistal portion, ventral view. 57: *Pachydrus globosus*; 58: *Hyphydrus aubei*. — 59–60. *Hovahydrus praetextus*. 59: Metasternum and anterior portion of metacoxa; 60: Paramere. — Different scale bars for Figs. 50, 51, 57, 58 (left, 1 mm); 44–46, 48, 59 (right inner, 0.5 mm); 60 (right middle, 0.5 mm); and 47, 49, 52–56 (right outer, 0.5 mm).

— Metasternal wing medially narrow (Fig. 40). Prosternal process with apex narrow to slightly enlarged and in narrow contact with metasternum (Fig. 33), or separated from metasternum (Fig. 35). Ventrolateral elytral carina short and apically provided with a distinct ligula (Fig. 58) (Hyphydrini) 3
2. Labrum not covered by anterior clypeal edge in anterior view. Body length 5.0–6.8 mm (Africa) .. *Heterhydrus*
— Labrum partly covered by anterior clypeal edge in anterior view, only anterior border and fringes visible. Body length 3.4–5.8 mm (America) ..... *Pachydrus*
3. Apex of prosternal process not reaching metasternum (Fig. 35) ..... *Andex*
— Apex of prosternal process reaching metasternum (Fig. 33) (Note: *Desmopachria (Pachiridis)* and *D. (Portmannia)* have a strongly impressed medial part of prosternal process-apex; only lateral lobes in contact with metasternum, Fig. 36) 4
4. Pronotum with posterior angle distinctly extended backwards (Fig. 24). Body length 1.0–3.0 mm (America) *(Desmopachria)* 5
— Pronotum with posterior angle not distinctly extended backwards (Figs. 22, 23 and 25–27) (Note: Pronotum laterobasally curved inwards in some species with body length 3.2–4.7 mm) (Palaearctis, Oriental, Ethiopian, Australian Regions) 11
5. Metatibia with longer spur serrate (Fig. 55) .... subg. *Nectoserrula*
— Metatibia with longer spur not serrate 6
6. Pronotum with basal striae (Fig. 32) .... subg. *Pachriodesma*
— Pronotum without basal striae 7
7. Elytra with impressed, sutural lines (clearly detectable at middle) ..... subg. *Pachriostrix*
— Elytra without impressed, sutural lines (rarely a few punctures at suture may suggest striae) 8
8. Male prosternal process with apex not modified 9
— Male prosternal process with apex medially strongly impressed, forked (Fig. 36) 10
9. Elytral microsculpture iridescent ... subg. *Hintonella*
— Elytra without or with non-iridescent microsculpture .. .. subg. *Desmopachria* s.str.
10. Elytral microsculpture iridescent .... subg. *Pachiridis*
— Elytra without or with non-iridescent microsculpture ... . subg. *Portmannia*
11. Elytron keeled (Fig. 28) ..... *Darwinhydrus*
— Elytron not keeled 12
12. Base of metatrochanter covered by small lobe of metacoxal process (approx. as in Fig. 42) 13
— Base of metatrochanter totally exposed (Fig. 41) .. 14
13. Prosternal process finely dentate (Fig. 38) .. *Microdytes*
— Prosternal process not dentate (Fig. 37). Elytron in most species blackish with yellowish humerobasal spot .... *Allopachria*
14. Clyepus with anterior margin beaded (Fig. 15); if bead indistinct, longer metatibial spur serrate (Fig. 56) .... *Hyphydrus*
— Clyepus with anterior margin without bead. Metatibia with longer spur not serrate 15
15. Body length 3.8–5.5 mm. Body shape more or less elongate 16
— Body length 1.9–3.1 mm. Body shape more or less globular 18
16. Pronotum with base sublaterally with broad excavation (Fig. 25) ..... *Primospes*
— Pronotum with base sublaterally not excavate 17
17. Body outline constricted at level of pronotal/elytral base (Fig. 22) ..... *Hydropeplus*
— Body outline not constricted at level of pronotal/elytral base ..... *Coelhydrus*
18. Penis with apex deeply bifurcate ..... *Hyphovatus*
— Penis with apex not bifurcate 19
19. Body dorsally covered with very fine, dense, evenly distributed punctation. Penis with apex dorsoventrally flattened, distinctly curved. Paramere without slender extension (Oriental Region) ..... *Agnoshydrus*
— Dorsal body punctation variable, always coarser and somewhat irregularly distributed. Penis with apex not dorsoventrally flattened and not distinctly curved. Paramere in most species provided with a slender extension (Madagascar) ..... *Hovahydrus*

4.2. Descriptions

Within each genus the species are listed in alphabetical order except when a well-founded phylogeny or species-group classification has been presented in previous studies.

4.2.1. Pachydrini n. trib.

Type genus: *Pachydrus* Sharp.

Diagnosis. — Body: Length approximately 3–7 mm, maximum width 2–4 mm. Black to dark brown or dark ferrugineous. Body robust, somewhat elongated. Lateral outline of body somewhat rounded, without distinct constriction at level of pronotal/elytral base. Pronotum distinctly narrower than elytra. — Head: Dorsal surface flattened with anterior margin rounded; frontally with a steep unbeaded edge. Dorsal surface totally reticulated. Antenna practically unmodified; segments almost equally long. Segments 4–10 apically slightly enlarged. — Pronotum: Posterior angle distinct; not extended backwards and base without broad sublateral excavation. Lateral bead uniformly narrow; only slightly wider medially than towards angles. — Elytron: Surface smooth, not keeled. Lateral epipleural margin located ventrally on body. Epipleural cavity totally delimited

by a fine rim. Epipleuron evenly narrowed from base to apex. Ventrolateral keel long and apically undulate (Fig. 57). — Ventral aspect: Prosternal process with apex posteriorly dilated, broadly connecting metasternum (Fig. 34). Enlarged apex frontally not delimited by a margin. Mesocoxae quite widely separated from each other. Metasternal wing medially broad (Fig. 39). Metacoxal processes broad, hind legs widely separated (Fig. 43). Metacoxae soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes reduced and not visible. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Apical spine-row of metatibia continuous; length of spines equal, short (Fig. 45). Metatibial spurs not modified; long and non-serrate. Posterior metatarsal claw robust, length of anterior claw about 1/3 of posterior claw. — Genitalia: Paramere lacks extension. Spermatheca not sclerotized.

Genera included: *Heterhydrus* (p. 67) and *Pachydrus* (p. 67).

Heterhydrus Fairmaire (Figs. 12, 21, 30, 34, 39, 43, 45, 48 and 53)

Heterhydrus Fairmaire, 1869: 186.

Type species: *Heterhydrus agaboides* Fairmaire, 1869, by monotypy.

History: Originally described as a monotypic genus of Dytiscidae. Sharp (1882) placed the genus in Bidessini. Transferred to Hyphydrini by Zimmermann (1919, 1920). Recently revised by Wewalka (1980). Here transferred to Pachydrini.

Diagnosis and description. — Body: Length 5.0–6.8 mm, width 3.0–3.8 mm. — Head: Frontal part of head flattened and strongly extended forming dorsally a flat frontal platform. Labrum visible in anterior view. — Elytron: Discal row of punctures clearly discernible although mixed with ordinary punctures; posteriorly row disappears. Dorsolateral row of punctures practically absent. Lateral row of punctures quite distinct and dense; posteriorly it becomes somewhat indistinct. Ordinary punctation fine to rather fine, fairly sparse to sparse, slightly irregularly distributed; outside lateral row of punctures (close to epipleuron) punctation fine and sparse. — Ventral aspect: Prosternal process distinctly dentate; apex of process strongly enlarged and in broad connection with metasternal fork. — Legs: Metatibia expands only a little from base to apex; its lateral surface provided with few punctures (Fig. 45). — Genitalia: Penis asymmetric in two species.

Material studied (male and female): *H. agaboides*: Madagascar, Suberbieville (2 exx. MZH). — *H. senegalensis*: 23 specimens from Ivory Coast, Ghana, Chad, Central African Republic, Nigeria and Zaire (all in MZH). — *H. adiaptus*: Holotype: Congo Belge PNU Mabwe 25–28.I.1949 (MAC); Paratype, Congo Belge PNU Mabwe, 31.I., 3.II.1949 (3 exx. MAC). — *H. ghanensis*: Nigeria EC St. Norcap nr Abakaliki 29.VI.1973 (16 paratypes MZH); Nigeria NC St. Zaria 2–3.VIII.1973 (4 paratypes MZH); Nigeria NC St. Badeggi rice fields 8–9.VIII.1973 (2 paratypes MZH); Sierra Leone Makeni 28.XI.1993 (4 exx. MZH). — *H. sudanensis*: Sudan, Upper Nile, Malakal 5–20.I. 1963 (22 exx. MZH); Sudan Eq. Nimule 11–13.III.1963 (1 ex. MZH).

The genus, in which five species are recognized, is restricted to the Ethiopian Region and Madagascar.

List of taxa:

Heterhydrus Fairmaire, 1869
- *senegalensis* (Aubé, 1838) (Eth)
- *adiaptus* Guignot, 1952 (Eth)
- *agaboides* Fairmaire, 1869 (Mad)
- *sudanensis* Zimmermann, 1927 (Eth)
- *ghanensis* Wewalka, 1980 (Eth)

Pachydrus Sharp (Fig. 57)

Pachydrus Sharp 1882: 338.

