DESCRIPTIONS OF NEW SPECIES OF DESMOPACHRIA BABINGTON

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Abstract

Four new species of Desmopachria Babington are described from Bolivia: D. amyae Miller, new species, D. challeti Miller, new species, D. signatoides Miller, new species, and D. volatidisca Miller, new species. The female genitalia of members of the genus are described and illustrated in detail for the first time. A discussion of the taxonomy and characters historically used for the classification of subgenera and species groups is presented. It is concluded that recognition of subgenera in the genus, despite the large size of the group and existence of good characters for grouping some species, is not desirable since some groups are weakly supported by character evidence and/or are probably paraphyletic. Use of all previous subgenus names is rejected. The species are organized into informal groups, most of which correspond with historically used subgenera. Several species are left ungrouped.

The genus Desmopachria Babington is one of the most speciose of New World dytiscid genera. As of this paper, 93 species are recognized in North and South America, and new species are commonly found. In fact, over half of the included species were described during only the last 20 years. Because of the size of the genus and relatively distinctive characters present in some of its members, it is tempting to subdivide the group into subgenera, or, at least, species groups. The resulting classification has not proven satisfactory in my opinion. This is not because characters are unavailable for grouping in many taxa, but rather because of the relative lack of distinctive characters in other species. As a result, distinctive species groups have been recognized as subgenera but the remaining morass of species have been lumped together in the dubious taxon, Desmopachria s. str. which is probably paraphyletic. Formal naming of only monophyletic taxa is a fundamental tenet of classification (Hennig 1966), and, so, good taxonomists should seek to recognize only taxa for which monophyly is evident from tests of character congruence. In this paper, I extend the review of the characters historically used for classifying the group presented by Young (1980) and myself (Miller 1999) and discuss the implications of character distributions among taxa for classification of the subgenera and species groups. I revise the classification of Desmopachria based on a conservative approach to formal taxon recognition. I also describe four new species bringing the total number of known species to 93. The species in this genus are most easily distinguished, at this time, by the shape of the male genitalia. Therefore, I present a synopsis of illustrations, mostly of male genitalia, from the disparate literature. This literature, which was mainly published by F. Young, spans nearly 20 years and is in several journals and mul-
tiple publications. This is intended to serve as a starting point for identification of material.

**Material and Methods**

Illustrations. New illustrations were made using drawing tubes on a Wild M3 dissecting microscope and on a Leitz Dialux 20 compound microscope. Drawings were scanned and digitized and plates were made using a computer. Illustrations reproduced from the literature were scanned using a Hewlett Packard ScanJet 6200C at 400 dpi resolution. The drawings were then edited using a bitmap editing program. Occasionally, enhancement of original drawings was deemed appropriate when the original quality was not good. An attempt was made only to enhance drawings, not to change shapes or communication of structures. In making the plates, arrangements, relative size and relative rotation of the images were altered when necessary.

Measurements. Measurements were made of new species using an ocular scale in a Wild M3C dissecting microscope at 40× magnification. Two measurements were taken, total length (TL) and greatest width (GW). The ratio, TL/GW, is provided as well to give an indication of shape. When available, a total of 10 specimens was measured at random from all available collection localities. When 10 were not available, all specimens were measured. The range and mean are provided for measurements.

Type Specimens. Holotypes of new species are placed in the Coleccion Cientifica del Departamento de Entomologia, Museo de Historia Natural “Noel Kempff Mercado,” Santa Cruz, Bolivia (MHNB) and United States National Museum of Natural History, Washington, D.C., USA (USNM). Paratypes are distributed in MHNB, USNM, the G.L. Challet Collection (GLCC), and/or my collection (KBMC).

Female Genitalia. The genitalia of females were extracted and examined following a method similar to that of Mazzoldi (1996). Genitalia were dissected from specimens either preserved in ethanol or dried. Dried specimens were first relaxed by brief immersion in lightly boiling water. To remove the structures of interest from a specimen, it was held between a thumb and forefinger and an insect pin was gently inserted between the third and fourth sterna. Using the apex of the pin, the connective tissue and terga were pulled apart resulting in the dissection of most of the abdomen from the body. The abdomen was then placed in hot 10% KOH for several minutes. The cleared structures were then placed in 4% acetic acid. During this time the structures were carefully teased apart with fine insect pins and the terga and sterna were separated from the genital structures and hindgut. The genitalia and gut were then placed in an aqueous solution of chlorazol black. When sufficiently stained the structures were washed in distilled water. The genitalia were examined in distilled water and glycerin. The glycerin tended to collapse structures such as the spermatheca unless immersed for an extended period of time. Therefore, the genitalia were first examined and drawn in distilled water using a drawing tube on a Wild M3C dissecting microscope. To examine finer details, the genitalia were mounted in glycerin on a microscope slide and examined using a Leitz Dialux 20 compound microscope.

*Desmopachria amyae* Miller, **new species**

Figs. 1–4, 15–16

**Diagnosis.** Very distinctive based on color pattern, lateral inflations and
Fig. 1. *Desmopachria amyae*, habitus. bar = 1.0 mm.
Fig. 2–14. Desmopachria spp., male genitalia. 2–4) D. amyae; 2) median lobe and left lateral lobe, dorsal aspect; 3) same, median lobe, right lateral aspect; 4) same, right lateral lobe, right lateral aspect; 5–7) D. challeti; 5) median lobe and left lateral lobe, dorsal aspect; 6) same, median lobe, right lateral aspect; 7) same, left lateral lobe, left lateral aspect; 8–10) D. signatoides; 8) median lobe and left lateral lobe, dorsal aspect; 9) same, median lobe, right lateral aspect; 10) same, right lateral lobe, right lateral aspect; 11–13) D. volatidisca; 11) median lobe, dorsal aspect; 12) same, median lobe, right lateral aspect; 13) same, right lateral lobe, right lateral aspect; 14) Desmopachria signatoides, left antenna, dorsal aspect. bars = 0.1 mm.

distinct furrows in elytra (Fig. 1), and distinctive male genitalia (Figs. 2–4). Median lobe in dorsal aspect robust, apically slightly expanded and with apex truncate (Fig. 2); in lateral aspect relatively straight (Fig. 3). Lateral lobe with distinct, medially-directed stout spine at apex (Fig. 2).

