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A new classification of the tribe Hygrotini Portevin, 1929 (Coleoptera: Dytiscidae: Hydroporinae)

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Abstract

The tribe Hygrotini Portevin, 1929 is currently composed of four genera, *Heroceras* Guignot, 1950, *Herophydrus* Sharp, 1880, *Hygrotus* Stephens, 1828 (with two subgenera, *Coelambus* Thomson, 1860, and *Hygrotus* s. str.), and *Hyphoporus* Sharp, 1880. A recent molecular phylogeny of the tribe with ca. 45% of the 137 described species of Hygrotini, including the type species of all genus-level taxa, revealed extended para- or polyphyly of the current genera and subgenera (Villastrigo *et al*., Zoologica Scripta, in press), for which reason a new classification of the tribe Hygrotini is proposed. Within Hygrotini only two genera are recognised: *Clemnius* **n. gen**. (with two subgenera: *Clemnius* s. str. with type species *Hyphydrus decoratus* Gyllenhal, 1810, and *Cyclopius* **n. subgen.** with type species *Hydroporus acaroides* LeConte, 1855) and *Hygrotus* (with four subgenera: *Coelambus*, *Hygrotus* s. str., *Hyphoporus* **n. stat.** and *Leptolambus* **n. subgen**. with type species *Dytiscus impressopunctatus* Schaller, 1783). Two genera are synonymised under *Hygrotus* s. str., *Herophydrus* **n. syn.** and *Heroceras* **n. syn.** The following 67 new combinations, for species thus far treated under the genera *Heroceras*, *Herophydrus*, *Hygrotus* and *Hyphoporus*, result from the new classification: *Clemnius* (s. str.) *berneri* (Young & Wolfe, 1984) **n. comb.**, *Clemnius* (s. str.) *decoratus* (Gyllenhal, 1810) **n. comb.**, *Clemnius* (s. str.) *hydropicus* (LeConte, 1852) **n. comb.**, *Clemnius* (s. str.) *laccophilinus* (LeConte, 1878) **n. comb.**, *Clemnius* (s. str.) *sylvanus* (Fall, 1917) **n. comb.**, *Clemnius* (*Cyclopius*) *acaroides* (LeConte, 1855) **n. comb.**, *Clemnius* (*Cyclopius*) *farctus* (LeConte, 1855) **n. comb.**, *Clemnius* (*Cyclopius*) *marginipennis* (Blatchley, 1912) **n. comb.**, *Hygrotus* (s. str.) *assimilis* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *bilardoi* (Biström & Nilsson, 2002) **n. comb.**, *H.* (s. str.) *capensis* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *confusus* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *descarpentriesi* (Peschet, 1923) **n. comb.**, *H.* (s. str.) *discrepatus* (Guignot, 1954) **n. comb.**, *H.* (s. str.) *endroedyi* (Biström & Nilsson, 2002) **n. comb.**, *H.* (s. str.) *gigantoides* (Biström & Nilsson, 2002) **n. comb.**, *H.* (s. str.) *gigas* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *goldschmidti* (Pederzani & Rocchi, 2009) **n. comb.**, *H.* (s. str.) *gschwendtneri* (Omer-Cooper, 1957) **n. comb.**, *H.* (s. str.) *hyphoporoides* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *ignoratus* (Gschwendtner, 1933) **n. comb.**, *H.* (s. str.) *inquinatus* (Boheman, 1848) **n. comb.**, *H.* (s. str.) *janssensi* (Guignot, 1952) **n. comb.**, *H.* (s. str.) *kalaharii* (Gschwendtner, 1935) **n. comb.**, *H.* (s. str.) *morandi* (Guignot, 1952) **n. comb.**, *H.* (s. str.) *muticus* (Sharp, 1882) **n. comb.**, *H.* (s. str.) *natator* (Biström & Nilsson, 2002) **n. comb.**, *H.* (s. str.) *nigrescens* (Biström & Nilsson, 2002) **n. comb.**, *H.* (s. str.) *nodieri* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *obscurus* (Sharp, 1882) **n. comb.**, *H.* (s. str.) *obsoletus* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *ovalis* (Gschwendtner, 1932) **n. comb.**, *H.* (s. str.) *pallidus* (Omer-Cooper, 1931) **n. comb.**, *H.* (s. str.) *pauliani* (Guignot, 1950) **n. comb.**, *H.* (s. str.) *quadrilineatus* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *reticulatus* (Pederzani & Rocchi, 2009) **n. comb.**, *H.* (s. str.) *ritsemae* (Régimbart, 1889) **n. comb.**, *H.* (s. str.) *rohani* (Peschet, 1924) **n. comb.**, *H.* (s. str.) *rufus* (Clark, 1863) **n. comb.**, *H.* (s. str.) *sjostedti* (Régimbart, 1908) **n. comb.**, *H.* (s. str.) *spadiceus* (Sharp, 1882) **n. comb.**, *H.* (s. str.) *sudanensis* (Guignot, 1952) **n. comb.**, *H.* (s. str.) *travniceki* (Šťastný, 2012) **n. comb.**, *H.* (s. str.) *tribolus* (Guignot, 1953) **n. comb.**, *H.* (s. str.) *variabilis secundus* (Régimbart, 1906) **n. comb.**, *H.* (s. str.) *variabilis variabilis* (Guignot, 1954) **n. comb.**, *H.* (s. str.) *verticalis* (Sharp, 1882) **n. comb.**, *H.* (s. str.) *vittatus* (Régimbart, 1895) **n. comb.**, *H.* (s. str.) *wewalkai* (Biström & Nilsson, 2002) **n. comb.**, *Hygrotus* (*Hyphoporus*) *anitae* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *aper* (Sharp, 1882) **n. comb.**, *H.* (*Hyphoporus*) *bengalensis* (Severin, 1890) **n. comb.**, *H.* (*Hyphoporus*) *bertrandi* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *caliginosus* (Régimbart, 1899) **n. comb.**, *H.* (*Hyphoporus*) *dehraduni* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *elevatus* (Sharp, 1882) **n. comb.**, *H.* (*Hyphoporus*) *geetae* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *josephi* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *kempi* (Gschwendtner, 1936) **n. comb.**, *H.* (*Hyphoporus*) *montanus* (Régim-

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bart, 1899) **n. comb.**, *H.* (*Hyphoporus*) *nilghiricus* (Régimbart, 1903) **n. comb.**, *H.* (*Hyphoporus*) *oudomxai* (Brancucci & Biström, 2013) **n. comb.**, *H.* (*Hyphoporus*) *pacistanus* (Guignot, 1959) **n. comb.**, *H.* (*Hyphoporus*) *pugnator* (Sharp, 1890) **n. comb.**, *H.* (*Hyphoporus*) *severini* (Régimbart, 1892) **n. comb.**, *H.* (*Hyphoporus*) *subaequalis* (Vazirani, 1969) **n. comb.**, *H.* (*Hyphoporus*) *tonkinensis* (Régimbart, 1899) **n. comb**.

Key words: Coleoptera, Dytiscidae, Hydroporinae, Hygrotini, phylogeny, new classification, new genus, new subgenera, new combinations, new synonyms

Introduction

The diving beetle tribe Hygrotini (Dytiscidae: Hydroporinae) is a relatively small and homogeneous lineage, with 137 species currently included in four genera: *Heroceras* Guignot, 1950, *Herophydrus* Sharp, 1880, *Hyphoporus* Sharp, 1880, and *Hygrotus* Stephens, 1828, the latter with two subgenera, *Hygrotus* s. str. and *Coelambus* Thomson, 1860 (Nilsson & Hájek 2017a). They have a predominantly Holarctic and Ethiopian distribution, with some species reaching the Oriental and the north of the Neotropical regions (Nilsson & Hájek 2017a).

The taxonomic history of Hygrotini has experienced several modifications since the original description of the tribe by Portevin (1929). Previous to this author, Sharp (1882: 389) listed *Coelambus* (in which he included species currently in *Hygrotus* and *Herophydrus*) as well as *Herophydrus* and *Hyphoporus* (both erected two years earlier) as the three first genera in his "Group Hydroporini". Portevin (1929: 180) excluded from Hydroporini the genera *Oxynoptilus* Schaum, 1867 (junior ojective synonym of *Hydrovatus* Motschulsky, 1853), *Hyphydrus* Illiger, 1802, and *Hygrotus*, and erected for these three genera the tribe Hygrotini, based on the common presence of an oblique epipleural carina near the elytral shoulders which separates the smaller anterior part (the genicular area or fossa, which receives the front- and midleg knees when the legs are folded; cf. Sharp 1882: 242) from the longer posterior part of the elytral epipleura. However, most authors continued to include *Hygrotus* and allied genera within the wider tribe Hydroporini as defined by Sharp (1882). Nilsson & Holmen (1995: 30) reinstated the tribe Hygrotini, excluding the genera *Hyphydrus* and *Hydrovatus* (which were already in their own tribes Hyphydrini and Hydrovatini respectively), but including the genus *Pseudhydrovatus* Peschet, 1924, which subsequently was shown to be a junior synonym of *Hydrovatus* (see Biström 2002).