Type species: *Pachydrus obesus* Sharp, 1882, subsequently designated by Guignot (1946: 113).

History: Originally described as a genus of Bidessini. Transferred to Hyphydrini by Zimmermann (1919, 1920). Young (1980) suggested that *Pachydrus* should be transferred from Hyphydrini to a separate tribe. It is here transferred to Pachydrini.

Diagnosis and description. — Body: Length 3.4–4.6 mm (*P. ritsemae*, 5.4–5.8 mm), width 2.1–2.8 mm (*P. ritsemae* 3.3–3.6 mm). — Head: Head frontally flat but less strongly extended (vide *Heterhydrus*). Anterior part of labrum clearly visible but basal part concealed by somewhat extended frontal part of head. — Elytron: Rows of punctures often hardly visible; mixed with ordinary punctures. Sometimes discal and lateral row of punctures partly discernible. Ordinary puncta-

tion variable in size and density; fine to quite coarse, somewhat sparse to dense. In some species puncture size variable but not divided into two different kinds. Elytral punctation always quite evenly distributed and also extended similarly to border against epipleura (cf. *Heterhydrus*). Sometimes separate punctures longitudinally somewhat extended. — Ventral aspect: Prosternal process quite strongly dentate; apex of process strongly enlarged and in broad connection with metasternal fork. Apex of prosternal process provided with a distinct, medial tubercle in *P. brevis* and *P. obesus*. — Legs: Metatibia expands moderately from base to apex; its lateral surface provided with a, in number, strongly reduced lateral row of punctures.

Material studied (male and female): *P. obesus*: Venezuela, Cagua 21.X.1960 (1 ex. coll. Young). — *P. globosus*: Brazil, Bahia Encruzilhada 7.IX.1972 (2 exx. MZH, 2 exx. coll. Young); Min. Ger. (1 ex. MZH); Boa Sorta (1 ex. MZH); Argentina, Pr. Chaco Resistencia 23.XII.1965 (2 exx. coll. Young). — *P. cribratus*: Colombia, Magdalena Is. Salamanca Parque Nat. 16.III.1968 (1 ex. coll. Young). — *P. princeps*: USA, Highlands Co. FLA, L. Placid 7–11.VIII.1966 (76 exx. MZH). — *P. cayennensis*: Mexico, Magatha (2 exx. coll. Young). — *P. brevis*: Trinidad: Nariva Swamp 30.VII.1963 (1 ex. coll. Young). — *P. obniger*: USA, FLA Monroe Co. Everglades Nat. Park 30.VII.1968 (1 ex. coll. Young); Bahamas: BWI, Long Isl. Deadmans Cay 11.III.1953 (1 ex. coll. Young). — *P. ritsemae*: Petit Brasil (lectotype RNHL); Same as lectotype (1 paralectotype RNHL).

Pachydrus, in which 9 species are recognized, occurs in the New World; Neotropis to Nearctis.

List of taxa:

Pachydrus Sharp, 1882
- *brevis* Sharp, 1882 (Neotr)
- *cayennensis* (Laporte de Castelnau, 1835) (Neotr)
- *cribratus* Sharp, 1882 (Mex, Carib)
- *globosus* (Aubé, 1838) (Neotr, Carib)
  - (*punctatus* Sharp, 1882)
- *obesus* Sharp, 1882 (Neotr)
- *obniger* (Chevrolat, 1863) (Carib)
- *politus* Sharp, 1882 (Neotr, Mex)
- *princeps* (Blatchley, 1914) (Nearc)
- *ritsemae* Régimbart, 1883 (Neotr)

4.2.2. Hyphydrini Sharp

Hyphydrini Sharp, 1882: 320, 370. Type genus: *Hyphydrus* Illiger.

Actobaenidae Gistel, 1856: 355. Type genus: *Actobaena* Gistel.

Diagnosis. — Body: Length 1–6.5 mm, width 0.7–4.3 mm. Shape globular to elongated, rarely dorsoventrally flattened. — Elytron: Ventrolateral keel short and apically provided with a distinct ligula (Fig. 58). — Ventral aspect: Apex of prosternal process narrow to somewhat enlarged; contact between apex and metasternum non-existing (one genus) or narrow to moderately broad. Metasternal wing medially narrow (Fig. 40). Metacoxal processes of normal width, hind legs not widely separated. Metacoxae not soldered to base of abdomen, except in *Desmopachria*. Posterior margin of ventral lamina of metacoxal processes visible as a suture, except in some species of *Desmopachria*. — Legs: Base of metatrochanter either totally exposed (Fig. 41) or partly covered by a minute, sharp extension from metacoxal process (approx. as in Fig. 42). Metatarsus with anterior claw shorter than posterior claw. — Genitalia: Spermatheca frequently well-sclerotized.

Twelve genera are recognized in Hyphydrini alphabetically as follows: *Agnoshydrus* (p. 72), *Allopachria* (p. 75), *Andex* (p. 68), *Coelhydrus* (p. 69), *Darwinhydrus* (p. 69), *Desmopachria* (p. 80), *Hovahydrus* (p. 79), *Hydropeplus* (p. 70), *Hyphovatus* (p. 71), *Hyphydrus* (p. 76), *Microdytes* (p. 74) and *Primospes* (p. 71).

Note. As Actobaenidae has not been cited as a valid name since it was first described, it should be suppressed and the well-known Hyphydrini conserved (Nilsson & Holmen 1995).

Andex Sharp (Figs. 10, 27, 31 and 35)

Andex Sharp 1882: 371.

Type species: *Andex insignis* Sharp, 1882, by monotypy.

History: *Andex* was originally described as a genus of Hyphydrini.

Diagnosis and description. — Body: Body length 5.3–6.3 mm, width 3.0–3.3 mm. Body shape elongate. Angle between pronotum and elytra very pronounced (Fig. 27). Pronotum much narrower than elytra and pronotal lateral outline rounded. — Head: Frontally between eyes non-margined and outline rounded. Antenna non-

modified; separate segments quite similar, long and almost equally broad (slightly enlarged apically). — Pronotum: Lateral bead uniformly narrow and distinct. Pronotal hind angle not posteriorly extended. — Elytron: Surface smooth, not keeled. Punctation simple, rather fine, somewhat irregularly and sparsely distributed. Discal row of punctures from base to elytral apex distinct. Dorsolateral row of punctures clearly discernible, more irregular than discal row and posteriorly rather indistinct. Lateral row of punctures sparse and rather indistinct. Separate punctures discernible from humeral to apical region. Epipleural cavity only partly delimited from rest of epipleuron because dividing rim partly reduced (Fig. 31). Lateral epipleural margin placed ventrally on body. — Ventral aspect: Prosternal process finely dentate; its apex quite narrow and it does not reach medio-frontal part of metasternum. Mesocoxae close to each other (Fig. 35). Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; its lateral surface provided with a dense row of punctures. Apical metatibial spine row continuous; length of separate spines variable, short to long. Metatibial spurs non-modified, quite long and not serrate. Anterior metatarsal claw about 1/2 the length of posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca not sclerotized.

Material studied (male and female): Brit. SW Africa Kamaggas VII.1904 L. Schultze S. (2 exx. MNHN); Cap (1 ex. MNHN).

Only one species, occurring in South Africa, is recognized in this genus.

List of taxa:

Andex Sharp, 1882
insignis Sharp, 1882 (Eth)

Coelhydrus Sharp

Coelhydrus Sharp 1882: 373.

Type species: *Coelhydrus brevicollis* Sharp, 1882, by monotypy.

History: *Coelhydrus* was originally described as a genus of Hyphydrini.

Diagnosis and description. — Body: Length 3.8–4.0 mm, width 2.2–2.4 mm. Body shape quite elongate although lateral outline somewhat rounded. Angle between pronotum and elytra almost absent, hardly visible. Pronotum somewhat narrower than elytra. — Head: Frontally between eyes without marginal bead; outline rounded. Antenna almost non-modified, segments 5–10 in apical half somewhat enlarged. — Pronotum: Posterior angle angulate but not extended posteriorly. Lateral bead uniformly narrow and distinct. — Elytron: Surface smooth, not keeled. With fine to rather fine, somewhat sparse and irregular punctation. All three rows of punctures discernible but rather sparse and somewhat irregular. Epipleural rim total. Epipleural lateral margin placed on ventral half of body. Epipleuron narrows abruptly approximately in middle. — Ventral aspect: Prosternal process distinctly dentate; apex reaching anteromedial part of metasternum. Mesocoxae rather narrowly separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanters totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base apically, its lateral surface with quite dense row of punctures. Apical metatibial spine row broken, medially with a gap lacking spines. Spine length unequal, short to medium long. Metatibial spurs somewhat sinuate; quite long and non-serrate. Length of last segment of pro- and mesotarsi almost equal to third segment. Anterior metatarsal claw about half as long as posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca not sclerotized.

Material studied (male and female): South Africa: Env. Cape Town 1899 (2 exx. MZH).

A monotypic genus confined to South Africa.

List of taxa:

Coelhydrus Sharp, 1882
brevicollis Sharp, 1882 (Eth)

Darwinhydrus Sharp (Fig. 28)

Darwinhydrus Sharp 1882: 373.

Type species: *Darwinhydrus solidus* Sharp, 1882, by monotypy.

History: *Darwinhydrus* was originally described as a genus of Hyphydrini.