**Description.** Measurements. n = 3, TL = 1.93–1.97 mm (\(\bar{x} = 1.96\)mm); GW = 1.43–1.46mm (\(\bar{x} = 1.45\)mm); TL/GW = 1.33–1.38 (\(\bar{x} = 1.35\)).

**Habitus** (Fig. 1). Moderately large for genus; broadly rounded laterally in dorsal aspect; greatest width slightly anterior of middle, posteriorly rounded; slightly flattened dorsoventrally.

**Coloration.** Head yellow. Pronotum yellow with posterior margin narrowly black. Elytron yellow with dark brown to black pattern (Fig. 1), dark brown or black along suture, black area expanded medially and along anterior margin, middle of disk extensively brown with fasciae extending posteriorly, apical region light brown. Antennae and palpi yellow. Pro- and mesothoracic legs...
Sculpture and structure. Head very finely and inconspicuously punctate; clypeal margin anteriorly produced and distinctly margined; antennae moderately short, antennomeres 4–9 anteroapically lobed. Pronotum impunctate except moderately but distinctly punctate laterally and broadly along pteromedia margin; without basal striae; lateral pronotal margin strongly rounded; lateral bead broad posteriorly, narrowed anteriorly. Elytron variably punctate, moderately and inconspicuously punctate over most of disk, apical area with

yellow; metathoracic legs brown. Thoracic sterna yellow-brown. Abdominal sterna yellow.

Figs. 15–20. 15–16) *D. amyae*, female genitalia; 15) right gonocoxosternite; 16) same, right gonocoxa; 17–20) *Desmopachria* species, female genitalia, ventral aspect; 17) *D. challeti*; 18) *D. volatidisca*; 19) *D. convexa*; 20) *D. youngi*. al = anterior lobe of gonocoxosternite, bc = bursa copulatrix, co = common oviduct, ds = spermathecal disc, fd = fertilization duct, fs = fertilization sac, gc = gonocoxa, gs = gonocoxosternite, ra = ramus, sd = spermathecal duct, sp = spermatheca, va = vagina. bars = 0.1 mm.
punctuation of two sizes, very fine and moderately coarse, interspersed; with four relatively distinctly impressed, longitudinal furrows near suture, medially, sublaterally and laterally (Fig. 1), punctures in furrows confluent; elytron laterally with elongate inflation extending along apical half, distinctly demarcated from disk of elytron by lateral furrow; epipleuron impunctate. Prosternum very short, with posteromedial tubercle. Prosternal process broad, apically pointed, shallowly concave. Metasternum, metacoxa and abdominal sterna impunctate. Legs unmodified.

**Male genitalia** (Figs. 2–4). Median lobe in ventral aspect broad basally, narrowed slightly medially and apically expanded and broadly truncate (Fig. 2); in lateral aspect moderately broad, tapered gradually to slightly rounded apex (Fig. 3). Lateral lobe in ventral aspect apically recurved with apex directed medially, apex with stout, robust spine directed medially, medial margin with long setae, apex with few long setae and numerous short setae (Fig. 2); in lateral aspect broad basally, evenly narrowed to slightly rounded apex (Fig. 4).

**Female genitalia** (Figs. 15–16). Gonocoxal apex with several long setae, apicominal margin with series of short setae (Fig. 15); gonocoxosternite with extremely long and apically bent anterior lobe, apicolateral margin with series of robust setae with apices curved, apicominal margin with few long, stout setae (Fig. 16). Other structures not examined.

**Variation.** This species is variable in extent of the maculation, degree of fragmentation and the relative darkness of color of the various regions of maculae.

**Taxonomy.** I have placed this species in the *D. striola* group based on the presence of elytral striae, but it does not resemble most of these species. This species may be similar to *D. varians* (which I have not seen) since Young (1980) mentions that it is dorsally patterned like members of the *D. variegata* group (see Discussion below for clarification of group classification) and lacks pronotal striae. Young (1990b) indicates that *D. varians* has very course punctures laterally on the base of the pronotum which are lacking in *D. amyae*.

**Etymology.** This beetle is named *amyae* after my wife, Amy Miller, because both are beautiful creatures.

**Natural History.** This species was collected from pools in a small, rocky, steep stream in a canyon in the Andean foothills of central Bolivia.

**Material Examined.** Holotype: ♂ in MHNB, labeled, “BOLIVIA: Dpto Sta Cruz. Prov. Florida, Rio del Sauce, 4.3km ENE Samaipata 01 Jul 1999 KB Miller, colr. 18°10′25″S 63°50′13″W 1669 m #2–21/ HOLOTYPE Desmopachria amyae K.B. Miller, 2000 [red label with double black line border].” Paratypes, 2 ♀♀, same data as holotype. The genitalia of the two female paratypes were damaged during dissection, and only a portion of the structures are described here.

Desmopachria challeti Miller, new species
Figs. 5–7, 17

**Diagnosis.** Distinguishable from other members of *D. convexa* group by shape of median lobe with lateral rami relatively broad and rounded apically (Fig. 5).

**Description.** Measurements. n = 4, TL = 1.54–1.65 mm (x̄ = 1.61 mm); GW = 1.05–1.10 mm (x̄ = 1.07 mm); TL/GW = 1.47–1.53 (x̄ = 1.51).

**Habitus.** Size average for genus; body robust, broadly rounded laterally, not
attenuate posteriorly; greatest width slightly anterior of middle; slightly dor-soventrally flattened.

**Coloration.** Head and pronotum yellow; elytron yellow laterally, basally and apically darker yellow-brown medially and along suture. Antennae and palpi yellow. Sterna and legs yellow.