The generic concepts within Hygrotini also suffered multiple changes. Thomson (1860) realised that *Hygrotus* sensu Stephens (1828) comprised two different morphological groups according to the aspect of the anterior margin of clypeus, establishing the genus *Coelambus* for the species without clypeal rim. The status of both *Coelambus* and *Hygrotus* has generated controversy among different authors, as the character of the clypeal rim in fact shows considerable variation (see Falkenström 1933, Balfour-Browne 1934, Anderson 1971, or Biström & Nilsson 2002, and the Appendix for a detailed discussion). Sharp (1882) considered *Coelambus* as a genus divided into different groups according to the morphology of the anterior part of the head and the clypeus, with *Dytiscus inaequalis* Fabricius, 1777 (the type species of the genus *Hygrotus*) included in his Group I. Other authors followed his criterion (e.g. Fall 1919), but Balfour-Browne (1940) and Hatch (1953) (among others) considered again *Coelambus* as a subgenus of *Hygrotus*, a treatment that has prevailed since then (although Miller & Bergsten 2016 recently re-established *Coelambus* as a valid genus, but without detailed discussion).

As for the other genera currently included in Hygrotini, Sharp (1880: cxlviii) erected within Hydroporini the new genus *Herophydrus* for what was known as *Hydroporus hyphydroides* Perris, 1864 (= *Hyphydrus guineensis* Aubé, 1838), plus five undescribed species from Africa and Madagascar, and the new genus *Hyphoporus* for *Hydroporus solieri* Aubé, 1838, and two other undescribed species. Two years later, Sharp (1882: 997; nec Branden 1885: 39) synonymised *H. hyphydroides* with *H. guineensis* and described the species mentioned in Sharp (1880) as new, five in *Herophydrus* and two in *Hyphoporus*. It is notable that in Sharp (1882) the current *Herophydrus musicus* (Klug, 1834) was maintained in the genus *Coelambus*.

The identity of the genera of Hygrotini has been problematic ever since. Guignot (1950) was the first author who characterised *Hyphoporus* and *Herophydrus* by using as main character the morphology of the male genitalia, asymmetric in the first and symmetric in the second. Finally, *Heroceras* was erected by Guignot (1950) for a species from Madagascar (*Herophydrus descarpentriesi* Peschet, 1923) with some peculiar characters (such as e.g. dilated antennae, see below).

Until recently the internal phylogeny of *Hygrotini* has only been addressed as part of wider studies on the

phylogeny of Dytiscidae, or the revision of particular genera. Remarkably, all published studies failed to recover the respective monophyly of *Hygrotus* and *Herophydrus*, either using molecular (Ribera *et al.* 2002, 2008; Abellán *et al.* 2013; Miller & Bergsten 2014) or morphological data, both of larvae (Alarie & Michat 2007) and adults (Miller 2001; Biström & Nilsson 2002). The phylogenetic position of the genera *Hyphoporus* and *Heroceras* has only been addressed using morphological data by Biström & Nilsson (2002), who found *Hyphoporus* as sister to the studied species of *Coelambus*, and *Heroceras* as sister to the species of *Herophydrus* plus *Hygrotus*.

In a previous work by the same authors (Villastrigo *et al*., in press) we reconstructed the evolution of the tolerance to salinity within tribe Hygrotini, which includes some of the few diving beetles able to live at salt concentrations more than double that of seawater (e.g. *Hygrotus salinarius* (Wallis, 1924) or *H. pallidulus* (Aubé, 1850); Timms & Hammer 1988, Picazo *et al*. 2010). With that purpose, a molecular phylogeny of the tribe was estimated, including ca. 45% of the described species. Results revealed that two of the four currently recognised genera of Hygrotini and one subgenus were para- or polyphyletic (*Hygrotus*, *Herophydrus* and subgenus *Coelambus*), and the monotypic *Heroceras* was deeply nested within a clade of Madagascan *Herophydrus*. The need of a new classification of Hygrotini in order to reconcile the taxonomic ordination of the tribe with its phylogeny was clear, but it was considered more appropriate to present the corresponding taxonomic changes in a separate work.

Material and methods

Phylogenetic data. We used the phylogeny of Hygrotini obtained in Villastrigo *et al.* (in press), which included sequence data from 99 specimens of 61 species representing all four currently recognised genera of Hygrotini (Table 1). Most importantly, the phylogeny included the type species of all nine genus-group names within Hygrotini (Nilsson & Hájek 2017a). Outgroups included a selection of species of Hydroporini, and trees were rooted on *Laccornis* Gozis, 1914, considered to be outside Hydroporini and Hygrotini and in a basal position within Hydroporinae (Ribera *et al.* 2008; Miller & Bergsten 2014).

For a detailed explanation of the methods used to obtain the molecular data and the phylogeny see Villastrigo *et al.* (in press). In summary, the phylogeny was built using fragments of seven genes in six sequencing reactions, three mitochondrial: (1) 5' end of cytochrome c oxidase subunit 1 (COI-5, the "barcode" fragment, Hebert *et al.* 2003), (2) 3' end of cytochrome c oxidase subunit 1 (COI-3), (3) 5' end of 16S RNA plus the Leucine tRNA plus 5' end of NADH dehydrogenase subunit I (16S); and three nuclear: (4) an internal fragment of the large ribosomal unit 28S RNA (28S), (5) an internal fragment of the small ribosomal unit, 18S RNA (18S) and (6) an internal fragment of Histone 3 (H3). Vouchers and DNA samples of all specimens used in the phylogeny are kept in the collections of the Institute of Evolutionary Biology (IBE, Barcelona) and Museo Nacional de Ciencias Naturales (MNCN, Madrid).

To reconstruct the phylogeny, sequences were aligned using the online version of MAFFT 7 with the G-INS-I algorithm (Katoh *et al.* 2009) and a fast Maximum Likelihood (ML) heuristic algorithm in RAxML-HPC2 (Stamatakis 2006) in the CIPRES Science Gateway (Miller *et al.* 2010), using a partition by genes with a GTR+G evolutionary model independently estimated for each partition and assessing node support with 100 pseudoreplicas with a rapid bootstrapping algorithm (Stamatakis *et al.* 2008).

Morphological data. Specimens were studied with an Olympus SZX16 stereomicroscope. For the figures, stacks of micrographs were made with a Canon EOS 650D camera attached to the stereomicroscope. These stacks were subsequently treated with the image stacking software Helicon Focus Pro version 6.4.1. For the SEM-micrographs, specimens were placed on stubs and coated with gold (Sputter Coater, Quorum Technologies Ltd., Ashford, England). Micrographs were taken with an ESEM XL30 (Philips, Amsterdam, The Netherlands) and Scandium FIVE software (Olympus, Münster, Germany) in the Phyletisches Museum (Jena, Germany). Adobe Photoshop CS5 software was used to retouch micrographs and ink drawings. Most ink drawings are reproduced from Fery (2003) with the permission of M.A. Jäch (Vienna, Austria); this is not mentioned in the legends of the figures.

To estimate the likely phylogenetic relationships of the species for which no molecular data could be obtained, and to complete the taxonomic rearrangement of the tribe Hygrotini (see below), we studied all described species of the subgenera *Hygrotus* and *Coelambus* with the only exceptions of *H.* (*Coelambus*) *artus* (Fall, 1919), known

only from the holotype and considered to be possibly extinct (see Anderson 1983), and *H.* (*Coelambus*) *femoratus* (Fall, 1901), which is likely a junior synonym of *H.* (*Coelambus*) *nubilus* (LeConte, 1855) (see Anderson 1983). Additionally, we have studied a selection of species of *Herophydrus* and *Hyphoporus* (see Table 1 for the studied material).

Species for which no molecular data were available were considered to be closely related to those showing a high morphological similarity, based both on external characters and on the female and male genitalia. For species without obvious close relatives we identified diagnostic characters or character combinations for the main clades in the phylogeny, and placed these species according to the presence or absence of these characters. We used Mesquite v3.20 (Maddison & Maddison 2017) to manually place all species in their estimated position in the phylogenetic tree (used as a backbone tree), and collapsed uncertain nodes to create polytomies.

Throughout the text of the present work, we follow the classification and nomenclature of Nilsson & Hájek (2017a, b) until we introduce our new classification. The following abbreviations are used in the text: TL (total length) and MW (maximum width); MNHN is used for "Muséum National d'Histoire Naturelle, Paris, France" and FSCA for "Florida State Collection of Arthropods, Gainesville, Florida, USA".

A new classification of the tribe Hygrotini

According to the phylogenetic results of Villastrigo *et al*. (in press) the monophyly of Hygrotini is recovered with strong support, as well as the division of Hygrotini into two clades (see Fig. 1, in which the former generic and subgeneric names are still used): (A) three Nearctic and one Palaearctic species of subgenera *Hygrotus* and *Coelambus* and (B) the remaining species of the tribe. The latter was in turn divided into four further clades: (B1) a group of Palaearctic species of *Coelambus* including *Hygrotus* (*Coelambus*) *confluens* (Fabricius, 1787) (the type species of *Coelambus*), (B2) the two sampled species of *Hyphoporus* (including its type species, *H. solieri*), (B3) a large group of species including *Heroceras*, all sampled *Herophydrus* (including its type species *H. guineensis*) and most species of *Hygrotus* s. str. (including its type species *H. inaequalis*) and (B4) the remaining species of *Coelambus*, in turn divided into two sister clades, one with mostly Palaearctic species and a second with mostly Nearctic species. The internal phylogeny of the main clades was in general in good agreement with the recognised species groups among *Hygrotus* and *Coelambus* based on morphology (see e.g. Anderson 1971, 1976, 1983; Fery 1992, 1995, 2003).

Given the para- or polyphyly of the genera *Hygrotus* and *Herophydrus* and of the subgenus *Coelambus* in their current concepts, we provide here a new classification of the tribe with the aim to avoid para- or polyphyletic genera and subgenera. This section includes brief descriptions of the principal diagnostic characters of the newly classified taxa, which were delimited according to the main clades of the phylogeny (see Table 1 for a complete checklist of the species of the tribe, and Fig. 2 for a dendrogram representing graphically the new classification).