Diagnosis and description. — Body: Length 3.2–3.9 mm, width 1.8–2.3 mm. Body somewhat elongate, dorsoventrally somewhat flattened. Lateral outline of body quite rounded. Angle between pronotum and elytra almost absent. Pronotum somewhat narrower than elytra. — Head: Frontally between eyes head non-margined (narrow frontal part posteriorly not distinctly delimited) but head medially, slightly posterior to frontal edge, somewhat depressed. Outline of frontal part of head rounded. Antenna almost non-modified; separate segments quite similar to each other; quite long and almost equally broad (segment 4 shorter than other segments; segments 5–10 in apical half slightly enlarged). — Pronotum: Base laterally slightly curved inwards. Distinctly delimited lateral bead uniformly narrow. — Elytron: Surface of elytron with three longitudinal keels; inner keel posteriorly in connection with lateral keel, which also forms lateral edge of elytron (Fig. 28). Rows of punctures absent. Total dorsal surface of elytron provided with quite dense, somewhat irregularly sized (coarse to fairly coarse) punctures. Lateral epipleural margin located on ventral side of body. Epipleuron narrows evenly from base to elytral apex. Epipleural cavity totally delimited by a fine rim. — Ventral aspect: Prosternal process quite finely dentate; its apex reaching metasternal fork. Mesocoxae rather narrowly separated. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Metatibia expands from base to apex; its lateral surface provided with a dense row of punctures. Apical row of spines on metatibia continuous; length of separate spines variable, rather short to medium. Metatibial spurs not modified; quite long and non-serrate. Metatibial claws slender; anterior claw about half as long as posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca not sclerotized.

Material studied: South Africa: Afr. australe 1906 (1 ex. MZH, 1 ex. MNHN); Stellenb. Cap. Colony (1 ex. MNHN); Brede 14.IX.1959 (2 exx. MNHN); Tzizikama For. 25.IX.1959 (10 exx. MNHN); Cap 20.IX.1959 (6 exx. MNHN); S. Afr. (15 exx. MNHN).

Only one species, occurring in South Africa, is recognized in this genus.

List of taxa:

Darwinhydrus Sharp, 1882
solidus Sharp, 1882

Hydropeplus Sharp (Figs. 14, 18, 22 and 44)

Hydropeplus Sharp 1882: 372.

Type species: *Hydroporus trimaculatus* Laporte de Castelnau, 1835, by monotypy.

History: *Hydropeplus* was originally described as a genus of Hyphydrini.

Diagnosis and description. — Body: Length 5.0–5.5 mm, width 2.9–3.3 mm. Body shape quite elongate; lateral outline still quite rounded. Angle between pronotum and elytra pronounced. Pronotum distinctly narrower than elytra. — Head: Frontally between eyes without marginal bead and outline rounded. Antenna non-modified; separate segments quite similar, long and almost equally broad (apically slightly enlarged). — Pronotum: Posterior angle somewhat rounded (not sharply angulate). Lateral bead uniformly narrow and totally, clearly discernible. Hind angle not extended posteriorly. — Elytron: Surface smooth, not keeled. Punctation simple, fine, densely and evenly distributed on total surface. All three rows of punctures indistinct, weakly developed. Lateral epipleural margin placed on ventral half of body. Epipleural cavity entirely delimited by a rim. Epipleuron narrows abruptly approximately in middle. — Ventral aspect: Prosternal process distinctly dentate; apex quite narrow and reaching anteromedial part of metasternum. Mesocoxae narrowly separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanters totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base towards apex; its lateral surface provided with a dense row of punctures. Apical metatibial spine row continuous; length of separate spines variable, short to long. Metatibial spurs non-modified, quite long and non-serrate. Last segment of pro- and mesotarsi about twice as long as segment 3. Anterior metatarsal claw about half as long as posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca clearly sclerotized.

Material studied (male and female): *H. trimaculatus*: South Africa: Tafelberg XI.1904 (10 exx. MZH); Table Mntn 15.XII.1950 (2 exx. MZH); Afr. australe 1908 (1 ex. MZH); S Cape Mtn Helderfontein (4 exx. TMP, 2 exx. MZH); Van Rhyn's Pass XI.1933 (7 exx. TMP, 3 exx. MZH); Disa Str. 2.XII.1900 (3 exx. TMP); Capl. Algoa Bay (1 ex. TMP). — *H. montanus*: South Africa: Tulbagh IV.1916 (1 ex. MZH); Cape-Cedarbg 8.XI.1983 (23 exx. TMP, 10 exx. MZH); Cape Mt Hawequas (1 ex. TMP); Tulbagh IV.1949 (1 ex. TMP).

Two species, restricted to South Africa, are recognized in this genus.

List of taxa:

Hydropeplus Sharp, 1882
montanus Omer-Cooper, 1965 (Eth)
trimaculatus (Laporte de Castelnau, 1835) (Eth)

Primospes Sharp (Fig. 25)

Primospes Sharp 1882: 372.

Type species: *Primospes suturalis* Sharp, 1882, by monotypy.

History: Originally described as a genus of Hyphydrini.

Diagnosis and description. — Body: Length 4.3–4.7 mm, width 2.5–2.7 mm. Body shape quite elongate; lateral outline still somewhat rounded. Angle between pronotum and elytra almost absent, hardly visible. Pronotum somewhat narrower than elytra. — Head: Frontally between eyes without marginal bead; outline quite rounded. Antenna non-modified; separate segments quite similar, quite long and apically slightly enlarged. — Pronotum: Base of pronotum laterally curved inwards so that hind angle is acute. Lateral bead uniformly narrow and clearly discernible. — Elytron: Surface smooth, not keeled. Punctation very fine, indistinct, sparse, and somewhat irregularly distributed. Discal row of punctures from base to apex quite distinct. Dorsolateral row of punctures in frontal half discernible although irregular and sparse; apically hardly visible. Lateral row of punctures also discernible although somewhat irregular and partly sparse. Lateral epipleural margin located on ventral half of body. Epipleural base delimited by a fine rim. Epipleuron narrows quite abruptly approximately in middle. — Ventral aspect: Prosternal process rather finely dentate; its apex quite narrow but reaches medial part of metasternum. Mesocoxae narrowly separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; its lateral surface with a dense row of punctures. Apical spine row of metatibia complete; spine length variable, short to quite long. Metatibial spurs non-modified, quite long and non-serrate. Apical segment of pro- and mesotarsi about twice as long as segment 3. — Genitalia: Paramere lacks long extension. Spermatheca sclerotized.

Material studied (male and female): South Africa, Cape Prov. Hopefield 31.X.1950 (2 exx. MZH); SA, Cape-Cedarbg 8.XI.1983 (1 ex. TMP, 1 ex. MZH).

A monotypic genus known only from South Africa.

List of taxa:

Primospes Sharp, 1882
suturalis Sharp, 1882 (Eth)

Hyphovatus Wewalka & Biström

Hyphovatus Wewalka & Biström 1994: 37.

Type species: *Hyphydrus dismorphus* Biström, 1984, by original designation.

History: Recently described as a genus of Hyphydrini with three species.

Diagnosis and description. — Body: Length 2.6–3.0 mm, width 1.8–2.0 mm. Body globular to quite globular; lateral outline rounded. Angle between pronotum and elytra almost absent, hardly visible. Pronotum clearly narrower than elytra. — Head: Frontally between eyes without marginal bead; head slightly depressed near anterior margin. Frontal outline rounded. Antenna practically non-modified; almost equal in length (segment 4 slightly shorter), segments 5–10 medium long and only slightly broader apically. Two basal segments slightly thickened. — Pronotum: Posterior angle quite distinct; not strongly extended backwards. Lateral bead uniformly narrow; discernible from fore to hind angle. — Elytron: Surface smooth, not keeled. Rows of punctures absent, not discernible. Punctation fine to somewhat coarse, quite

dense and quite evenly distributed. Lateral epipleural margin located on ventral side of body. Epipleural cavity totally delimited by a fine rim. Epipleuron narrows quite abruptly near middle. — Ventral aspect: Prosternal process finely dentate; apex quite narrow and reaching metasternal fork. Mesocoxae quite narrowly separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia from close to base almost to apex evenly broad; its lateral surface provided with a quite dense row of punctures. Apical metatibial spine row continuous; length of spines almost equal, quite long. Metatibial spurs not modified, quite long, almost straight and non-serrate. Anterior metatarsal claw slightly longer than half length of posterior claw. — Genitalia: Paramere lacks long extension. Sclerotized spermatheca absent.

Material studied (male and female): *Hyphovatus dismorphus*: Thailand 14.XI.1988 Khao Yai N.P. Jäch leg. (2 exx. coll. Wewalka, 1 ex. MZH). Material of the two additional species associated with *Hyphovatus* have been examined earlier (Wewalka & Biström 1994).

Three species, distributed in the Oriental Region, are thus far recognized in this genus.