**Sculpture and structure.** Head very finely and inconspicuously punctate; anterior clypeal margin dorsoventrally compressed and distinctly beaded; antennae moderately short, antennomeres 6–10 anteroapically lobed. Pronotum very finely and inconspicuously punctate; without basal striae; lateral pronotal margins broadly rounded; lateral bead narrow, slightly broader posteriorly; epipleuron impunctate. Elytron finely punctate over most of surface, more coarsely punctate apically. Prosternum short, with posteromedial tubercle. Prosternal process broad medially, broadly acuminate apically, medially shallowly concave. Metasternum, metacoxae and abdominal sterna impunctate. Legs not modified.

**Male genitalia** (Figs. 5–7). Median lobe in dorsal aspect strongly bifid into two, elongate, lateral rami, rami broad apically, broadly rounded, lateral margins sinuate, basally broadly bifurcate (Fig. 5); in lateral aspect basally with broad section, apically with elongate portion medially expanded, apex narrowly rounded (Fig. 6). Lateral lobe apically with articulable lobe long, apically pointed, apex of lateral lobe truncate with small areas of setae (Fig. 5), in lateral aspect very broad medially (Fig. 7).

**Female genitalia** (Fig. 17). Spermatheca globular, spermathecal cap oblique with distinctive invaginated lobe; fertilization duct elongate, tightly contorted, moderately broad; posterior lobes of gonocoxae reduced; apex of vagina with rami; gonocoxosternites rounded, anterior lobe robust, anteriorly expanded, posterior margin of gonocoxosternite with region of short setae, apex with few, stout setae.

**Variation.** This species varies somewhat in the depth of coloration of the elytron.

**Taxonomy.** This species is a member of the *D. convexa* group (see Discussion below for information about species groups) as evident from the presence of a distinct, apical, articulable lobe on the lateral lobe and deeply bifid median lobe (Fig. 5).

**Etymology.** This species is named *challeti* in honor of the collector of the type series, G.L. Challet.


**Desmopachria signatoides** Miller, **new species**
Figs. 8–10, 14

**Diagnosis.** Distinguishable from other members of *D. convexa* group by shape of male genitalia (Figs. 8–10); median lobe in dorsal aspect elongate, narrow, apically deeply bifid and with rami slender and apically pointed (Fig. 8); articulable spur of lateral lobe short and lateral lobe broad apically in dorsal aspect (Figs. 8, 10).
Description. Measurements. n = 1, TL = 1.29 mm; GW = 0.88 mm; TL/GW = 1.46.

Habitus. Small; broadly rounded laterally in dorsal aspect, posteriorly rounded; dorsoventrally slightly flattened; brown with indistinct yellow maculae.

Coloration. Head and pronotum yellow. Elytron brown with irregular yellow maculae anteriorly and with elytral apex yellow. Antennae and palpi yellow. Pro- and mesothoracic legs yellow; metathoracic legs brown. Prosternum black; other thoracic and abdominal sterna yellow.

Sculpture and structure. Head very finely and sparsely punctate, but punctures distinct; anterior clypeal margin produced anteriorly and distinctly beaded; antennae short, antennomeres 6–10 short, cylindrical, together very compact (Fig. 14). Pronotum impunctate medially, indistinctly punctate laterally and along basal margin; lateral margin moderately rounded; lateral bead very narrow, slightly widened anteriorly. Elytron with punctures very fine and sparse, but distinct; epipleuron narrow, impunctate. Prosternum narrow, transversely strongly carinate and produced anteriorly, medial tubercle absent; prosternal process broad, apically broadly acuminate, surface slightly convex. Metasternum impunctate. Metacoxa very finely punctate, punctures inconspicuous. Abdominal sterna impunctate; sternum six with apicomедial tumidity, apex margined and with medial furrow extending from tumidity to apex.

Male genitalia (Figs. 8–10). Median lobe in ventral aspect anteriorly broad and widely bifurcate, posteriorly with elongate, narrow section, with lateral margins slightly divergent with deep apical emargination making apex strongly bifid (Fig. 8); in lateral aspect with medial broad area, apical portion elongate-curved with apex narrowly rounded (Fig. 9). Lateral lobe in ventral aspect moderately broad, divided into two sections, apical section apically broad with laterally acute-pointed apex, with small region of setae subapically, posteriorly with distinct articulable lobe or spur; in lateral aspect with anterior portion very broad and robust, apical portion narrow with articulable lobe distinctly visible medially (Fig. 10).

Female. Unknown.

Taxonomy. This species is a member of the *D. convexa* group (see Discussion below for clarification of group classification) based on the presence of an articulable spur on the lateral lobe, though it differs from all other species except *D. signata* Zimmermann in the shape of the male genitalia and the presence of elytral maculae. The species appears to be closely related to *D. signata* since both have maculate elytra and a bifid median lobe. However, the median lobe appears to be considerably longer and differently shaped in *D. signatoides* (see Figs. 8–10, 32).

Etymology. This species is named *signatoides* for its similarity to the species *D. signata* in shape of male genitalia and elytral maculation.

Natural History. The single specimen of this species was collected from an artificial cattle watering pond in a relatively dry area of the Bolivian lowlands.

Material Examined. Holotype: ♂ in MHNB, labeled, “♂/ BOLIVIA: Dpto. Sta Cruz. Prov. Chiquitos 2.2km E San Jose. artificial cattle pond 26 June 1999 KB Miller, colr./ 17°51’00”S 60°43’02”W 315m #2–12/ HOLOTYPE Desmopachria signatoides K.B. Miller, 2000 [red label with double black line border].’’ This species is known only from the holotype.

Desmopachria volatidisca Miller, new species

Figs. 11–13, 18

Diagnosis. Distinguishable from other species by distinctive and complicated shape of male genitalia (Figs. 11–13); median lobe very robust with
three pairs of apical rami (Figs. 11–12); lateral lobe very broad in lateral aspect with apicoventral truncate process (Fig. 13).

**Description.** Measurements. n = 10, TL = 1.57–1.74 mm (x = 1.69 mm); GW = 1.05–1.16 mm (x = 1.13 mm); TL/GW = 1.48–1.53 (x = 1.50).