Tribe Hygrotini Portevin, 1929: 180, as tribe of subfamily Hydroporinae.

Type genus: *Hygrotus* Stephens, 1828: 38.

Diagnosis. Within Hydroporinae, species of Hygrotini are usually characterised by the following combination of characters:

- metepisternum (metepiventrite in Miller & Bergsten 2016: 139) reaching mesocoxal cavities, not separated by mesepimeron (in contrast to members of Vatellini);
- apices of elytra and last abdominal ventrite not acuminate (in contrast to members of Methlini);
- prosternal process elongate with apex narrowly pointed or rounded (in contrast to members of Hydrovatini);
- dorsal (anterior) margin of metafemur separated from metacoxal lobe by metatrochanter (in contrast to members of Laccornellini and Laccornini);
- humeral portion of epipleuron with oblique carina delimiting genicular fossa (character shared with members of Hydrovatini, Hyphydrini and genus *Rhithrodytes* Bameul, 1989 in Hydroporini; cf. Fery 2013, 2016; see Fig. 53 for *Rhithrodytes agnus* Foster, 1992, and Figs 49–52 for some *Hygrotus* species).

- metatarsal claws equal in length, with exception of members of *C. saginatus*-group (see Fery 1992, 1995, 2003) and in contrast to members of Hyphydrini and Pachydrini (see e.g. Pederzani 1995; Miller & Bergsten 2016).

None of these characters is, however, an unambiguous synapomorphy of the group. We introduce here a potentially unambiguous synapomorphy of tribe Hygrotini, recognised by one of us (H.F.). In many members of Hydroporinae the antennal cavities in the fronto-lateral part of the head are rather deep and more or less conical (much flatter e.g. in Hyphydrini), allowing the movement of the first antennomere (the scape). These cavities are delimited dorsally by the anterior border of the clypeus ("b" in Figs 3–6). Inside each cavity there is a capsule in which the base of the scape (the condyle) is articulated. This capsule is delimited by a distinct more or less circular carina ("a" in Figs 3–6). In all studied species of Hygrotini there is an additional–more or less semicircular–carina ("c" in Figs 4–6) which is closer to the border of the clypeus and surrounds in part the other carina. In the species of Hydroporini this additional carina is not present (see Fig. 3 for *Hydroporus dorsalis* (Fabricius, 1787) or fig. 33 in Fery & Bouzid 2016 for *Tassilodytes parisii* (Gridelli, 1939)). In a few species of Hygrotini the second carina is difficult to observe or is very narrow (as in e.g. *Heroceras descarpentriesi* and *Hygrotus* (*Coelambus*) *salinarius*), but is nevertheless clearly perceptible when the specimens are properly illuminated and orientated. However, in most specimens studied of *Hygrotus* (*Coelambus*) *masculinus* (Crotch, 1874), the second carina is reduced to a short piece near the mandible.

According to the phylogeny reconstructed in Villastrigo *et al.* (in press) the tribe Hygrotini is divided into two well supported monophyletic lineages, which are considered here with generic rank. Each of these two lineages is in turn divided into generally well supported clades, which are treated as subgenera. In some cases these clades have lower support in the molecular phylogeny, and are also not well defined morphologically (see below and Appendix for a discussion on the clypeal bead, the main character used so far to differentiate genera and subgenera within Hygrotini), so we opted for a subgeneric rather than a generic rank.

Due to the new classification 67 species are for the first time included in the genus *Clemnius* **n. gen**. or in *Hygrotus*, thus their names becoming new combinations. We have listed all these species in Table 1 marked with "**n. comb.**" These changes have also generated some homonymies which will be resolved in a separate work (H. Fery, manuscript in preparation).

The genera and subgenera are treated below in the same order as in Fig. 2, starting from the lower part of the figure.

Genus *Clemnius* n. gen.

Type species: *Hyphydrus decoratus* Gyllenhal, 1810: XVI, by present designation.

The new genus *Clemnius* **n. gen**. includes eight described species distributed in the Nearctic (including the north of Mexico, sometimes treated as Neotropical) and in the Palaearctic zoogeographical region (Fig. 2 and Table 1).

Diagnosis. In the new classification *Clemnius* **n. gen**. is one of two genera of the tribe Hygrotini. All species of this and the second genus *Hygrotus* have two carinae in each antennal cavity (see Figs 4–6), a unique character among the entire subfamily Hydroporinae. The new genus—which corresponds to clade A in Fig. 1—is a heterogeneous assembly of relatively small species with different morphological characters. It is subdivided into two sister-clades each treated as a subgenus: *Cyclopius* **n. subgen.** and *Clemnius* s. str. **n. subgen.** (see Fig. 2).

Subgenus *Cyclopius* n. subgen.

Type species: *Hydroporus acaroides* LeConte, 1855: 294, by present designation.

The subgenus *Cyclopius* **n. subgen.** contains three species of the former subgenus *Hygrotus* (see Fig. 2 and Table 1).

TABLE 1. Checklist of all 137 species of Hygrotini with original, new and former (Nilsson & Hájek 2017a) generic and subgeneric names; last three columns indicating new combinations, distribution and methods applied to material studied. See Villastrigo *et al*. (in press) for details on the specimens used in the molecular phylogeny and accession numbers of the sequences.

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
1	*acaroides*	(LeConte, 1855)	*Hydroporus*	*Clemnius*	*Cyclopius*	*Hygrotus*	*Hygrotus*	n. comb.	NA	morphological & molecular
2	*aequalis*	Falkenström, 1932	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	PL	morphological
3	*ahmeti*	Hájek, Fery & Erman, 2005	*Hygrotus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
4	*anitae*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	PL	only literature
5	*aper*	(Sharp, 1882)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR, PL	only literature
6	*armeniacus*	(Zaitzev, 1927)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
7	*artus*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	only literature
8	*assimilis*	((Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
9	*bengalensis*	(Severin, 1890)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	morphological
10	*berneri*	Young & Wolfe, 1984	*Hygrotus*	*Clemnius*	*Clemnius*	*Hygrotus*	*Coelambus*	n. comb.	NA	morphological
11	*bertrandi*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	PL	only literature
12	*bilardoi*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
13	*bruesi*	(Fall, 1928)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
14	*caliginosus*	(Régimbart, 1899)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
15	*capensis*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
16	*caspius*	(Wehncke, 1875)	*Hydroporus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
17	*chinensis*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
18	*cleopatrae*	(Peyron, 1858)	*Hydroporus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	PL	morphological
19	*collatus*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
20	*compar*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
21	*confluens*	(Fabricius, 1787)	*Dytiscus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
22	*confusus*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
23	*corpulentus*	(Schaum, 1864)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
24	*curvilobus*	Fery, Sadeghi & Hosseinie, 2005	*Hygrotus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological

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TABLE 1. (Continued)

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
25	*curvipes*	(Leech, 1938)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
26	*decoratus*	(Gyllenhal, 1810)	*Hyphydrus*	*Clemnius*	*Clemnius*	*Hygrotus*	*Hygrotus*	n. comb.	PL	morphological & molecular
27	*dehraduni*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	PL	only literature
28	*descarpentriesi*	(Peschet, 1923)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Heroceras*	—	n. comb.	AF	morphological & molecular
29	*discrepatus*	(Guignot, 1954)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
30	*dissimilis*	(Geminger & Harold, 1868)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
31	*diversipes*	Leech, 1966)	*Hygrotus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
32	*elevatus*	(Sharp, 1882)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR, PL	morphological
33	*endroedyi*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
34	*enneagrammus*	(Ahrens, 1833)	*Hydroporus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
35	*falli*	(Wallis, 1924)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
36	*farctus*	(LeConte, 1855)	*Hydroporus*	*Clemnius*	*Cyclopius*	*Hygrotus*	*Hygrotus*	n. comb.	NA	morphological
37	*femoratus*	(Fall, 1901)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	only literature
38	*flaviventris*	(Motschulsky, 1860)	*Hydroporus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
39	*fontinalis*	Leech, 1966	*Hygrotus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
40	*fraternus*	(LeConte, 185	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA, NT	morphological
41	*fresnedai*	(Fery, 1992)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
42	*fumatus*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
43	*geetae*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
44	*gigantoides*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
45	*gigas*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological
46	*goldschmidti*	(Pederzani & Rocchi, 2009)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
47	*gschwendtneri*	(Omer-Cooper, 1957)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
48	*guineensis*	(Aubé, 1838)	*Hyphydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	AF, PL	morphological & molecular
49	*heros*	(Sharp, 1882)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	AF	morphological

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TABLE 1. (Continued)