List of taxa:

Hyphovatus Wewalka & Biström, 1994
- *manfredi* Wewalka & Biström, 1994 (Or)
- *prapatensis* Wewalka & Biström, 1994 (Or)
- *dismorphus* (Biström, 1984) (Or)

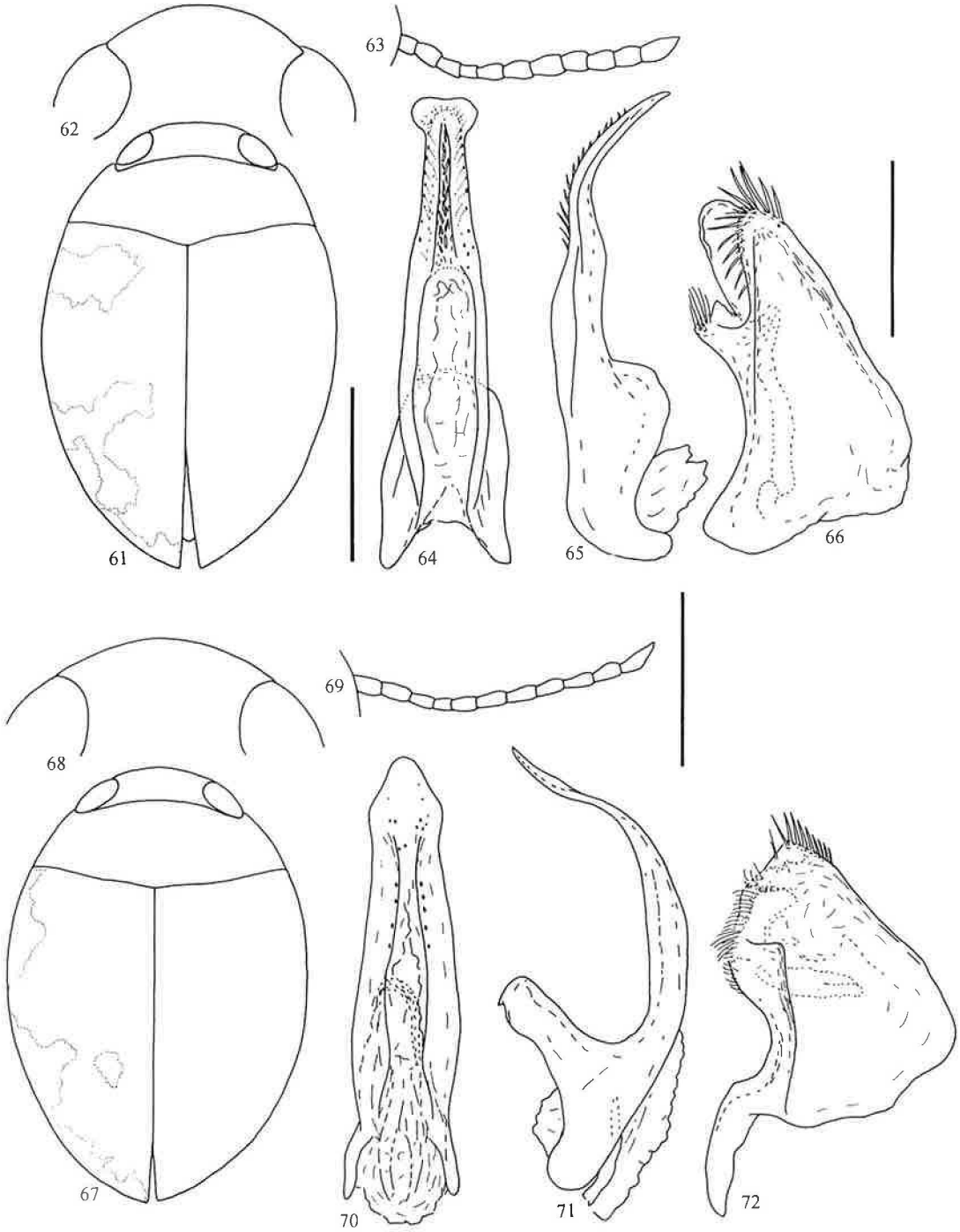
Agnoshydrus n. gen. (Figs. 2, 5, 49–51 and 61–72)

Type species: *Hydrovatus laccophiloides* Régimbart, 1888, by present designation.

Note. Zimmermann (1924) suggested that the type species should be transferred to *Allopachria*, whereas Vazirani (1977) placed it in *Microdytes*.

Diagnosis and description. — Body: Length 2.25–2.36 mm, width 1.55–1.60 mm. Shape globular; dorsoventrally slightly flattened. Lateral outline rounded. Angle between pronotum and elytra indistinct. Pronotum distinctly narrower than elytra. Body dorsally covered with very fine, dense, evenly distributed punctation. — Head: Frontally between eyes without marginal bead; outline rounded (medially indistinctly truncated). Antenna almost non-modified with segments almost equally long and broad (deviations as follows: segment 3 a little more slender; segment 4 slightly more slender and short; segment 11 a little prolonged). Almost unicoloured, pale ferrugineous to pale brown. — Pronotum: Pronotal hind angle quite distinct; posteriorly not extended; base laterally not strongly curved inwards. Lateral bead very fine; from apex to base almost equally narrow. Pale brownish to pale ferrugineous, laterally slightly paler, pale brownish to yellowish. — Elytron: Elytral surface smooth, non-keeled. Rows of punctures absent, except for a very indistinct, fragmented lateral row. Lateral margin of epipleuron located on ventral aspect of body. Epipleural cavity totally delimited by a fine rim. Epipleuron narrows distinctly at level of first sternite. — Ventral aspect: Prosternal process smooth, without denticulae. Apex of prosternal process somewhat enlarged; reaching metasternal fork. Mesocoxae moderately separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; lateral surface provided with a quite dense row of punctures. Apical spine row of metatibia complete; length of spines variable, of medium length to long. Metatibial spurs in one species practically unmodified; quite long, almost straight, non-serrate. In the other species spurs strongly modified; short, broad, outline curved. Anterior metatarsal claw slightly more than half the length of posterior claw. Metatrochanter and -femur posteriorly provided with a hairtuft; in one species hairtuft reduced to some hairs. — Male genitalia: Paramere lacks long, slender extension. Penis apex flattened, strongly bent. — Female: Slerotized spermatheca absent.

Two species have so far been recognized, both with an Oriental distribution.



Figs. 61–72. *Agnoshydrus*. — 61–66. *A. laccophiloides*. 61: Habitus; 62: Head, frontal aspect; 63: Antenna; 64–65: Penis. (64. Dorsal view, 65. Lateral view); 66: Paramere. — 67–72. *A. densus*. 67: Habitus; 68: Head, frontal aspect; 69: Antenna; 70–71: Penis. (71. Dorsal view, 72. Lateral view.); 72: Paramere. — Different scale bars for Figs. 61, 67 (left, 1 mm); 62, 63, 68, 69 (middle, 0.5 mm), and 64–66, 70–72 (right, 0.2 mm).

Key to species

1. Metatrochanter and -femur provided with dense hairtufts in male (Fig. 50); metatibial spurs slender, of medium length, almost straight ..... *A. densus*
— Metatrochanter and -femur provided with a few hairs (Fig. 51); metatibial spurs short, broad, outline curved (Fig. 49) ..... *A. laccophiloides*

A. laccophiloides (Régimbart)

Hydrovatus laccophiloides Régimbart 1888: 612 (orig. descr.); 1899: 231; Zimmermann 1920: 34; 1924: 195 (? belongs to *Allopachria*).

Microdytes laccophiloides (Régimbart, 1888): Vazirani 1977: 24; Satô 1981: 68.

Type locality: Bhamo, Burma.

Type material studied: Holotype, male: Bhamo Birmania Fea VI.1885/typus/*laccophiloides* Rég./*Hydrov. laccophiloides* Régb. typus!/*Hydrovatus laccophiloides* Rég. det. Régimbart (MCG).

Description. — Body: Length 2.36 mm, width 1.60 mm. Habitus as in Fig. 61. — Head: Pale brown to yellowish. Submat, meshes of microsculpture minute, very fine and indistinct. Frontal aspect (Fig. 62). Antenna pale brown (Fig. 63). — Pronotum: Pale brown to yellowish; anteriorly and posteriorly with vague, slightly darker areas. Submat, very finely microsculptured; meshes minute, indistinct. Lateral outline almost straight; anteriorly curved inwards. — Elytron: Dark ferrugineous to dark brown, with somewhat vague pale brown areas (Fig. 61). Submat, very finely microsculptured; meshes minute, indistinct. Epipleuron very finely punctate and submat, indistinctly microsculptured. — Ventral aspect: Ferrugineous to pale brownish. Punctation very fine, dense and almost evenly distributed. Slightly mat, microsculpture indistinct. — Legs: Pale brown to brown or ferrugineous. Pro- and mesotarsi rather slender. Metatibial spurs as in Fig. 49. — Male genitalia: Figs. 64–66.

Distribution: Burma; only known from type locality.

Ecology: Unknown.

A. densus n. sp.

Type locality: About 50 km S Pakse, near Ban Phatoumphone, Prov. Champasak, S-Laos.

Type material: Holotype, male: S-Laos: Prov. Champasak/ca. 50 km S Pakse/Umg. Ban Phatoumphone/23–24.V.1996, 50–100 m/leg. Schillhammer (1a), at light (NMW). Paratypes: 2 females with same data as holotype (NMW, MZH); 1 male, C-Laos: Prov. Viangchan, Phou Khao Khouay NP, Nam Leuk, env. Tad Leuk Waterf., 1–8.VI.1996, 200 m, at light (15a), leg. Schillhammer (NMW); 1 male, Thailand, Tap Tan, 20 km WNW Uthai Thani, 260 km NW Bangkok, 15.I.1979, leg. W. Thielen/*Hydrovatus laccophiloides* Rég., det. M. Brancucci 83 (coll. Wewalka).