**Habitus.** Moderately sized for genus; rounded laterally in dorsal aspect, elongate oval; rounded laterally; greatest width slightly posterad of middle; rounded posteriorly; slightly flattened dorsoventrally; medium brown to yellow brown.

**Coloration.** Head and pronotum evenly yellow. Elytron brown to yellow brown, basally with poorly-defined yellow areas medially. Antennae and palpi yellow. Pro- and mesothoracic legs yellow; metathoracic legs yellow-brown. All sternae yellow.

**Sculpture and structure.** Head finely punctate; clypeal margin anteriorly produced, strongly beaded; antennae short, antennomeres 6–10 anteroapically lobed. Pronotum evenly, finely punctate; lateral pronotal margins strongly rounded; lateral bead slightly expanded anteriorly. Elytron with punctuation distinct, but fine and sparse, finer and less dense laterally and posteriorly; epipleuron narrow, very finely and inconspicuously punctate, punctures sparse. Prosternum very short, medially with posterior tubercle. Prosternal process broad medially, posteriorly acuminate. Metasternum impunctate. Metacoxae very finely and inconspicuously punctate. Abdominal sternite impunctate. Legs not unusually modified.

**Male genitalia** (Figs. 11–13). Median lobe extremely complex, laterally and dorsoventrally very broad and robust, medially hollow; apically multi-lobate with very distinctive, posteriorly-directed rami, apex with flattened, laterally broad lobes (Figs. 11–12). Lateral lobe in lateral aspect broad, apicoventrally with a pronounced, subrectangular projection, posterior surface with few, short setae (Fig. 13).

**Female genitalia** (Fig. 18). Spermatheca large, globular, spermathecal cap with large, distinctive anterior lobe; gonocoxae absent, apex of vagina with large, triangular, thickened membranous region; gonocoxosternites elongate-triangular, anterior lobe robust, anteriorly hooked, posterolateral margin of gonocoxosternite with region of short setae, apex with few, stout setae.

**Variation.** This species varies in color with some members laterally more lightly colored on the elytron. The basal elytral diffuse pale area varies in extent from nearly absent to rather broad.

**Taxonomy.** I have placed this species in the *D. glabricula* group (see Discussion below for clarification of group classification) since its median and lateral lobes are extremely robust (Figs. 11–13).

**Etymology.** This species is named *volatidisca* from the Latin words, *volatis*, meaning “flying”, and *discus*, meaning “saucer”, in reference to the general shape of specimens (like small, spherical spaceships).

**Natural History.** This species was collected from a pool in a slow stream, a cattail marsh and an artificial cattle watering pond in the Bolivian lowlands.

**Material Examined.** *Holotype*: ♂ in MHN, labeled, “♂/ BOLIVIA: Dpto Sta Cruz Prov Velasco 2.5 km SE San Ignacio, cattail marsh, 20 June 1999, K.B. Miller, colr/ 16°23′24″S 60°57′13″W 325m #2–7/ HOLOTYPE Desmopachria volatidisca K.B. Miller, 2000 [red label with double black line border].” *Paratypes*: 1, same data as holotype; 6 labeled, “BOLIVIA: Dpto Sta Cruz Prov. Velasco, 2.8 km SSW San Ignacio, marsh, 22 June 1999/ 16°24′11″S 60°58′26″W, 383m #2–8/ PARATYPE Desmopachria volatidisca K.B. Miller, 2000 [blue label with black line border];” 1 labeled, “BOLIVIA:
Dpto Sta Cruz Prov. Chiquitos, 2.2 km E San Jose, artificial cattle watering pond, 26 June 1999 KB Miller, colr./ 17°51′00″S 60°43′02″W 315m #2–12/ PARATYPE Desmopachria volatidisca K.B. Miller, 2000 [blue label with black line border];” 11 labeled, “BOLIVIA: Dpto Sta Cruz Prov. Chiquitos, 2.7 km S San Jose, pool in stream, 27 June 1999 KB Miller, colr./ 17°52′20″S 60°44′28″W 333m #2–15/ PARATYPE Desmopachria volatidisca K.B. Miller, 2000 [blue label with black line border];” 3 labeled, “BOLIVIA: Dpto Sta Cruz Prov. Chiquitos, San Jose, mud puddle 28 June 1999 KB Miller, colr./ 17°50′52″S 60°44′16″W 326m #2–16/ PARATYPE Desmopachria volatidisca K.B. Miller, 2000 [blue label with black line border];” 33 labeled, “BOLIVIA: Prov Sta Cruz Prov. Chiquitos, 1.3 km WSW San Jose, pool in stream, 28 June 1999 KB Miller, colr./ 17°51′13″S 60°44′53″W 320m #2–17/ PARATYPE Desmopachria volatidisca K.B. Miller, 2000 [blue label with black line border].”