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
50	*hydropicus*	(LeConte, 1852)	*Hydroporus*	*Clemnius*	*Clemnius*	*Hygrotus*	*Hygrotus*	n. comb.	NA, NT	morphological & molecular
51	*hyphoporoides*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
52	*ignoratus*	(Gschwendtner, 1933)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
53	*impressopunctatus*	(Schaller, 1783)	*Dytiscus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	H	morphological & molecular
54	*inaequalis*	(Fabricius, 1777)	*Dytiscus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	PL	morphological & molecular
55	*infuscatus*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
56	*inquinatus*	(Boheman, 1848)	*Hydroporus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
57	*inscriptus*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
58	*intermedius*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	NA	morphological
59	*janssensi*	(Guignot, 1952)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
60	*josephi*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
61	*kalaharii*	(Gschwendtner, 1935)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
62	*kempi*	(Gschwendtner, 1936)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR, PL	only literature
63	*laccophilinus*	(LeConte, 1878)	*Hydroporus*	*Clemnius*	*Clemnius*	*Hygrotus*	*Coelambus*	n. comb.	NA	morphological & molecular
64	*lagari*	(Fery, 1992)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
65	*lernaeus*	(Schaum, 1857)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
66	*lutescens*	(LeConte, 1852)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA, NT	morphological & molecular
67	*marginipennis*	(Blatchley, 1912)	*Coelambus*	*Clemnius*	*Cyclopius*	*Hygrotus*	*Hygrotus*	n. comb.	NA	morphological
68	*marklini*	(Gyllenhal, 1813)	*Hyphydrus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	H	morphological & molecular
69	*masculinus*	(Crotch, 1874)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
70	*montanus*	(Régimbart, 1899)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
71	*morandi*	(Guignot, 1952)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	OR	only literature
72	*musicus*	(Klug, 1834)	*Hydroporus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	AF, OR, PL	morphological & molecular
73	*muticus*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	AF	morphological & molecular
74	*natator*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature

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TABLE 1. (Continued)

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
75	*nigrescens*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
76	*nigrescens*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
77	*nigrolineatus*	(Steven, 1808)	*Hyphydrus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
78	*nilghiricus*	(Régimbart, 1903)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR, PL	only literature
79	*nodieri*	(Régimbart, 1895)	*Coelambus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	AF	morphological & molecular
80	*novemlineatus*	(Stephens, 1829)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	H	morphological & molecular
81	*nubilus*	(LeConte, 1855)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA, NT [PC]	morphological
82	*obscureplagiatus*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
83	*obscurus*	(Sharp, 1882)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
84	*obsoletus*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
85	*orthogrammus*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
86	*oudomxai*	(Brancucci & Biström, 2013)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
87	*ovalis*	(Gschwendtner, 1932)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
88	*pacistanus*	(Guignot, 1959)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	PL	only literature
89	*pallidulus*	(Aubé, 1850)	*Hydroporus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
90	*pallidus*	(Omer-Cooper, 1931)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
91	*parallellogrammus*	(Ahrens, 1812)	*Dytiscus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
92	*patruelis*	(LeConte, 1855)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
93	*pauliani*	(Guignot, 1950)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
94	*pectoralis*	(Motschulsky, 1860)	*Hydroporus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
95	*pedalis*	(Fall, 1901)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
96	*picatus*	(Kirby, 1837)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
97a	*polonicus polonicus*	(Aubé, 1842)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
97b	*polonicus sahlbergi*	(Sharp, 1882)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
98	*pugnator*	(Sharp, 1890)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature

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TABLE 1. (Continued)

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
99	*punctilineatus*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Coelambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
100	*quadrilineatus*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological
101	*quinquelineatus*	(Zetterstedt, 1828)	*Hyphydrus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	PL	morphological & molecular
102	*reticulatus*	(Pederzani & Rocchi, 2009)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
103	*ritsemae*	(Régimbart, 1889)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
104	*rohani*	(Peschet, 1924)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	molecular
105	*rufus*	(Clark, 1863)	*Hyphydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological
106	*saginatus*	(Schaum, 1857)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
107	*salinarius*	(Wallis, 1924)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
108	*sanfilippoi*	(Fery, 1992)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
109	*sayi*	J. Balfour-Browne, 1944	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	NA	morphological & molecular
110	*sellatus*	(LeConte, 1866)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
111	*semenowi*	(Jakovlev, 1899)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
112	*semivittatus*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
113	*severini*	(Régimbart, 1892)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR, PL	morphological
114	*sjostedti*	(Régimbart, 1908)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
115	*solieri*	(Aubé, 1838)	*Hydroporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	—	PL	morphological & molecular
116	*spadiceus*	(Sharp, 1882)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	molecular
117	*stefanschoedli*	Fery, Sadeghi & Hosseinie, 2005	*Hygrotus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological
118	*subaequalis*	(Vazirani, 1969)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	only literature
119	*sudanensis*	(Guignot, 1952)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
120	*suturalis*	(LeConte, 1850)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
121	*sylvanus*	(Fall, 1917)	*Coelambus*	*Clemnius*	*Clemnius*	*Hygrotus*	*Coelambus*	n. comb.	NA	morphological
122	*thermarum*	(Darlington, 1928)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological
123	*tonkinensis*	(Régimbart, 1899)	*Hyphoporus*	*Hygrotus*	*Hyphoporus*	*Hyphoporus*	—	n. comb.	OR	morphological & molecular

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TABLE 1. (Continued)

n	species	authors	original genus	genus in this work	subgenus in this work	genus in Nilsson & Hájek 2017a	subgenus in Nilsson & Hájek 2017a	new combination	distribution	methods applied
124	*travniceki*	(Šťastný, 2012)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological
125	*tribolus*	(Guignot, 1953)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
126	*tumidiventris*	(Fall, 1919)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
127	*turbidus*	(LeConte, 1855)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA	morphological & molecular
128	*unguicularis*	(Crotch, 1874)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	H	morphological & molecular
129	*urgensis*	(Jakovlev, 1899)	*Coelambus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological & molecular
130a	*variabilis secundus*	(Régimbart, 1906)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
130b	*variabilis variabilis*	(Guignot, 1954)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
131	*vaziranii*	Nilsson, 1999)	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	—	PL	only literature
132	*versicolor*	(Schaller, 1783)	*Dytiscus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	*Hygrotus*	—	PL	morphological & molecular
133	*verticalis*	(Sharp, 1882)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	morphological & molecular
134	*vittatus*	(Régimbart, 1895)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
135	*wardii*	(Clark, 1862)	*Hydroporus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	NA, NT	morphological
136	*wewalkai*	(Biström & Nilsson, 2002)	*Herophydrus*	*Hygrotus*	*Hygrotus*	*Herophydrus*	—	n. comb.	AF	only literature
137	*zigetangco*	Fery, 2003	*Hygrotus*	*Hygrotus*	*Leptolambus*	*Hygrotus*	*Coelambus*	—	PL	morphological

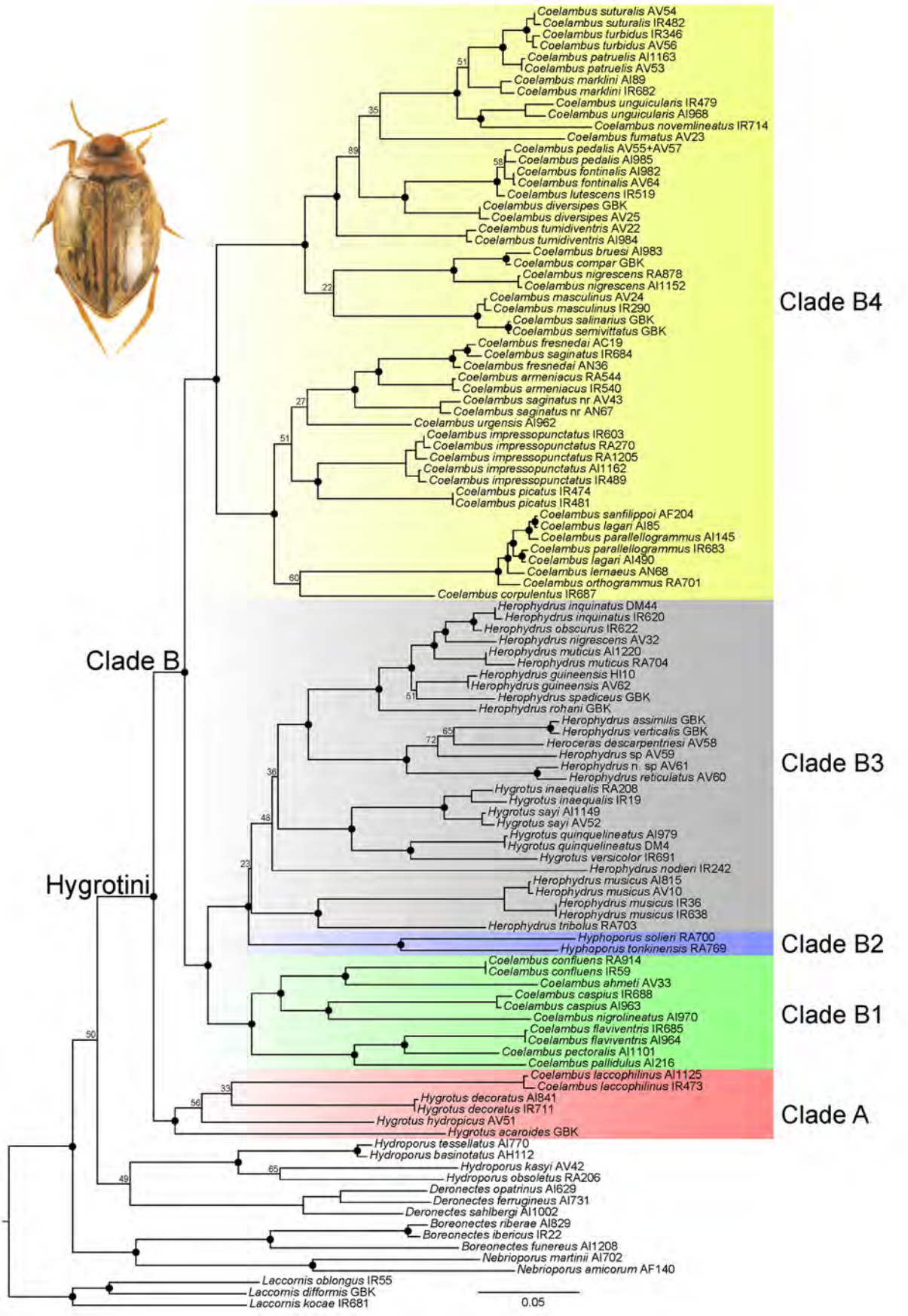


FIGURE 1. Phylogeny of Hygrotini, modified from Villastrigo *et al*. (in press). Numbers above nodes are bootstrap support values. Note that here the former generic and subgeneric names are still used.