Description (only differences from the redescription above are recognized). — Body: Length 2.25–2.30 mm, width 1.55–1.60 mm. Habitus as in Fig. 67. — Head: Pale ferrugineous. Frontal aspect (Fig. 68). Antenna (Fig. 69). — Pronotum: Ferrugineous, laterally slightly paler, pale ferrugineous (gradual change from darker to paler area). — Elytron: Dark ferrugineous, with somewhat vague pale ferrugineous areas (Fig. 67). — Legs: Metatibia with spurs non-modified; almost straight and slender. Metatrochanter and -femur with dense hairtufts in male (Fig. 50), first protarsal segment slightly delated in male. — Male genitalia: Figs. 70–72.

Distribution: Laos, Thailand.

Ecology: Unknown.

Microdytes J. Balfour-Browne (Figs. 7 and 8)

Microdytes J. Balfour-Browne 1946: 106.

Type species: *Microdytes belli* J. Balfour-Browne, 1946, by original designation.

History: *Microdytes* was originally introduced as a distinct genus and two species were associated with it (Balfour-Browne 1946). Guignot (1954) introduced *Nipponhydrus* as a subgenus of *Microdytes* and associated the name *flavomaculatus* Kamiya to it. Nilsson and Wewalka (1994) synonymized *Nipponhydrus* with *Allopachria*. Future studies will show if the genus *Microdytes* must be further splitted.

Diagnosis and description. — Body: Length 1.5–2.3 mm, width 1.0–1.6 mm. Shape of body globular; some species a little elongated. Angle between pronotum and elytra absent to indistinct and hardly visible. Pronotum in most species distinctly narrower than elytra; in a few species moderately narrower than elytra. — Head: A few species have a strikingly broad head relative to the body. Between eyes head variable; generally without marginal bead (one species with a very thin medial bead discernible), but rarely in frontal half of head with two, shallow, wide depressions. Fron-

tal outline sometimes rounded, sometimes medially straightened or almost angulated and in middle excavated. Rarely head ends abruptly. Antenna also variable; sometimes almost unmodified, quite slender and of medium length. In some species external segments short, broad (rarely these segments enlarged, broader than long). In a few species two basal segments strongly enlarged. — Pronotum: Pronotal hind angle distinct, not posteriorly extended, neither base laterally curved inwards. Lateral outline of pronotum almost straight to somewhat rounded, with fine and evenly broad marginal bead. — Elytron: Elytral surface smooth, not keeled. A few species exhibit a quite shallow, lateral furrow. Punctation generally fine to very fine, sparse to almost absent. A few species have a little coarser, more irregularly sized and denser punctation. Rows of punctures generally hardly visible or absent. Sometimes a quite indistinct basal and lateral row of punctures may be discerned. Lateral margin of epipleuron located on ventral side. Epipleural cavity totally delimited. Epipleuron narrows quite abruptly near first abdominal segment. — Ventral aspect: Prosternal process finely dentate. Apex of prosternal process somewhat enlarged, reaching metasternal fork. Mesocoxae moderately separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a very fine line. — Legs: Minute basal part of metatrochanter covered by a small lobe of metacoxal process. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; most species with lateral surface provided with a quite dense row of punctures. In some species the row of punctures consists of very fine, hardly visible punctures. Apical metatibial spine row continuous; separate spines variable in length, rather short to quite long. Metatibial spurs not modified, straight and medium long. Anterior metatarsal claw between 1/2 to 1/3 shorter than posterior claw. — Genitalia: Paramere lacks long and slender extension. Spermatheca not sclerotized.

Material studied (male and female): *M. belli*: Kanara/Ind. or. (1 ex. coll. Wewalka). — *M. championi*: Nepal, 20 km NW Pokhara Lumie 1 600 m 2.V.1984 (2 exx. coll. Wewalka). — *M. maculatus*: Bhutan, Bhakta B. Sarbhang 31.VIII.1981 (1 ex. coll. Wewalka) — *M. pasiricus*: Pasir 3.XII.1928/*pasiricus* Csiki Paratype (1 ex. MNHN). — *M. uenoi*: Taiwan, Taipei Gongliao 12.XI.1992 (1 ex. coll. Wewalka). Additionally we have examined 17 specimens belonging to 9 so far undescribed species, from Thailand, Malaysia and Indonesia.

At present nine species from the Oriental Region have been recognized in the genus.

List of taxa:

Microdytes J. Balfour-Browne, 1946
- *belli* J. Balfour-Browne, 1946 (Or)
- *championi* J. Balfour-Browne, 1946 (Or)
- *elgae* Hendrich & Balke, 1995 (Or)
- *maculatus* (Motschulsky, 1859) (Or)
- *pasiricus* (Csiki, 1938) (Or) n. comb.
  - (*simplicior* (Csiki, 1938))
  - (*unicolor* (Csiki, 1938))
- *sabitae* Vazirani, 1968 (Or)
- *taiwanus* Satô, 1990 (Or)
- *tomokunii* Satô, 1981 (Or)
- *uenoi* Satô, 1972 (Or)

Allopachria Zimmermann (Figs. 4, 9, 17, 26, 29, 37 and 52)

Allopachria Zimmermann 1924: 194.

Type species: *Allopachria quadripustulata* Zimmermann, 1924, by monotypy.

History: *Allopachria* was originally described as a monobasic genus of Hyphydrini. Vazirani (1977) transferred the genus to Bidessini, whereas Nilsson *et al.* (1989) returned it to Hyphydrini. Nilsson and Wewalka (1994) synonymized *Nipponhydrus* with *Allopachria*. The female holotype of the type species is seemingly lost (Hendrich & Balke 1995).

Diagnosis and description. — Body: Length 1.6–3.0 mm, width 1.1–2.1 mm. Body shape quite globular although dorsoventrally somewhat flattened (especially distinct in larger species). Lateral outline of body rounded; angle between pronotum and elytra absent to indistinct. Pronotum at hind angle only slightly narrower than elytra. In all but one of the examined species each elytron basally with a distinctly delimited pale brown to yellowish, humeral spot. Deviating species with body almost totally black. — Head: Shape of frontal edge between eyes variable. In most examined species outline rounded and often medially straightened; outline sometimes almost angulate. Rarely with fine marginal bead, or head surface slightly depressed posterior to frontal edge. In a few species head mediofrontally narrowly but distinctly turned upwards. Shape of antenna surprisingly variable. In males often modified. In one

species segments 5–10 distinctly flattened. In a few species segments 4–5 asymmetric; laterally variously expanded. Often segments only with minor modifications, separate segments rather short to medium in length; for instance external segments may be short while basal segments distinctly longer. — Pronotum: Posterior angle quite sharp; not extended posteriorly, neither base laterally distinctly curved inwards. Lateral outline rounded to almost straight; marginal bead posteriorly dilated (in one species only moderately so). — Elytron: Elytral surface smooth, not keeled, sometimes with lateral furrows. Anterolateral angle often extended forwards and visible from above (reaching a short distance past pronotal hind angle). Punctation rather fine to very fine, sparse to fairly dense and quite evenly distributed. Sometimes punctation almost absent. Punctures may vary in size but are not clearly of two different kinds. Rows of punctures often absent. Rarely discal row basally and lateral row discernible, although they are weakly developed. Lateral margin of epipleuron generally placed on ventral side of body (in *A. bimaculata* placed laterally and visible from above). Epipleural cavity totally delimited. Epipleuron narrows quite abruptly near first abdominal segment. — Ventral aspect: Prosternal process not dentate; outline of process in lateral view finely uneven but no separate process may be discerned. Apex of process a little enlarged; reaching metasternal fork. Distance between mesocoxal cavities medium to quite short. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Metacoxal process with minute lobe that covers a small part of base of metatrochanter. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; its lateral surface provided with a medium dense row of punctures. Apical metatibial spine row continuous; length of spines variable, medium to long. Metatibial spurs non-modified, fairly long, straight and non-serrate. Anterior metatarsal claw between 1/2 to 1/4 shorter than posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca non-sclerotized.

Material examined (male and female): *A. bimaculata*: Mt. Okyama Is. Okinoerabu 7.VIII.1958/Paratype (1 ex. coll. Wewalka); Mikyo, Tokunoshima I. 10.IV.1968 (1 ex. coll. Wewalka). — *A. flavomaculata*: Wara-Gawa Gifu Pref. 24.VIII.1967 (2 exx. coll. Wewalka); Fukuoka VI.1953 (2 exx. MNHN). — *A. quadripustulata*: Indonesia Siberut Toteburu-Bakeuluk 17.II.1991 (1 ex. coll. Wewalka). — *A. wangi*: Taiwan, Taipei 3.VII.1992/paratype (1 ex. coll. Wewalka); Taiwan, Keelung City 10.VIII.1990/paratype (1 ex. coll. Wewalka). — Additionally, material of six different undescribed species from Thailand, Vietnam, China and Hong Kong have been examined (10 exx. coll. Wewalka).

Seven species are thus far recognized in the genus. At least six new species will be introduced by Wewalka in separate articles. *Allopachria* is widely distributed in the Oriental Region and Japan.