Female Genitalia

Because female genitalia have not been previously described in any detail for this genus (though the spermatheca of D. tarda Spangler was illustrated by Spangler (1973)). I present here a description of the structures as evident from dissection of the species D. challeti (Fig. 17), D. volatidisca (Fig. 18), D. convexa (Aubé) (Fig. 19) and D. youngi Miller (Fig. 20). I have also examined female genitalia of several other species not illustrated here. The bursa copulatrix ranges from short and inconspicuous (e.g., Fig. 18) to longer and more evident (Figs. 19–20). A bursal gland is absent. The spermathecal duct is moderately long and very slender and attaches at the end of the bursa. At the insertion of the spermathecal duct into the spermatheca is a flattened circular disc, the “spermathecal disc,” through the center of which the spermathecal duct passes. The spermathecal disc may have irregular or smooth surfaces, and there appear to be fine setae or gland ducts attached to the disc around its margin. This feature may be a useful character for phylogenetic analysis and its distribution in the Hyphydrini should be investigated further. The spermatheca is robust and globular. There is a distinct differentiated region anteriorly on the spermatheca which is typically annulated. This region in some species is very large and multiannulated (Fig. 20) but in others forms a distinct, rounded, flattened cap (Figs. 18–19). In D. convexa and D. challeti there is a distinct, invaginated lobe medially on the cap (Figs. 17, 19) which may be a good synapomorphy for some species. The fertilization duct is moderately long and slender and opens into a large sac-like structure, the “fertilization sac” which attaches to the common oviduct together forming the vagina. The apex of the vagina is bordered ventrally by the rami (sensu Liebsherr and Will 1998) (Fig. 20) or the rami are lacking (Figs. 17–19). The gonocoxae are typical of hydroporines with a posterior triangular portion with long anterior “apodemes” (Figs. 15, 17, 19–20). The gonocoxae are reduced in some taxa (e.g., Figs. 17, 19) or are entirely absent (e.g., Fig. 18). Reduced gonocoxae may be a good synapomorphy for some taxa within the genus, and the distribution of this character should be eventually explored further. The goncoxosternites vary in shape (probably at the species level) but are relatively typical in general shape to other members of the Hydroporinae, i.e., laterally broad with a distinct, long anterior lobe. The distribution and nature of the setae on the goncoxosternites and the gonocoxae may provide good phylogenetic characters.
Discussion

Biström et al. (1997) presented a phylogenetic analysis of Hyphydrini and Pachydrini. In their analysis they proposed several characters which supported the monophyly of Desmopachria within Hyphydrini. Because inference of relationships within Desmopachria depends to a certain extent on character state distributions in the outgroup as well as evidence for the monophyly of the group, a brief discussion of their analysis is warranted. A reanalysis of their data set using NONA (Goloboff 1995) and the commands “hold 5000”, “hold/20”, “mult*20” and “max*” yielded 192 trees (length = 38, CI = 71, RI = 83). These are the same results they obtained except fewer trees were found, probably because NONA retains only trees supported by unambiguous evidence under all possible optimizations. When the commands “amb = ” and “max*” were employed in NONA, 576 trees were found which is closer to the 510 Hennig86 trees and the 624 PAUP 3.1.1 trees they found. The consensus tree of the most parsimonious trees obtained in my analysis is identical to theirs.

Use of the outgroups Laccornis des Gozis and Methles Sharp may present a potential problem in their analysis. Wolfe (1985) and others have suggested that Laccornini and Methlini are near the base of the Hydroporinae. Therefore, assessment of character states present in the other tribes of Hydroporinae and their inclusion in the analysis may alter the internal topology of Hyphydrini + Pachydrini. Although outgroups do not need to be the most closely related taxon (Nixon and Carpenter 1993), I believe that in this case inclusion of members of other tribes of Hydroporinae will significantly influence the internal topology of Hyphydrini + Pachydrini. The authors clearly recognize this and point out the fact that their analysis does not address relationships between the tribes of Hydroporinae. Nevertheless, the authors conclude that Hyphydrini as used in the historical sense (i.e., including Heterhydrus Fairmaire and Pachydrus Sharp) is polyphyletic despite the fact that their analysis did not adequately address this question nor support this conclusion. Indeed, the authors present two rather strong morphological characters supporting the monophyly of Hyphydrini + Pachydrini, reduction of the metacoxal lobes and reduction of the anterior metatarsal claw. Although they point out that a reduced anterior metatarsal claw is present in other dytiscids, it is not present in other Hydroborinae except in a few, isolated lineages and seems certainly to be an independently derived synapomorphy for Hyphydrini + Pachydrini. Although the conclusion that Hyphydrini in the historical sense is polyphyletic seems premature to me, a reanalysis of the genera is beyond the scope of this project.

Biström et al. (1997) present several characters supporting monophyly of Desmopachria, and this genus (3 terminals representing 17 species) is one of the only clades resolved in the consensus tree. Unambiguous synapomorphies of Desmopachria in their analysis include: 1) antennomeres 1–2 wider than following segments (apparently also present in some Microdytes Balfour-Browne (Biström et al. 1997) though not coded as such in their matrix), 2) antennomeres 5–10 short and slightly expanded in apical half (seemingly also present in several other taxa (Miller, unpubl. observation) and absent in some Desmopachria such as D. signatoides (Fig. 14)), 3) labial palpus with apical pair of sensilla widely separated, 4) maxillary palpus with one apical sensillum and 5) pronotum with posterolateral angles produced posteriorad. Two characters are homoplasious in the most parsimonious trees, but support monophyly of Desmopachria including: 1) metacoxae fused to visible abdominal
sternite 1 and 2) metatibia with apical transverse row of spines discontinuous medially. Based on this evidence (though certainly subject to change with improved sampling of outgroup taxa) monophyly of Desmopachria is a relatively strong hypothesis.

Several subgenera have been recognized in Desmopachria. The first is the subgenus Nectoserrula characterized by the presence of a serrate anterior metatibial spur. This character state is also present in some Hyphydrus, but optimizes as independently acquired in each of these taxa in the cladograms of Biström et al. (1997).

A bifurcate male prosternal process with a distinct pit between the lateral rami is characteristic of two groups, Pachiridis Young and Portmannia Young. This seems to be an extremely strong synapomorphy since the state does not appear in similar form anywhere else in the Dytiscidae. Young (1980) chose to recognize Pachiridis based on the presence of iridescent cuticle, similar to the state in Hintonella Young. This type of coloration seems like a weaker character to me than does the modified prosternal process. Therefore, I hypothesize monophyly of Pachiridis and Portmannia. The subgenus Hintonella is characterized by strongly protuberant clypeal margin that is scoop shaped and thin in males, but less strongly modified in females (Young 1980).

A sutural stria was used by Young (1980, 1990b) and Guignot (1950) to unite the heterogeneous assemblage of species in the subgenus Pachriostrix. Many of the species in this group are very dissimilar in other characters and I regard the sutural stria as a relatively weak character for inferring relationship. In particular, several species in other groups (such as Pachriodesma) have sutural striae which may leave Pachriostrix without a synapomorphy.