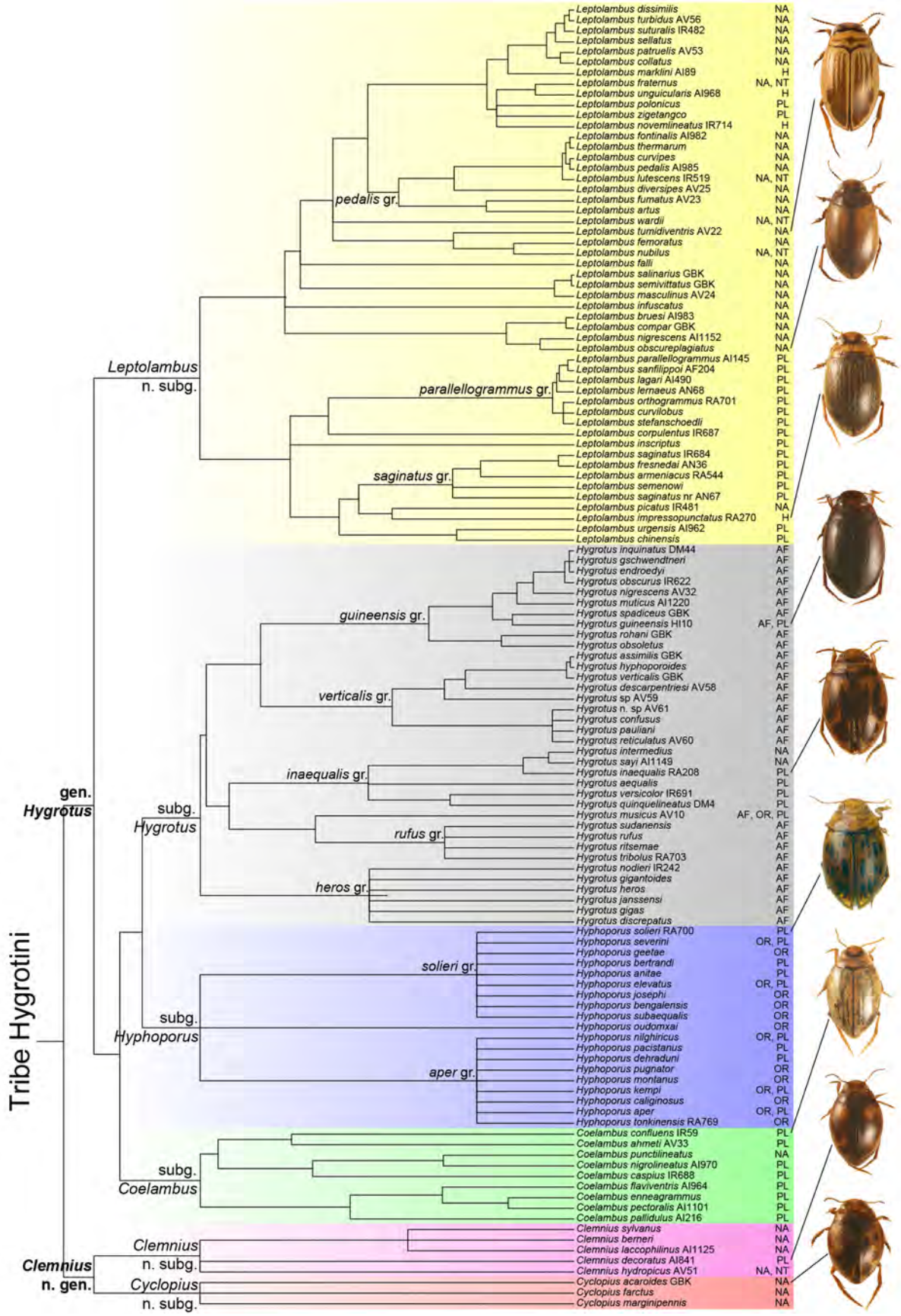
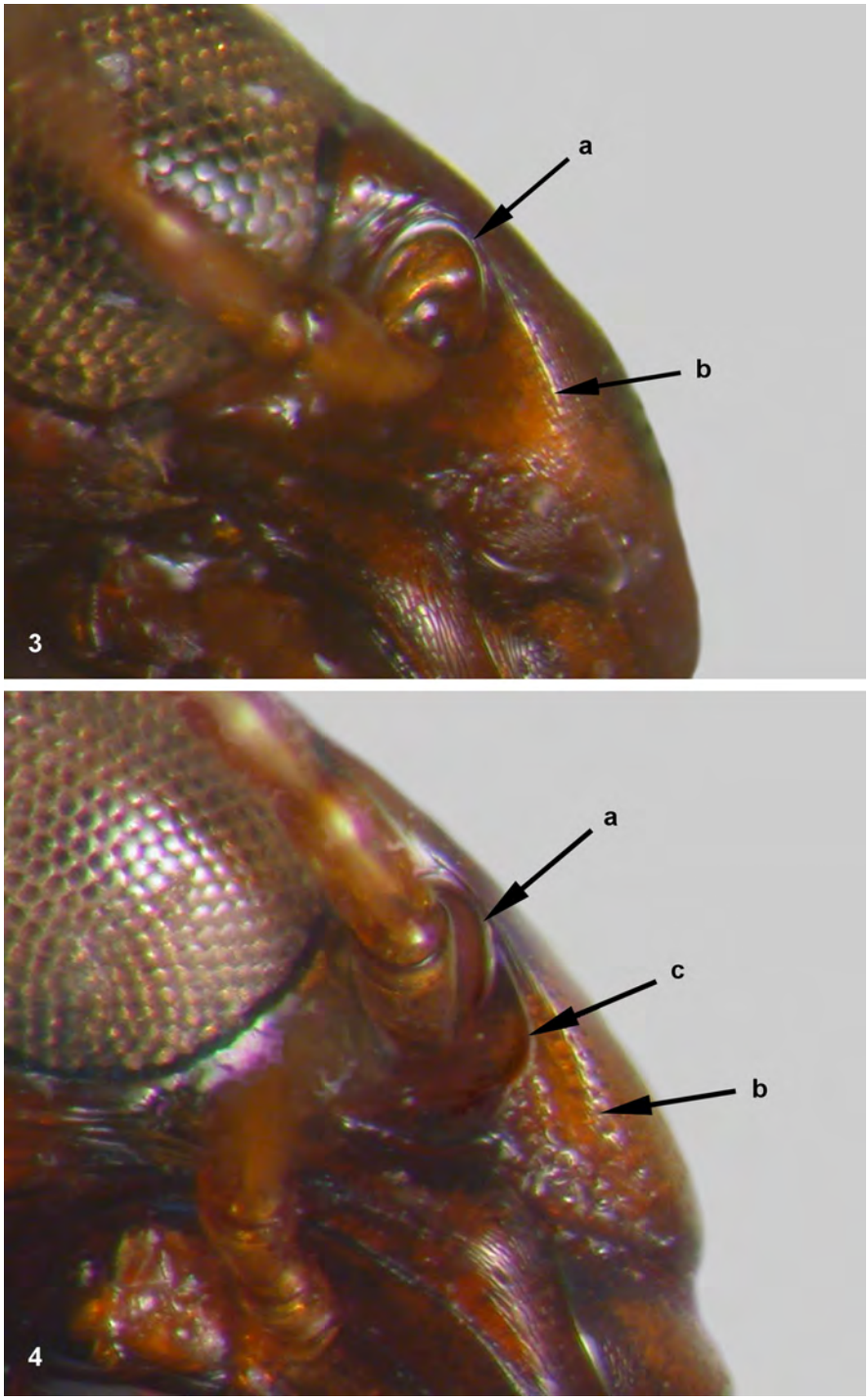