List of taxa:

Allopachria Zimmermann, 1924
(*Nipponhydrus* Guignot, 1954)
- *barong* Hendrich & Balke, 1995 (Or)
- *bimaculata* (Satô, 1972) (Or)
- *flavomaculata* (Kamiya, 1938) (Pal)
  - (*f. kumozuensis* Satô, 1958)
  - (*f. narusei* Satô, 1958)
- *quadrimaculata* (Satô, 1981) (Or)
- *quadripustulata* Zimmermann, 1924 (Or)
- *umbrosa* Zimmermann, 1927 (Or)
- *wangi* Nilsson & Wewalka, 1994 (Or)

Hyphydrus Illiger (Figs. 15, 19, 23, 33, 38, 40, 41, 46, 54, 56 and 58)

Hyphydrus Illiger 1802: 369.

Type species: *Hydrachna gibba* Fabricius, 1801, as designated by Latreille (1810); junior synonym of *Dytiscus ovatus* Linnaeus, 1761.

History: The genus was originally delimited and introduced under the name *Hydrachna* by Fabricius (1801) but this generic name turned out to be preoccupied by *Hydrachna* Müller, 1776, associated with Acarina. *Hyphydrus* was introduced by Illiger (1802) for the species names *gibba, ovalis* and *scripta* which he did not accept to be attributed to the same genus as *hermanni* (now in the genus *Hygrobia*). Four subgenera were distinguished in the genus during the 20th century but this classification was rejected by Biström (1982a). Since the last revision numerous new species have been described by different authors. The present review of the tribe Hyphydrini suggests a splitting of *Hyphydrus* sensu Biström in three different genera.

Diagnosis and description. — Body: Length 2.8–6.5 mm, width 1.9–4.3 mm. Shape of body quite globular, or somewhat elongated (*lyratus* group occurring in Australia and the Oriental Region). Angle between pronotum and elytra in most species absent (pronounced at least in a few species). Pronotum distinctly narrower than elytra. — Head: Between eyes with marginal bead (bead

rarely indistinct or absent); outline of head frontally rounded to angulate (medially straight). In one species head mediofrontally extended. In a few species frontal margin delimited by a deep and narrow furrow. Antenna slender, comparatively long; separate segments quite similar. — Pronotum: Hind angle generally quite sharp, not posteriorly extended; pronotal base laterally not distinctly curved inwards. Pronotal outline rounded to straight; lateral marginal bead uniformly narrow. — Elytron: Surface smooth, not keeled. Punctation simple or somewhat irregularly sized; in some species distinctly of two different kinds. Sometimes with four rows of punctures; a sutural row, a discal, a dorsolateral and a lateral row. Rows often disappear posteriorly. In some species one or some of the rows are absent or very indistinct. Most often discal and lateral rows are present. Lateral margin of epipleuron placed on ventral side of body. Epipleural cavity well delimited. Epipleuron narrows posteriorly quite abruptly at level of first abdominal sternite. — Ventral aspect: Prosternal process distinctly dentate; its apex quite narrow and reaching metasternal fork. Distance between mesocoxae quite short. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia in most species groups except for extreme base equally broad; in a few species groups metatibia narrows quite gradually from base to apex. Lateral surface of metatibia in most species provided with a dense row of punctures; in a few species punctures densely distributed almost over total surface (medial row of punctures then indistinct). Apical metatibial spine row continuous; length of spines unequal, medium to long. Metatibial spurs variable; often comparatively long and straight, rarely curved or apically sinuate. In one species group longer spur distinctly serrate. Anterior metatarsal claw between 1/4 to 1/3 shorter than length of posterior claw. — Genitalia: Paramere lacks long extension. Spermatheca clearly sclerotized.

Material studied (male and female): Practically all species associated with the genus *Hyphydrus* have been examined.

129 species are recognized in Palaearctis, the Ethiopian, the Oriental, and the Australian Regions.

List of species

Hyphydrus Illiger, 1802
(*Hydrachna* Fabricius, 1801 nec Müller)
(*Actobaena* Gistel, 1856)
(*Pachytes* Montrouzier, 1869 nec Defrance)
(*Allophydrus* Zimmermann, 1930)
(*Apriophorus* Guignot, 1936)
(*Aulacodytes* Guignot, 1936)
madagascariensis Wehncke, 1877 (Mad)
assinicus Régimbart, 1889 (Eth)
flaviceps Zimmermann, 1926 (Eth)
parvicollis Sharp, 1882 (Eth)
decemmaculatus Wehncke, 1877 (Or, Austr)
(*curvipes* Régimbart, 1891)
effeminatus Watts, 1978 (Austr)
contiguus Wehncke, 1877 (Austr)
elegans (Montrouzier, 1860) (Or, Austr)
(*blanchardii* Clark, 1862)
(*australis* Clark, 1862)
(*caledoniae* Clark, 1862)
(*illigeri* Perroud, 1864)
(*bifasciatus* Macleay, 1871)
(*nitidicornis* Broun, 1881)
(*gibbicollis* Régimbart, 1891)
dani Biström, Balke & Hendrich, 1993 (Or)
l. lyratus Swartz, 1808 (Or, Austr)
(*nigronotatus* Clark, 1863)
(*bisulcatus* Clark, 1863)
(*fossulipennis* Macleay, 1871)
l. foveolatus Régimbart, 1891 (Or)
l. flavicans Régimbart, 1892 (Or)
l. xanthomelas Régimbart, 1877 (Or)
grandis Laporte de Castelnau, 1835 (Pal, Eth)
(*major* Sharp, 1882)
caffer Boheman, 1848 (Eth)
residuus Omer-Cooper, 1971 (Eth)
alluaudi Régimbart, 1889 (Eth)
linnavuorii Biström, 1982 (Eth)
umilis Bilardo & Rocchi, 1995 (Eth)
tristiculus Guignot, 1951 (Eth)
agnitus Guignot, 1952 (Eth)
funebris Guignot, 1956 (Eth)
alfredi Bilardo & Rocchi, 1986 (Eth)
bistroemi Bilardo & Rocchi, 1986 (Eth)
(*hiekei* Biström, 1986)
microreticulus Bilardo & Rocchi, 1986 (Eth)
amplimaculatus Bilardo & Rocchi, 1995 (Eth)
mbandouensis Bilardo & Rocchi, 1990 (Eth)
ater Bilardo, 1982 (Eth)
schoutedeni Gschwendtner, 1930 (Eth)
sphaeroidalis Biström, 1982 (Eth)
fuscus Omer-Cooper, 1931 (Eth)
ovatus (Linnaeus, 1761) (Pal)
(*ferrugineus* Linnaeus, 1767)
(*sphaerius* De Geer, 1774)
(*grossus* Müller, 1776)
(*gibbus* Fabricius, 1777)