Pachriodesma was originally united based on the presence of impressed basal stria on the pronotum (Guignot 1949; Young 1980). Later, Young (1990b) transferred several species from the subgenus Pachriostrix to Pachriodesma including D. varians Wehcke which apparently lacks pronotal striae. Presence of pronotal striae may be a good synapomorphy for this group, but the lack of striae in D. varians would seem to disclude this species from the group. The presence of basal striae in many members of Bidessini could influence the optimization of this character in a cladistic analysis.

The last subgenus, Desmopachria s. str., consists of the species left over when other groups with apparently good synapomorphies are removed. The formal naming of only monophyletic groups is fundamental to modern Linnaean classification schemes (Hennig 1966). Ideally, formal names convey information about phylogenetic relationships. That is, when two species are placed in the same formally-named taxon, it can be assumed that the species are more closely related phylogenetically to each other than either is to a species in a different taxon. There are no good synapomorphies known for the subgenus Desmopachria s. str. However, it should also be pointed out that there is also no strong evidence the subgenus is not monophyletic, i.e., there are no species evidently more closely related to species in other subgenera than to other members of Desmopachria s. str. Nevertheless, without strong evidence for relationships within and between subgenera such as Pachriostrix and Desmopachria s. str., it seems to me undesirable to continue recognizing formal subgenera in this genus. Although recognition of formal groups that are not demonstrably monophyletic may be a convenience, especially in a group as large and diverse as Desmopachria, it ultimately undermines the classification as groups are continually recognized and elevated leaving behind increasing numbers of probable paraphyletic taxa. A similar situation exists in
Dytiscidae in the tribe Bidessini where considerable well-meaning taxonomic work has led to numerous groups that are probably not monophyletic (e.g., see Miller 1998; Miller 2000). In Bidessini, only a thorough cladistic analysis using a variety of character systems will likely lead to an understanding of relationships between the genera and an improved (i.e., more predictive) classification. To avoid the problems inherent to an taxonomic program of excessive splitting and elevation of taxa (such as in Bidessini), I strongly recommend a conservative approach to the classification of Desmopachria until such time as a thorough cladistic analysis, including as many species and character systems as possible, can lead to strong hypotheses of relationships.

To this end, rather than formal recognition of subgenera of Desmopachria, I have chosen to present a new classification that, instead, informally recognizes only species groups. As a result, numerous taxa are left ungrouped but informal names are still employed for ease of communication of information and as an aid for remembering groups of species. I suggest that this is a better system than recognition of ambiguous, possibly para- or polyphyletic taxa until a more detailed cladistic analysis can be executed and a classification erected based upon it. It also removes the necessity of the use of bulky trinomials when discussing single species and the inconvenient formal change in names when species are moved from one subgenus to another as has happened considerably and would certainly happen in the future as well.

Within the previously recognized Desmopachria s. str. there are several characters which appear to be synapomorphies. One of these is the presence of a preapical, articulable spur on the lateral lobes. Young (1980, 1981b) used this character to recognize his D. convexa-grana group. This group is also characterized by a median lobe that is deeply bifid or consists primarily of lateral rami. In addition, the D. nitida group is characterized by deeply bifid lateral lobes. Other species groups recognized by Young (1980) are less strongly supported by characters such as color or general shape of the median lobe, etc. Of these groups I recognize only his D. leechi-glabricula group (my D. glabricula group) since its members have genitalia that are superficially similar in being strongly robust.

**Key to the Species Groups of Desmopachria**

1. Anterior metatibial spine serrate ........................................ D. vicina group
1’. Anterior metatibial spine not serrate ........................................ 2

2. Pronotum with basal striae .................................................. D. dispersa group
2’. Pronotum without basal striae .................................................. 3

3. Prosternal process sexually dimorphic, male process apically strongly forked, area between rami forming a deep pit, female process not as in male ............................................................................. D. portmanni group
3’. Prosternal process not sexually dimorphic, not forked in either sex .... 4

4. Elytron with a distinct sutural stria ........................................ D. striola group
4’. Elytron without a distinct sutural stria ........................................ 5

5. Anterior clypeal margin sexually dimorphic, in males strongly modified, thin, translucent and strongly up-turned, anteriorly beaded in female, but not as strongly modified as in male ............................... D. ubangoides group
5’. Anterior clypeal margin not sexually dimorphic, anteriorly beaded in both sexes ................................................................. 6

6. Lateral lobes deeply bifid, apex divided into two long rami (e.g., Figs. 54–55) ................................................................. D. nitida group
6'. Lateral lobes not deeply bifid ........................................ 7
7. Lateral lobes with an anteapical, articulable process (e.g., Figs. 5, 7, 8, 10)
   ................................................................................. D. convexa group
7'. Lateral lobes without an anteapical, articulable process .......... 8
8. Median and lateral lobes very strongly robust and heavily sclerotized (e.g.,
   Figs. 11–13) ........................................................................ D. glabricula group
8'. Median and lateral lobes not strongly robust and sclerotized ........
   ............................................................................. ungrouped species

Revised Classification of Desmopachria

Desmopachria Babington, 1840
   syn. Nectoserrula Guignot, 1949
   syn. Pachriodesma Guignot, 1949
   syn. Pachriostrix Guignot, 1950
   syn. Pachridis Young, 1980
   syn. Portmannia Young, 1980
   syn. Hintonia Young, 1980 (not Reichart, 1973, replaced by Hintonella Young (1981a))
   syn. Hintonella Young, 1981
D. convexa group
   =D. convexa-grana group sensu Young (1980, 1981b). A key to most species is provided by Young (1981b). Young (1990a) suggested that D. pulvis Guignot is similar to D. signata Zimmermann based on the shape of the male genitalia and other characters, therefore I have placed it within this group. Drawings are reproduced from Young (1981b, 1990a).
   D. aspera Young, 1981 (Fig. 21)
   D. cenchramis Young, 1981 (Fig. 22)
   D. challeti Miller, new species (Figs. 5–7, 17)
   D. circularis Sharp, 1882 (Fig. 23)
   D. convexa (Aubé, 1838) (Fig. 24)
   D. deflocata Young, 1981 (Fig. 25)
   D. glabella Young, 1981 (Fig. 26)
   D. grana (LeConte, 1855) (Fig. 27)
   D. isthmia Young, 1981 (Fig. 28)
   D. laesslei Young, 1981 (Fig. 29)
   D. lewisi Young, 1981 (Fig. 30)
   D. majuscula Young, 1990 (Fig. 31)
   D. pulvis Guignot, 1958
   D. signata Zimmermann, 1921 (Fig. 32)
   D. signatoides Miller, new species (Figs. 8–10, 14)
   D. tarda Spangler, 1973 (Fig. 33)