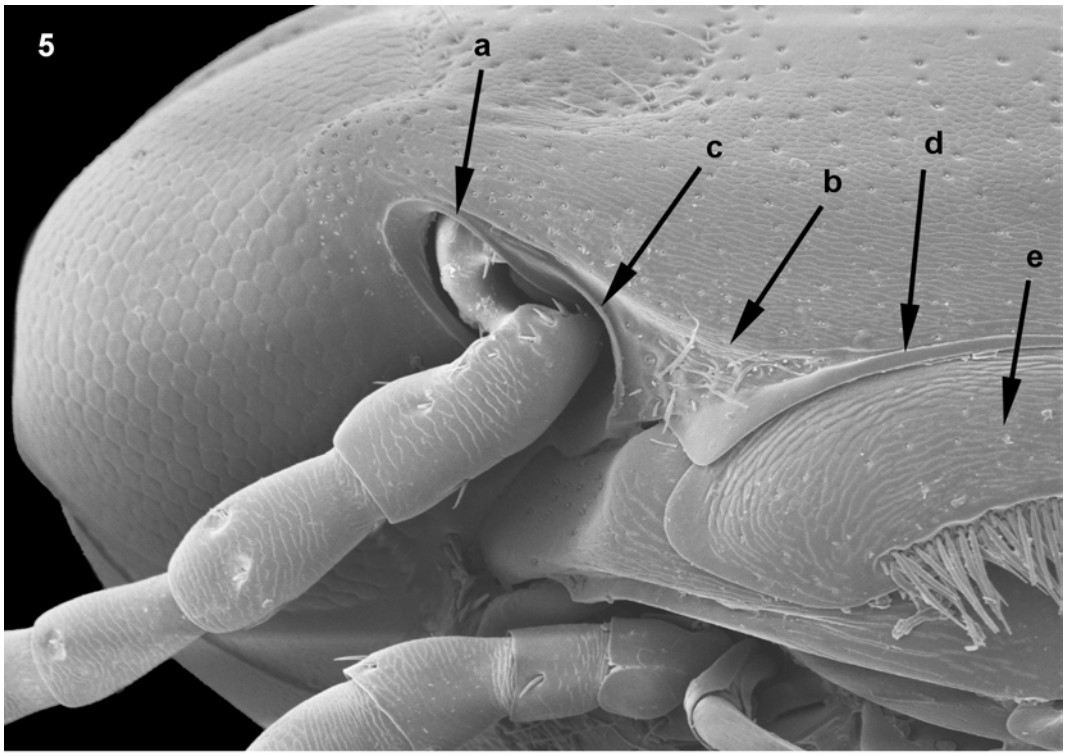
FIGURE 2. Dendrogram showing the new classification of Hygrotini. A number of species without molecular data (no voucher number) have been inserted near morphologically similar species with molecular data. Acronyms refer to biogeographical regions.

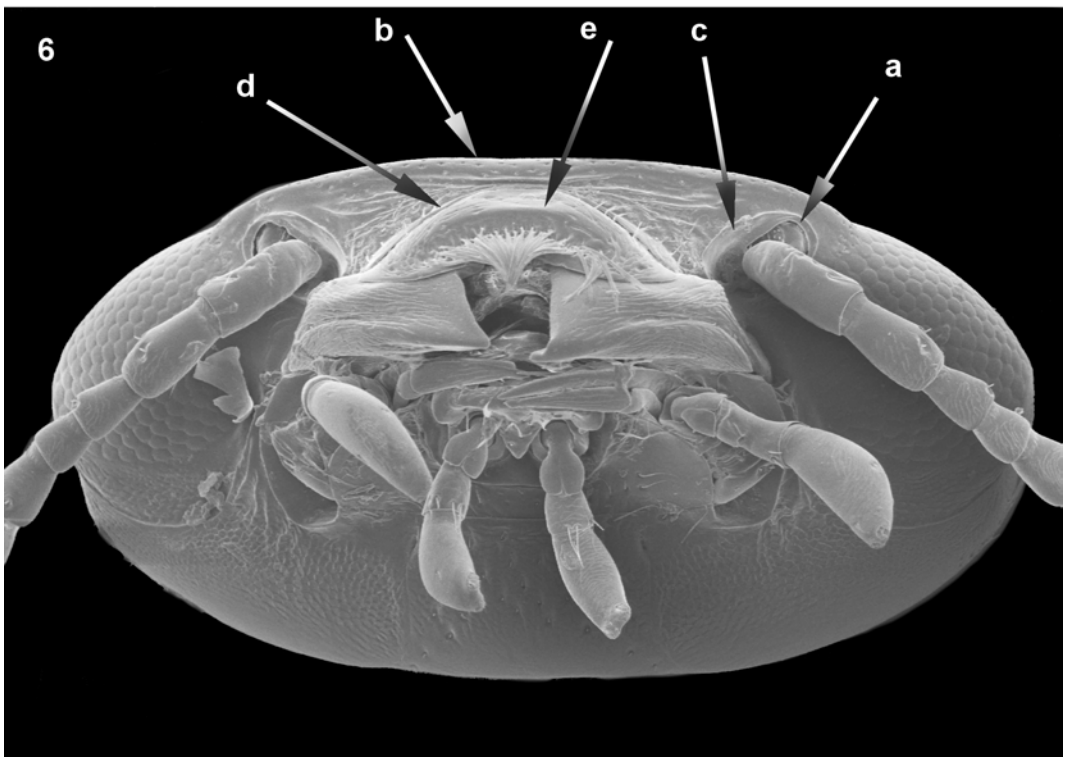


FIGURES 3–4. Antennal cavities of: (3) *Hydroporus dorsalis* (Hydroporini) and (4) *Hygrotus* (*Leptolambus*) *lagari* (Fery, 1992) (a: carina delimiting capsule for scape; b: fronto-lateral border of clypeus; c: second carina).

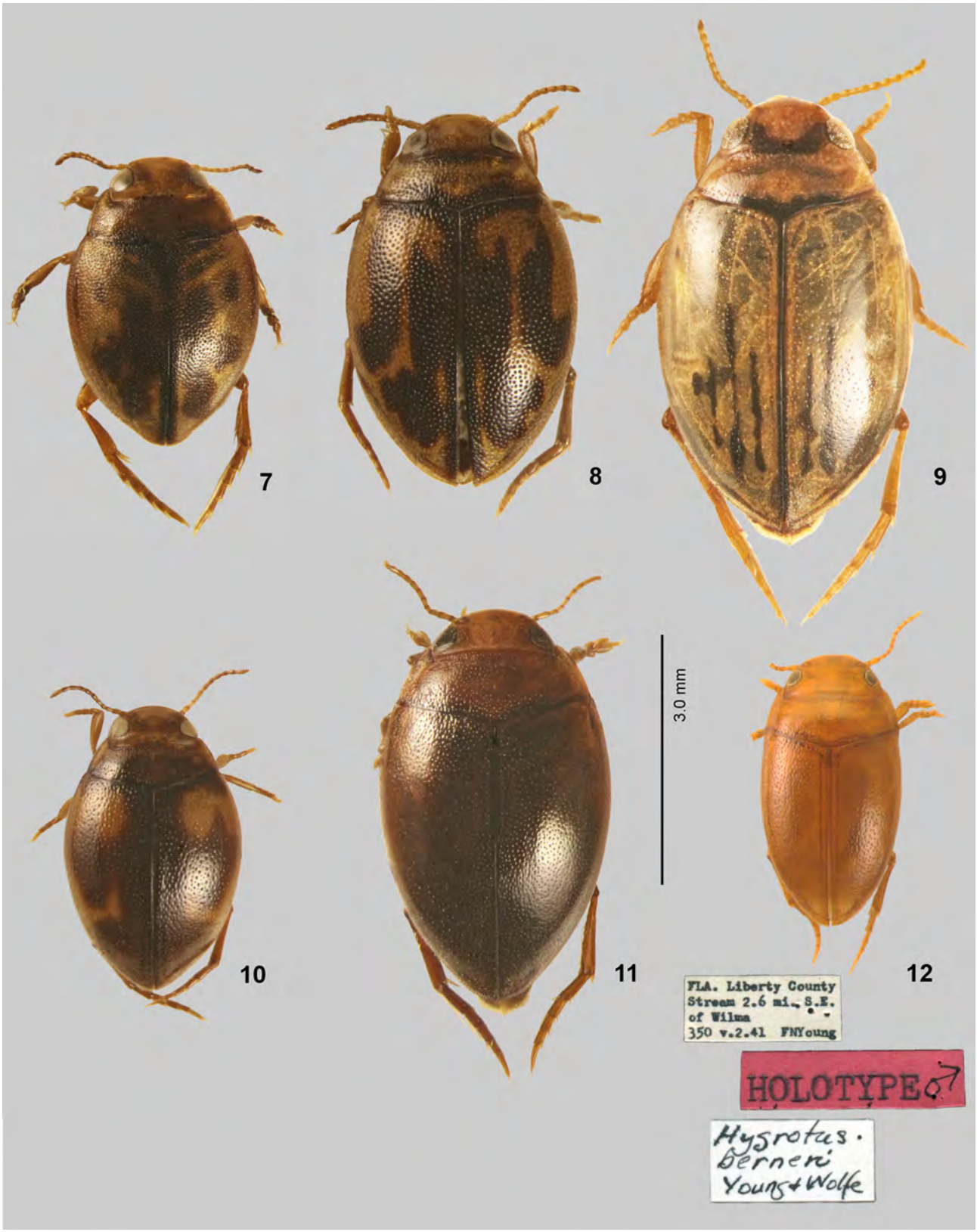
Diagnosis. Body shape subglobose (TL/MW ca. 1.35–1.6); body size small (TL 2.1–2.6 mm) (cf. Fig. 7 for *Clemnius* (*Cyclopius*) *acaroides*). Head with anterior clypeal margin truncate and slightly emarginated, border not produced forwards; bead broadly interrupted medially (*C*. (*Cyclopius*) *acaroides* and *C*. (*Cyclopius*) *marginipennis* (Blatchley, 1912)) or absent (*C*. (*Cyclopius*) *farctus* (LeConte, 1855)); antennomeres simple, not broadened. Elytra with margin in lateral view rather strongly ascending to shoulder (similar to Fig. 54); epipleuron comparably broad, broader than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably small angle (< ca. 135°; similar to Fig. 49). Colour pattern of elytra variable, from yellowish with dark vittae to more or less uniformly dark brownish or blackish; venter brownish to dark brownish, partly paler.

Males with last abdominal ventrite with deep medial depression, its anterior margin with two long spines projecting backwards and more posteriorly with two rather short ones directed perpendicular to surface (see fig. 24B in Larson *et al*. 2000), a unique character in Hygrotini and also in Dytiscidae. Median lobe symmetric, robust in *C*. (*Cyclopius*) *acaroides* (Fig. 19) and *C*. (*Cyclopius*) *marginipennis*, but very thin in *C*. (*Cyclopius*) *farctus*. Parameres with condylar process short, forming an obtuse angle with distal part (see Fig. 29; cf. figs. 10–12 in Anderson 1971). Male metatarsal claws of equal length.