(*ovalis* Illiger, 1798)
(*variegatus* Stephens, 1829)
sanctus Sharp, 1882 (Pal)
anatolicus Guignot, 1957 (Pal)
(*carrarai* Sanfilippo, 1963)
aubei Ganglbauer, 1892 (Pal)
(*variegatus* Aubé, 1836 nec Stephens)
l. laeviventris Sharp, 1882 (Pal)
l. tsugaru Nakane, 1993 (Pal.)
falkenstromi Gschwendtner, 1939 (Pal)
(*brincki* Guignot, 1946)
j. japonicus Sharp, 1873 (Pal)
(*frontalis* Sharp, 1882)
(*paromoeus* Guignot, 1954)
j. vagus Brinck, 1943) (Pal)
detectus Falkenström, 1936 (Pal)
(*pieli* Guignot, 1936)
(*chinensis* Hlisnikovsky, 1954)
(*orientalis* v. *reductus* Hlisnikovsky, 1954)
orientalis Clark, 1863 (Pal, Or)
(*eximius* Clark, 1863)
maculiceps Régimbart, 1906 (Eth)
(*basilewskyi* Guignot, 1960)
sjoestedti Biström, 1982 (Eth)
perforatus Régimbart, 1895 (Eth)
(*p.* v. *degener* Guignot, 1952)
(*p.* v. *alogus* Guignot, 1952)
(*scitulus* Omer-Cooper, 1958)
fluviatilis Pederzani, 1988 (Eth)
variolosus Régimbart, 1906 (Eth)
(*v.* v. *patens* Guignot, 1954)
burgeoni Gschwendtner, 1930 (Eth)
silfverbergi Biström, 1982 (Eth)
nigrovittatus Régimbart, 1906 (Eth)
komghaensis Omer-Cooper, 1965 (Eth)
pederzanii Biström, 1982 (Eth)
villiersi Guignot, 1947 (Eth)
opaculus Régimbart, 1895 (Eth)
(*caviceps* Régimbart, 1904)
quadrisulcatus Bilardo & Rocchi, 1986 (Eth)
satyrus Bilardo & Pederzani, 1978 (Eth)
occultus Bilardo & Rocchi, 1995 (Eth)
silvanus Bilardo, 1982 (Eth)
camerunensis Biström, 1982 (Eth)
lanzai Bilardo & Rocchi, 1986 (Eth)
vasalloi Bilardo & Rocchi, 1990 (Eth)
congoanus Biström, 1982 (Eth)
essoni Bilardo & Rocchi, 1995 (Eth)
coccinelloides Zimmermann, 1923 (Or)
keiseri Mouchamps, 1959 (Or)
separandus Régimbart, 1895 (Mad, Eth)
(*oncodes* Guignot, 1955)
trophis Guignot, 1955 (Mad)
barysomus Guignot, 1958 (Eth)
sylvester Guignot, 1955 (Mad)
(*spissus* Guignot, 1960)
bigamus Guignot, 1956 (Mad)
inopinatus Omer-Cooper, 1971 (Eth)
stipator Guignot, 1942 (Eth)
cycloides Régimbart, 1889 (Eth)
(*circularis* Régimbart, 1895)
(*pelates* Guignot, 1953)
(*lamottei* Legros, 1958)
(*malawiensis* Omer-Cooper, 1971)
(*nigeriensis* Omer-Cooper, 1971)
zambiensis Pederzani, 1988 (Eth)
delibatus Guignot, 1947 (Eth)
? (*brownei* Bertrand, 1948)
gabonicus Régimbart, 1895 (Eth)
(*vicinus* Bertrand & Legros, 1975)
quadriguttatus Guignot, 1956 (Eth)
malkini Guignot, 1959 (Eth)
odiosus Guignot, 1952 (Eth)
omercooperae Guéorguiev, 1975 (Eth)
caryerus Guignot, 1942 (Eth)
(*legrosi* Guéorguiev, 1975)
(*guignoti* Guéorguiev, 1975)
tuberosus Guignot, 1954 (Eth)
cuppeni Biström, 1984 (Mad)
facilis Biström, 1987 (Eth)
dissimilis Biström, 1983 (Eth)
maculifer Guignot, 1959 (Eth)
soni Biström, 1982 (Eth)
signatus Sharp, 1882 (Eth)
(*grossus* Sharp, 1882)
(*aethiopicus* Balfour-Browne, 1944)
subsignatus Bilardo & Rocchi, 1990 (Eth)
pictus Klug, 1834 (Pal, Eth)
(*lugubris* de Borre, 1870)
wittei Gschwendtner, 1938 (Eth)
puncticollis Sharp, 1882 (Eth)
abyssinicus Peschet, 1916 (Eth)
maculatus Babington, 1841 (Pal, Eth)
(*crassus* Wollaston, 1867)
(*africanus* Sharp, 1882)
(*a.* v. *borkuanus* Bruneau de Miré & Legros, 1963)
lasiosternus Guignot, 1942 (Eth)
(*bertrandi* Guéorguiev, 1975)
pavani Bilardo & Rocchi, 1986 (Eth)
stipes Sharp, 1882 (Mad)
(*scriptus* v. *soarezicus* Alluaud, 1897)
scriptus (Fabricius, 1798) (Eth)
distinctus Aubé, 1838 (Eth)
lentiginosus Guignot, 1934 (Eth)
ditylus Guignot, 1953 (Eth)
gschwendtneri Guignot, 1942 (Or)
(*pictus* v. *indicus* Gschwendtner, 1935 nec Sharp)
(*p.* v. *nalinie* Vazirani, 1968)
(*lindemannae* Guignot, 1959)
boettcheri Biström, 1982 (Or)
schoedli Wewalka & Biström, 1993 (Or)
sumatrae Régimbart, 1880 (Or)
(*assamensis* Vazirani, 1968)
pulchellus Clark, 1863 (Or)
(*orbicularis* Régimbart, 1899)
(*wui* Gschwendtner, 1933)

(*jeanneli* Guignot, 1934)
jacobsoni Biström, 1982 (Or)
fangensis Biström & Satô, 1988 (Or)
intermixtus (Walker, 1858) (Or)
(*indicus* Sharp, 1882)
gibbosus Biström, 1984 (Or)
eldenbecki Biström, 1982 (Or)
ceramensis Wewalka & Biström, 1993 (Or)
loriae Régimbart, 1891 (Or)
holomelas Biström, 1984 (Or)
renardi Severin, 1890 (Or)
birmanicus Régimbart, 1888 (Or)
holmeni Biström, 1983 (Or)
excoffieri Régimbart, 1899 (Pal, Or)
celebensis Biström, 1983 (Or)
jaechi Wewalka & Biström, 1989 (Or)
eremita Guignot, 1954 (Eth)
circumflexus Klug, 1853 (Eth)
(*hardenbergi* Zimmermann, 1926)
conradsi Gschwendtner, 1933 (Eth)
(*opiparus* Guignot, 1934)
brancuccii Biström, 1981 (Eth)
celox Biström, 1987 (Eth)
prinzi Wewalka & Biström, 1989 (Eth)
spangleri Biström, 1985 (Eth)
imitator Biström, 1984 (Eth)
aequatorialis Biström, 1983 (Eth)
concii Bilardo & Rocchi, 1986 (Eth)
nasutus Bilardo & Pederzani, 1978 (Eth)
esau Biström, 1982 (Eth)
prozeskyi Biström, 1982 (Eth)
impressus Klug, 1833 (Eth)
(*cocquerelii* Fairmaire, 1869)
(*flavicollis* Régimbart, 1895)

Hovahydrus Biström (Figs. 59 and 60)

Hovahydrus Biström 1982b: 430.

Type species: *Hyphydrus praetextus* Guignot, 1952, by original designation.

History: Originally described as a genus of Hyphydrini including four species, previously assigned to the genus *Hyphydrus*.

Diagnosis and description. — Body: Length 1.9–3.1 mm, width 1.4–2.1 mm. Body shape quite globular; only a little elongated. Angle between pronotum and elytra almost absent. Pronotum distinctly narrower than elytra. — Head: Between eyes without marginal bead, but frontal edge sharp; posterior to edge somewhat depressed. Frontal outline rounded to slightly angulate (edge medially slightly straightened). Antenna almost non-modified; separate segments quite similar and medium long (segments 1–2 slightly enlarged; 3 slender; 4 a little shorter than other segments; 5–10 apically slightly enlarged). — Pronotum: Hind angle quite pronounced, not posteriorly extended; base laterally not strongly curved inwards. Lateral outline of pronotum almost straight to rounded; marginal bead uniformly narrow. — Elytra: Elytral surface smooth, non-keeled. Punctation slightly variable (not of two different kinds); quite dense to somewhat sparse and slightly irregularly distributed. Rows of punctures almost totally absent; an irregular, lateral row of punctures may sometimes be discerned. Lateral margin of epipleuron placed ventrally on body. Epipleuron narrows quite evenly from entirely delimited epipleural cavity to elytral apex. — Ventral aspect: Prosternal process distinctly dentate; apex quite narrow and reaching metasternal fork. Mesocoxae rather narrowly separated from each other. Metacoxae not soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a suture. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; its external surface provided with a dense row of punctures. Apical spine row of metatibia continuous; length of spines somewhat variable, medium long to long. Metatibial spurs non-modified; medium long and almost straight, non-serrate. Anterior metatarsal claw about half the length of posterior claw. — Genitalia: Paramere with a long, slender extension except in *H. minutissimus* (cf. illustrations in Biström 1982b: 432). Attribution of this species to *Hovahydrus* is, thus, to be regarded uncertain.

Material studied (male and female): *H. praetextus*: Madagascar, Mt Tsaratanana 1 800 m, X.1949/Paratype (4 exx. MNHN). — *H. sinapi*: Madagascar, Ihanarandriana, rte Ambatolampy VIII.1953, Millot/Allotype (1 ex. MNHN). — *H. perrieri*: Madagascar, Tsiafa javona VI.1947, 2 500 m (1 ex. MNHN); Madagascar, riv. Itremo VIII.1949 (2 exx. MNHN). — *H. minutissimus*: Madagascar, Ambolitantely 13.XI.1991 Walther leg. (2 exx. MZH).

With some hesitation four species, occurring in Madagascar, are recognized in *Hovahydrus*.

List of species:

Hovahydrus Biström, 1982
minutissimus (Régimbart, 1903) (Mad)
praetextus (Guignot, 1952) (Mad)
perrieri (Fairmaire, 1898) (Mad)
sinapi (Guignot, 1955) (Mad)

Desmopachria Babington (Figs. 3, 6, 11, 12, 16, 20, 24, 32, 36, 47 and 55)

Desmopachria Babington 1841: 16.

Type species: *Desmopachria nitida* Babington, 1841, by monotypy.

Subgenera: *Nectoserrula* Guignot 1950a: 152. Type species: *Hyphydrus mendozanus* Steinheil, 1869, by original designation. — *Pachriodesma* Guignot 1950a: 152. Type species: *Hydroporus latissimus* LeConte, 1851, by original designation. — *Pachriostrix* Guignot 1950b: 3. Type species: *Desmopachria grouvellei* Régimbart, 1895, by original designation. — *Pachiridis* Young 1980: 307, 311. Type species: *Desmopachria iridis* Young, 1980, by original designation. — *Portmannia* Young 1980: 307, 310. Type species: *Hydroporus portmanni* Clark, 1862, by original designation. — *Hintonella* Young 1981: 212. Type species: *Desmopachria ubangoides* Young, 1980, by original designation. Synonym: *Hintonia* Young 1980: 307, 314, preoccupied by *Hintonia* Reichart, 1973; Torridincolidae, Coleoptera.

History: *Desmopachria* was first described as a monobasic genus close to *Hygrotus* Stephens (Babington 1841). Sharp (1882) placed the genus in Bidessini and associated 13 species with it. Zimmermann (1919, 1920) transferred *Desmopachria* to Hyphydrini. After this a number of subgenera have been described. Future systematic studies will reveal whether some (or all) subgenera in fact deserve generic rank.