D. dispersa group
   =Desmopachria (Pachriodesma) Guignot (1949) and sensu Young (1980). Desmopachria varians Wehnecke is excluded from the group since it lacks basal striae even though it was included in D. (Pachriodesma) by Young (1990b). Male genitalia have not been figured except for D. latissima (LeConte), but color patterns are useful for separating the North American species. Drawings are reproduced from Young (1980).
   D. brevicollis Régimbart, 1903

*D. dispersa* (Crotch, 1873) (Fig. 34)
*D. latissima* (LeConte, 1851) (Figs. 35, 39)
*D. mexicana* Sharp, 1882 (Fig. 36)
*D. mutchleri* Blatchley, 1919 (Fig. 37)
*D. sanfilippoi* Guignot, 1957
*D. seminola* Young, 1951 (Fig. 38)
*D. suturalis* Sharp, 1884
*D. glabricula* group
*D. aphromoscela* Miller, 1999 (Figs. 40–42)
*D. flavida* Young, 1981 (Fig. 43)
*D. glabricula* Sharp, 1882 (Fig. 44)
*D. leechi* Young, 1981 (Figs. 45–46)
*D. strigata* Young, 1981 (Fig. 47)
*D. volatidisca* Miller, new species (Figs. 11–13, 18)
*D. volvata* Young, 1981 (Figs. 48–49)
*D. zimmermani* Young, 1981 (Fig. 50)
D. nitida group

= D. nitida group sensu Young (1980, 1986). I have assigned the species D. phacoides Guignot, D. subnotata Zimmermann and D. subtilis Sharp to this group based on the illustration of the genitalia of D. subnotata (Figs. 68–69) and Young’s (1980) implication that the other two species are similar. Drawings are reproduced from Miller (1999) and Young (1980, 1986, 1989).

D. darlingtoni Young, 1989 (Fig. 51)
D. draco Miller, 1999 (Figs. 52–55)
D. granoides Young, 1986 (Figs. 56–57)
D. liosomata Young, 1986 (Figs. 58–59)
D. margarita Young, 1990 (new name for D. glabricula Sharp, 1887:752 nec Sharp, 1887:18) (Fig. 60)
D. nitida Babington, 1841 (Figs. 61–63)
D. nitidoides Young, 1990 (Fig. 64)
D. phacoides Guignot, 1950
D. psarammo Miller, 1999 (Figs. 65–67)
D. rhea Miller, 1999 (Figs. 68–72)
D. subnotata Zimmermann, 1921 (Figs. 73–74)
D. subtilis Sharp, 1882
D. zelota Young, 1990 (Figs. 75–76)

D. portmanni group


D. aldessa Young, 1980 (Figs. 77–79)
D. aurea Young, 1980 (Figs. 80–82)
D. iridis Young, 1980 (Figs. 83–85)
D. novacula Young, 1980 (Figs. 86–88)
D. basicollis Guignot, 1949
D. bryanstoni Clark, 1862 (Fig. 89)
  syn. D. polita Sharp, 1882
D. decorosa Young, 1995 (Fig. 90)
D. dispar Sharp, 1882 (Fig. 91)
D. goias Young, 1995 (Fig. 92)
D. laevis Sharp, 1882 (Fig. 93)
D. mutata Sharp, 1882 (new name for D. bryanstoni Sharp, 1882 nec Clark, 1862) (Fig. 94)
D. niger Zimmermann, 1923
D. nitidissima Zimmermann, 1928
D. pittieri Young, 1995 (Fig. 95)
D. portmanni Clark, 1862 (Fig. 96)
D. sobrina Young, 1995 (Fig. 97)
D. specula Sharp, 1887 (Fig. 98)
D. variegata Sharp, 1882 (Fig. 99)
D. youngi Miller, 1999 (Figs. 100–102)
D. zetha Miller, 1999 (Fig. 103)

D. striola group

Figs. 34–50. *Desmopachria dispersa* and *D. glabricula* groups, all male genitalia, median and lateral lobes, unless otherwise indicated. 34–38) *D. dispersa* group, habit; 34) *D. dispersa*; 35) *D. latissima*; 36) *D. mexicana*; 37) *D. matchleri*; 38) *D. seminola*; 39) *D. latissima*; 40–42) *D. aphronoscela*; 40) median and lateral lobes, dorsal aspect; 41) same, right lateral lobe, right lateral aspect; 42) same, male mesotibia, a = left mesotibia, posterior aspect, b = left mesotibia, anterior aspect; 43) *D. flavida*; 44) *D. glabricula*; 45–46) *D. leechi*, male genitalia; 45) apex of lateral lobe, lateral aspect; 46) same, median and lateral lobes; 47) *D. strigata*; 48–49) *D. volvata*; 48) median and lateral lobes, dorsal aspect; 49) same, median lobe and left lateral lobe, ventral aspect; 50) *D. zimmermani*.