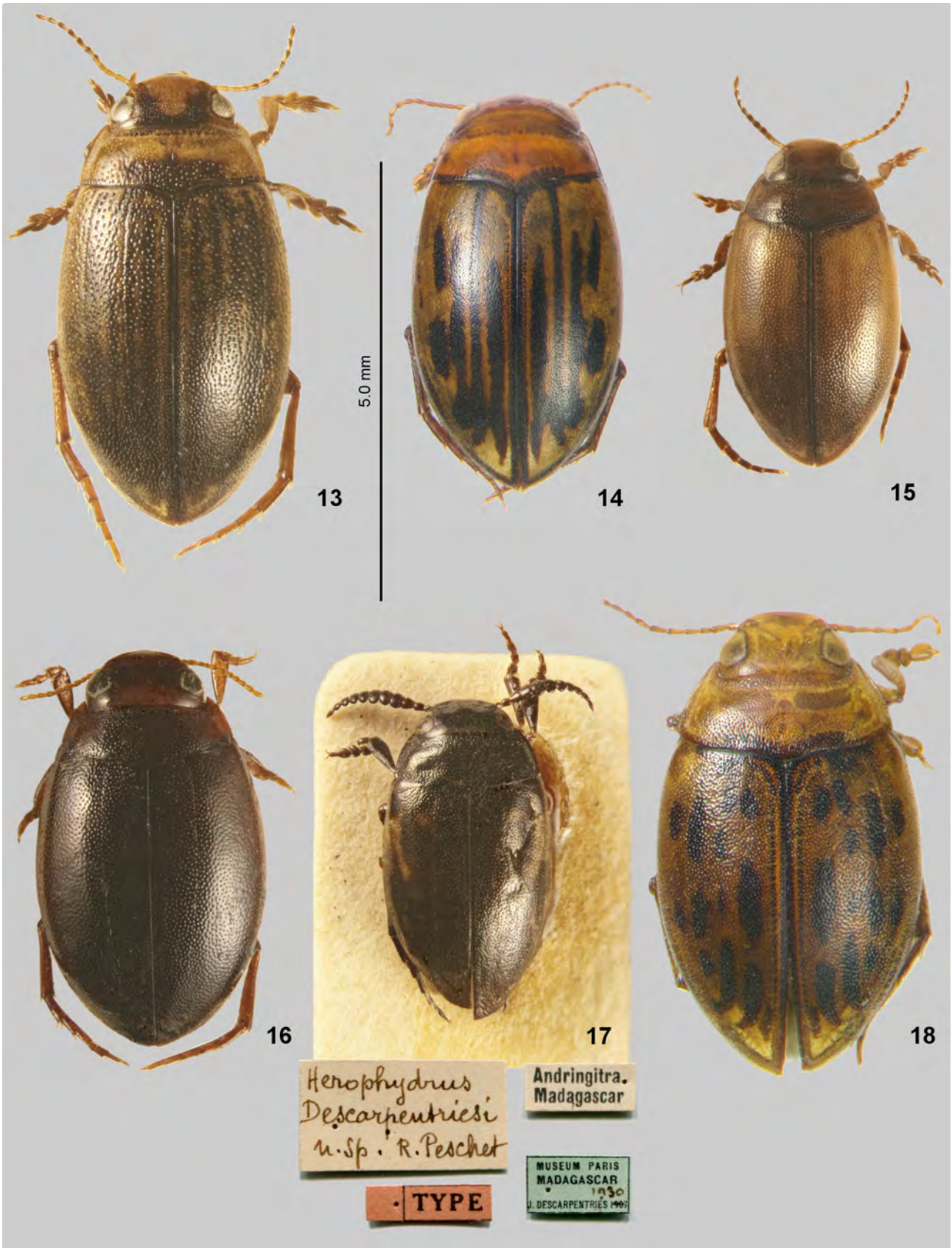




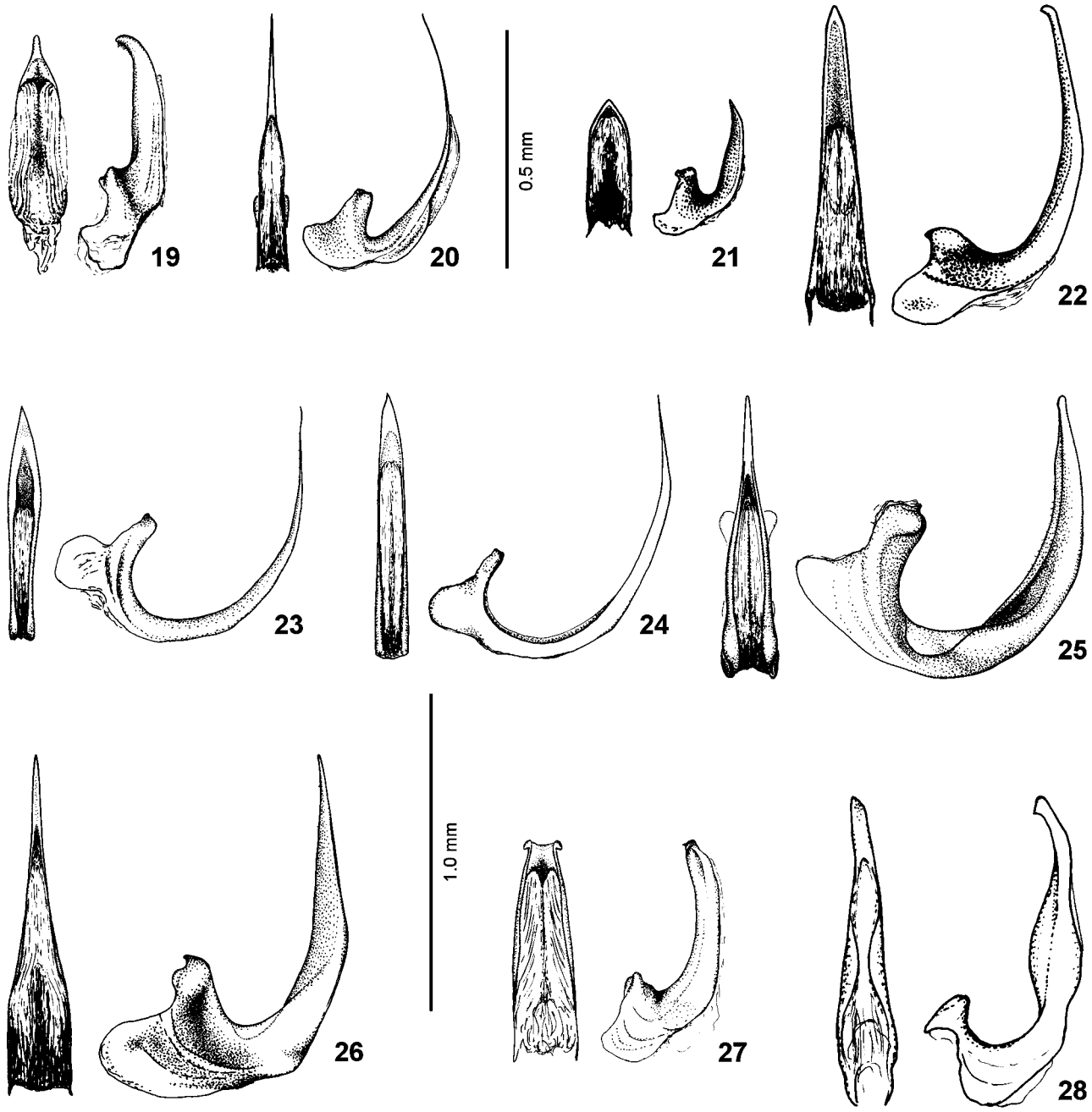
FIGURES 5–6. SEM micrographs with details of head and antennal cavities of: (5) *Hygrotus* (*Leptolambus*) *impressopunctatus* (frontal view) and (6) *Hygrotus* (s. str.) *inaequalis* (oblique ventral view) (a, b and c as in Figs 3–4; d: clypeal stripe; e: labrum).



FIGURES 7–12. Habitus of: (7) *Clemnius* (*Cyclopius*) *acaroides*, (8) *Hygrotus* (s. str.) *inaequalis*, (9) *Hygrotus* (*Coelambus*) *confluens*, (10) *Clemnius*. (s. str.) *decoratus*, (11) *Clemnius* (s. str.) *laccophilinus* and (12) *Clemnius* (s. str.) *berneri* (male holotype and labels).



FIGURES 13–18. Habitus of: (13) *Hygrotus* (*Leptolambus*) *impressopunctatus*, (14) *H*. (*Leptolambus*) *orthogrammus*, (15) *H*. (*Leptolambus*) *obscureplagiatus*, (16) *H*. (s. str.) *guineensis*, (17) *H*. (s. str.) *descarpentriesi* (male syntype and labels) and (18) *H*. (*Hyphoporus*) *solieri* (Figs 14 and 18 are reproduced from Fery *et al*. 2012 with the permission of F. Gusenleitner, Linz, Austria).