Diagnosis and description. — Body: Length 1.1–3.0 mm, width 0.7–2.0 mm. Shape quite globular; a few species have a slightly elongated body. Lateral outline of body quite rounded. Angle between pronotum and elytra absent or indistinct. Pronotum distinctly narrower than elytra. — Head: In most species head between eyes rounded, medially sometimes straightened; with fine marginal bead. In some species margin flattened, forming quite narrow, upwards turned rim. In a few species head frontally angulate; medially straight and bent upwards. Antenna somewhat modified; segments 1–2 quite large; segment 3 slender, long; segment 4 short; segments 5–10 short, quite broad; segment 11 of same width as segments 5–10 but distinctly longer. — Pronotum: Posterior angle sharp; distinctly extended backwards. Lateral bead uniformly narrow. Some species have two basal striae as in many species of Bidessini. — Elytra: Surface smooth. Punctation simple, fine to quite coarse, dense to rather sparse; sometimes almost impunctate. Punctures variable; evenly distributed to concentrated frontally and at suture. Rarely size of punctures variable; very fine punctures somewhat irregularly mixed with coarser punctures. Rows of punctures often absent or very indistinctly discernible. Rarely discal and lateral rows and very seldom also dorsolateral rows of punctures discernible. Lateral margin of epipleuron placed ventrally on body. Epipleural cavity totally delimited. Epipleuron narrows quite distinctly near first abdominal segment. — Ventral aspect: Prosternal process finely dentate. Apex of prosternal process in most species reaching metasternal fork; in a few species medial part of prosternal process-apex strongly impressed so that only lateral lobes reach metasternal fork. Distance between mesocoxae moderate. Metacoxae soldered to base of abdomen. Posterior margin of ventral lamina of metacoxal processes visible as a weak suture or totally reduced. — Legs: Base of metatrochanter totally exposed. Metafemur not reaching metacoxal process. Metatibia expands from base to apex; lateral surface provided with a quite sparse to dense row of punctures. Apical metatibial spine row with medial gap. Length of spines variable; rather short to quite long. Metatibial spurs in most species non-modified; straight and moderately long to long. In a few species longer spur serrate. Length of anterior metatarsal claw between 1/5 to 1/2 of posterior claw. — Genitalia: Paramere lacks long, slender extension. Spermatheca distinctly sclerotized.

Material studied (male and female): *Desmopachria* s.str.: *D. nitida*: Sao Paulo (1 ex.MNHN); Matto Gross Corumba (2 exx. MNHN). — *D. attenuata*: Brasil/Type (MNHN); Gouadloupe (1 ex. MNHN). — *D. grana*: Florida Liberty Co. Yellow Cr. SE Telogia 5.VI.1982 (1 ex. MZH). — *D. convexa*: Indiana Monroe Co. Bloomington 4.VII.1990 (2 exx. MZH). — *Nectoserrula*: *D. punctatissima*: Neuquen 1907 (3 exx. MNHN). — *D. vicina*: Mexico Vera Cr./cotype (1 ex. MNHN). — *D. mendozana*: Argent. Neuquen (3 exx. MNHN). — *D. concolor*: Paraguay R. Alta Parama Ihamisi (1 ex. MNHN); Paraguay XII.1936 (1 ex. MNHN); Brasil V.1954 (1 ex. MNHN). — *Pachiridis*: *D. iridis*: Brasil Pará Aldeia Yavaruhu 11–25.II.1966 (2 exx. MZH). — *Pachriodesma*: *D. brevicollis*: Argent. Pampas Grande/type (MNHN). — *D. sanfilippoi*: Venezuela St Falcon/San Luis/paratype (3 exx. MNHN). — *D. mexicana*: Granjuato (1 ex. MNHN); Sonora VI.1956 (1 ex. MNHN); Arizona Tucson/Bear Canyon (1 ex. MNHN); *D. dispersa*: Texas McLennan Co. 4.X.1980 (2 exx. MZH). — *Pachriostrix*: *D. grouvellei*: Brasil/Matto Grosso (1 ex. MZH). — *Portmannia*: *D. laevis*: Brasil Boa Sorta (2 exx. MNHN); Brasil (1 ex. MNHN). — *D. bryantstoni*: Mexico S.L. Potosi 22.XII.1948 (1 ex. coll. Young). — *D. portmanni*: Texas Davis Mts. (2 exx. coll. Young); Arizona Cochise Co. 11.VII.1956 (1 ex. coll. Young). — *D. variegata*: Mexico (3 exx. coll. Young); Honduras (1 ex. coll. Young). — *D. basicollis*: Costa Rica/para-

type (3 exx. MNHN). — *D. sobrina*: Panama/paratype (1 ex. coll. Young). — *D. zethus*: Mexico/paratype (2 exx. coll. Young). Additionally I have studied a number of different, unnamed specimens of *Desmopachria*. No material of the subgenus *Hintonella* has been examined.

With some hesitation, in all 79 species are recognized in this genus. The range of the genus covers North to South America.

List of taxa:

Desmopachria Babington, 1841

Subgenus *Desmopachria* Babington, 1841
aspera Young, 1981 (Nearc, Carib)
attenuata Regimbart, 1895 (Neotr)
balfourbrownei Young, 1990 (Neotr)
bifasciata Zimmermann, 1921 (Neotr)
cenchramis Young, 1981 (Nearc)
circularis Sharp, 1882 (Neotr)
convexa (Aube, 1838) (Nearc)
darlingtoni Young, 1989 (Carib)
defloccata Young, 1981 (Mex, Nearc)
flavida Young, 1981 (Mex)
geijskesi Young, 1990 (Neotr)
glabella Young, 1981 (Carib)
glabricula Sharp, 1882 (Neotr)
grana (LeConte, 1855) (Nearc)
granoides Young, 1986 (Neotr)
hylobates Young, 1993 (Neotr)
isthmia Young, 1981 (Neotr)
laesslei Young, 1981 (Carib)
leechi Young, 1981 (Nearc)
lewisi Young, 1981 (Carib)
liosomata Young, 1986 (Neotr)
majuscula Young, 1990 (Neotr)
(?) *margarita* Young, 1990 (Neotr)
nitida Babington, 1841 (Neotr)
nitoides Young, 1990 (Neotr)
ovalis Sharp, 1882 (Neotr)
phacoides Guignot, 1950 (Neotr)
pulvis Guignot, 1958 (Neotr)
signata Zimmermann, 1921 (Neotr)
striga Young, 1990 (Neotr)
strigata Young, 1981 (Neotr)
subfasciata Young, 1990 (Neotr)
subnotata Zimmermann, 1921 (Neotr)
subtilis Sharp, 1882 (Neotr)
tarda Spangler, 1973 (Carib)
voltata Young, 1981 (Neotr)
zelota Young, 1990 (Neotr)
zimmermani Young, 1981 (Mex)

Subgenus *Hintonella* Young, 1981
(*Hintonia* Young, 1980)
minuta (Young, 1980) (Neotr)
siolii (Young, 1980) (Neotr)
ubangoides (Young, 1980) (Neotr)

Subgenus *Nectoserrula* Guignot, 1950
concolor Sharp, 1882 (Neotr)
mendozana (Steinheil, 1869) (Neotr)
punctatissima Zimmermann, 1923 (Neotr)
vicina Sharp, 1882 (Mex)

Subgenus *Pachiridis* Young, 1980
aldessa Young, 1980 (Neotr)
aureus Young, 1980 (Neotr)
iridis Young, 1980 (Neotr)
novacula Young, 1980 (Neotr)

Subgenus *Pachriodesma* Guignot, 1950
brevicollis Regimbart, 1903 (Neotr)
dispersa (Crotch, 1873) (Nearc)
latissima (LeConte, 1851) (Nearc)
mexicana Sharp, 1882 (Mex, Nearc)
mutchleri Blatchley, 1919 (Nearc)
sanfilippoi Guignot, 1957 (Neotr)
seminola Young, 1951 (Nearc)
suturalis Sharp, 1884 (Neotr)
varians Wehncke, 1877 (Neotr)

Subgenus *Pachriostrix* Guignot, 1950
ferrugata Regimbart, 1895 (Neotr)
fossulata Zimmermann, 1928 (Neotr)
grouvellei Regimbart, 1895 (Mex)
paradoxa Zimmermann, 1923 (Neotr) (loc. accord. Trémoullies 1995)
ruginosa Young, 1990 (Neotr)
striola Sharp, 1887 (Neotr)

Subgenus *Portmannia* Young, 1980
basicollis Guignot, 1949 (Neotr)
bryantstoni Clark, 1862 (Mex)
(*polita* Sharp, 1882)
decorosa Young, 1995 (Mex)
dispar Sharp, 1882 (Mex)
goias Young, 1995 (Neotr)
laevis Sharp, 1882 (Neotr)
mutata Sharp, 1882 (Neotr)
niger Zimmermann, 1923 (Neotr) (loc. accord. Trémoullies 1995)
nitidissima Zimmermann, 1928 (Neotr) (loc. accord. Trémoullies 1995)
pittieri Young, 1995 (Neotr)
portmanni Clark, 1862 (Mex)
sobrina Young, 1995 (Neotr)
speculum Sharp, 1887 (Neotr)
variegata Sharp, 1882 (Mex)
zethus Young, 1995 (Mex)

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