*D. amyae* Miller, new species (Figs. 1–4, 15–16)
*D. chei* Miller, 1999 (Figs. 104–105)
*D. ferrugata* Réginhart, 1895
*D. fossulata* Zimmermann, 1928 (Fig. 106)
*D. grouselli* Réginhart, 1895 (Fig. 107)
*D. rugiosa* Young, 1990 (Figs. 108–109)
*D. striola* Sharp, 1887 (Figs. 110–111)
*D. ubangoides* group
= *Desmopachria* (Hintonella) Young (1981a). Drawings are reproduced from Young (1980).
*D. minuta* Young, 1980 (Figs. 112–113)
*D. sioli* Young, 1980 (Fig. 114)
Figs. 51–76. All male genitalia, median and lateral lobes, unless otherwise indicated.  
51) D. darlingoni; 52–55) D. draco; 52) median lobe, dorsal aspect; 53) median lobe, right lateral aspect; 54) Right lateral lobe, dorsal aspect; 55) right lateral lobe, right lateral aspect; 56–57) D. granoides; 56) median and lateral lobes; 57) same, lateral lobe, lateral aspect; 58–59) D. liosomata; 58) median and lateral lobes; 59) same, lateral lobe, lateral aspect; 60) D. margarita; 61–63) D. nitida; 61) median and lateral lobes; 62) same, apex of median lobe, lateral aspect; 63) same, lateral lobe, lateral aspect; 64) D. nitidoides; 65–67) D. psarammo; 65) median lobe and right lateral lobe, dorsal aspect; 66) same, median lobe and lateral lobe, right lateral aspect; 67) same, left elytron; 68–72) D. rhea; 68) median lobe and right lateral lobe, dorsal aspect; 69) same, median lobe, ventral aspect; 70) same, median lobe, right lateral aspect; 71) same, right lateral lobe, right lateral aspect; 72) same, right lateral lobe, ventral aspect; 73–74) D. subnotata; 73) median and lateral lobes; 74) same, lateral lobe, lateral aspect; 75–76) D. zelota; 75) median and lateral lobes; 76) same, median and lateral lobes, lateral aspect.

D. ubangoides Young, 1980 (Fig. 115)
D. vicina group
    =Desmopachria (Nectoserrula) Guignot (1949) and sensu Young (1980).
Drawings are reproduced from Young (1980).
D. concolor Sharp, 1882
Figs. 77–103. Desmopachria portmanni group, male genitalia, all median and lateral lobes unless otherwise indicated. 77–79) D. aldessa; 77) median and lateral lobes; 78) same, lateral lobe, lateral aspect; 79) same, median lobe, lateral aspect; 80–82) D. aurea; 80) median and lateral lobes; 81) same, lateral lobe, lateral aspect; 82) same, median lobe, lateral aspect; 83–85) D. iridis; 83) median and lateral lobes; 84) lateral lobe, lateral aspect; 85) lateral lobe, lateral aspect; 86–88) D. novacula; 86) median and lateral lobes; 87) lateral lobe, lateral aspect; 88) median lobe, lateral aspect; 89) D. bryanstoni; 90) D. decorosa; 91) D. dispar; 92) D. goias; 93) D. laevis; 94) D. mutata; 95) D. pittieri; 96) D. portmanni; 97) D. sobrina; 98) D. specula; 99) D. variegata; 100–102) D. youngi; 100) median and right lateral lobe, dorsal aspect; 101) same, right lateral lobe, right lateral aspect; 102) same, median lobe, right lateral aspect; 103) D. zetha.

D. mendozana Steinheil, 1869 (Figs. 116–117)
D. punctatissima Zimmermann, 1923
D. vicina Sharp, 1882
ungrouped species
D. attenuata Régaumbart, 1895 (Figs. 118–120)
D. balfourbrownet Young, 1990 (Figs. 121–123)
Figs. 104–125. Desmopachria striola, D. ubangooides and D. vicina groups and ungrouped species, male genitalia, all median and lateral lobes unless otherwise indicated. 104–105 D. chei; 104) median and lateral lobes, dorsal aspect; 105) right lateral lobe, right lateral aspect; 106) D. fossulata; 107) D. grouveli; 108–109) D. ruginosa; 108) median and lateral lobes; 109) same, median and lateral lobes, lateral aspect; 110–111) D. striola; 110) median and lateral lobes; 111) same, median and lateral lobes, lateral aspect; 112–113) D. minuta; 112) median and lateral lobes; 113) same, left elytron; 114) D. sioli; 115) D. ubangooides; 116–117) D. mendozana; 116) median and lateral lobes; 117) lateral lobe, lateral aspect; 118–120) D. attenuata; 118) median and lateral lobes; 119) same, lateral lobe, lateral aspect; 120) same, median lobe lateral aspect; 121–123) D. balfourbrownei; 121) median and lateral lobes; 122) same, median lobe, lateral aspect; 123) same, left elytron; 124–125) D. bifasciata; 124) median and lateral lobes; 125) same, habitus.

D. bifasciata Zimmermann, 1921 (Figs. 124–125)
D. bolivari Miller, 1999 (Figs. 126–128)
D. geijskesi Young, 1990 (Fig. 129)
D. hylobates Young, 1993 (Figs. 130–131)
D. ovalis Sharp, 1882 (Fig. 132)
D. paradoxa Zimmermann, 1923
D. striga Young, 1990 (Figs. 133–134)
Figs. 126–140. Ungrouped Desmopachria species. 126–128) *D. bolivari*; 126) median and lateral lobes, dorsal aspect; 127) same, right lateral lobe, right lateral aspect; 128) same, median lobe, right lateral aspect; 129) *D. geijkeskesi*; 130–131) *D. hylobates*; 130) median and lateral lobes; 131) same, lateral lobe, lateral aspect; 132) *D. ovalis*; 133–134) *D. striga*; 133) median and lateral lobes; 134) same, lateral lobe, lateral aspect; 135) *D. subfasciata*; 136–140) *D. taniae*; 136) right lateral lobe, dorsal aspect; 137) same, median lobe, dorsal aspect; 138) same, right lateral lobe, right lateral aspect; 139) same, median lobe, right lateral aspect; 140) same, left elytron.

*D. subfasciata* Young, 1990 (Fig. 135)

*D. taniae* Miller, 1999 (Figs. 136–140)

*D. varians* Wehncke, 1877

*D. variolosa* Régimbart, 1895

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