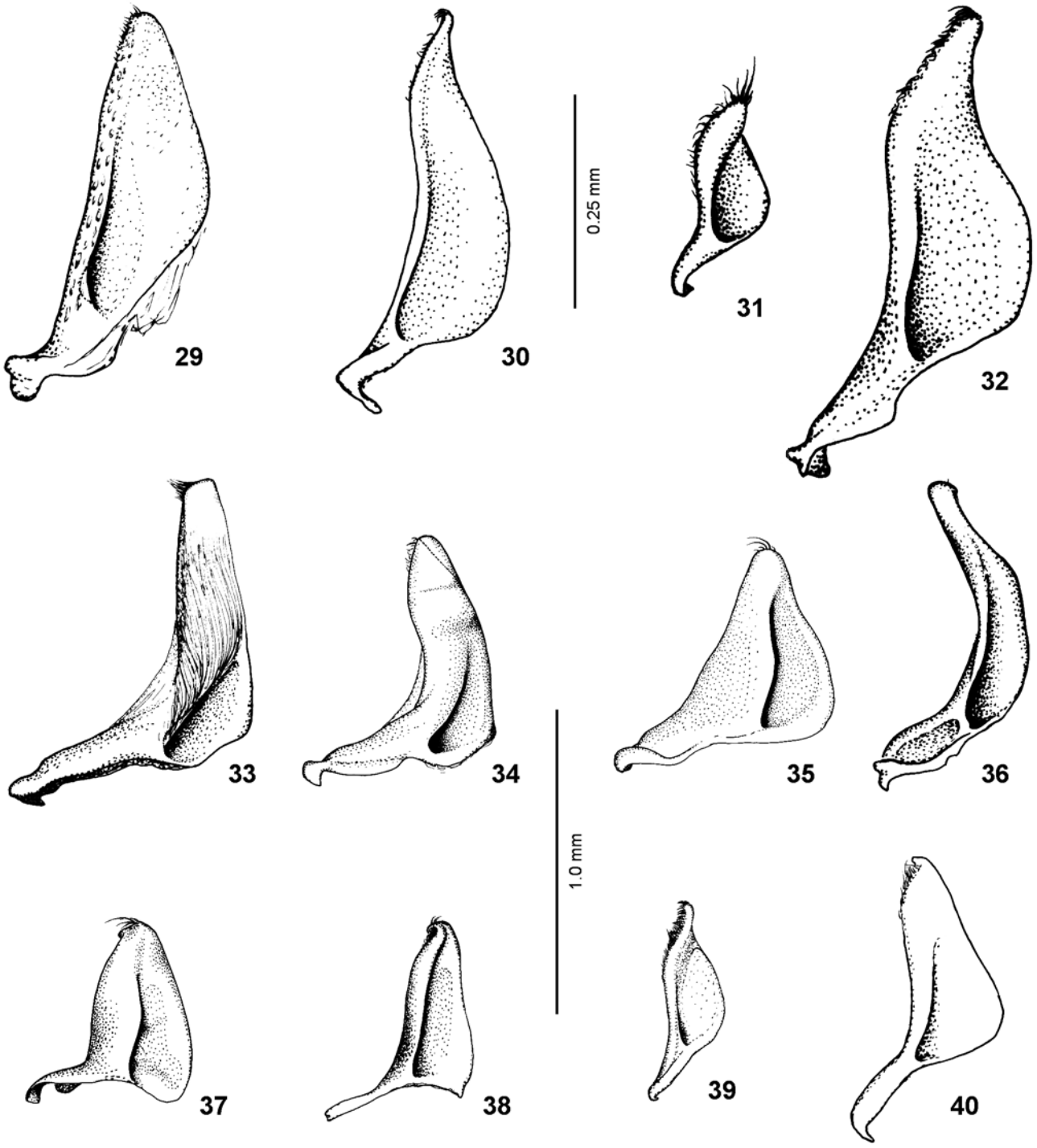


FIGURES 19–28. Median lobe in ventral and lateral view of: (19) *Clemnius* (*Cyclopius*) *acaroides*, (20) *Clemnius* (s. str.) *berneri*, (21) *Clemnius* (s. str.) *decoratus*, (22) *Hygrotus* (s. str.) *inaequalis*, (23) *H.* (*Coelambus*) *enneagrammus*, (24) *H.* (*Coelambus*) *confluens*, (25) *H.* (*Leptolambus*) *parallellogrammus*, (26) *H.* (*Leptolambus*) *impressopunctatus*, (27) *H.* (s. str.) *guineensis* and (28) *H.* (*Hyphoporus*) *tonkinensis* (Fig. 28 is a modified reproduction of figs 3 and 4 in Brancucci & Biström 2013).

Etymology. From the Greek χύκλος (kyklos = circle), referring to the semicircular shape of the clypeus of the species of the subgenus. The gender of the name is masculine.

Distribution. Nearctic: Canada and USA.

Main habitat types. Species of this subgenus are typically known from lentic freshwater habitats; Blatchley (1912: 330) reported *C.* (*Cyclopius*) *marginipennis* from "shallow brackish ponds".



FIGURES 29–40. Left paramere of: (29) *Clemnius* (*Cyclopius*) *acaroides*, (30) *Clemnius* (s. str.) *berneri*, (31) *Clemnius* (s. str.) *decoratus*, (32) *Hygrotus* (s. str.) *inaequalis*, (33) *H*. (*Leptolambus*) *fresnedai*, (34) *H.* (*Leptolambus*) *impressopunctatus*, (35) *H*. (*Leptolambus*) *parallellogrammus*, (36) *H*. (*Leptolambus*) *nubilus*, (37) *H*. (*Coelambus*) *enneagrammus*, (38) *H*. (*Coelambus*) *confluens*, (39) *H*. (s. str.) *guineensis* and (40) *H*. (*Hyphoporus*) *tonkinensis* (Fig. 40 is a modified reproduction of fig. 5 in Brancucci & Biström 2013).

Subgenus *Clemnius* s. str. n. subgen.

Type species: *Hyphydrus decoratus* Gyllenhal, 1810: XVI, by present designation.

The subgenus *Clemnius* **n. subgen.** contains five species of the former genus *Hygrotus*, subgenera *Hygrotus* and *Coelambus* (see Fig. 2 and Table 1).

Diagnosis. Body shape oval, either almost globose (TL/MW ca. 1.6) (see Fig. 10 for *C.* (s. str.) *decoratus*) or more elongated, "navicular" (TL/MW 1.7–1.8) (see Fig. 11 for *C.* (s. str.) *laccophilinus* (LeConte, 1878)), with MW short behind pronotum and distinctly before mid-length (still somewhat more elongated in *C*. (s. str.) *berneri* Young & Wolfe, 1984, with TL/MW ca. 2.05; see Fig. 12 for holotype and its labels; FSCA); body size small (TL 2.1–3.3 mm). *Clemnius* (s. str.) *decoratus* and *C*. (s. str.) *hydropicus* (LeConte, 1852) with anterior clypeal margin evenly and semicircularly rounded, with border produced forwards and bead complete as in subgenus *Hygrotus* s. str. In contrast *Clemnius* (s. str.) *laccophilinus*, *C.* (s. str.) *berneri* and *C*. (s. str.) *sylvanus* (Fall, 1917) with anterior clypeal margin truncate and slightly emarginated, with border not produced forwards and bead absent. Antennomeres simple, not broadened. Elytra with margin in lateral view moderately ascending to shoulder (similar to Fig. 55); epipleuron comparably broad, broader than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably small angle (< ca. 135°; similar to Fig. 49). Elytra either dark, uniformly testaceous or with yellowish-brown dots, but not vittate; venter brown or testaceous. Last abdominal ventrite without deep depression.

Aedeagus with median lobe symmetric, robust in *C*. (s. str.) *decoratus* (Fig. 21) and *C*. (s. str.) *hydropicus* (cf. fig. 13 in Anderson 1971) or distally very narrow in *C*. (s. str.) *berneri* (Fig. 20), *C*. (s. str.) *laccophilinus* and *C.* (s. str.) *sylvanus* (cf. also figs 1A and 2A in Anderson 1976). Parameres with condylar process rather short and forming an obtuse angle with distal part (Figs 30 and 31; cf. also figs 1B and 2B in Anderson 1976). Male metatarsal claws of equal length.

Etymology. From the Greek χλεμμύς (klemmys = tortoise); referring to the almost hemispherical body shape of most species. The gender of the generic name is masculine.

Distribution. Palaearctic (Europe, Russia and Kazakhstan), Nearctic and Neotropical (northern part of Mexico).

Main habitat types. The subgenus includes species typical of lentic freshwater environments.

Notes: Within the subgenus there are two clear groups of species according to body shape and genital morphology, one formed by *C*. (s. str.) *decoratus* and *C*. (s. str.) *hydropicus* (body shape more globular, aedeagus robust with short medial lobe), and the other by *C*. (s. str.) *berneri*, *C*. (s. str.) *laccophilinus* and *C*. (s. str.) *sylvanus* (body shape more elongated, "navicular", aedeagus slender with elongated median lobe). The phylogenetic relationships of the species for which molecular data were available are poorly supported (Fig. 1), but in any case we never recovered these two groups as respectively monophyletic. We thus refrain from splitting *Clemnius* **n. subgen.** into two taxa corresponding to these two groups, at least until more evidence becomes available.

Genus *Hygrotus* Stephens, 1828

Type species: *Dytiscus inaequalis* Fabricius, 1777: 239, by subsequent designation of Curtis (1835: pl. 531).

The genus *Hygrotus* as here defined includes 129 described species (two of them bitypic) distributed in the Nearctic (including the north of Mexico), Palaearctic, Afrotropical and Oriental zoogeographical regions (Fig. 2 and Table 1). One Nearctic species was introduced to Hawaii (see below), which belongs to the Pacific region.

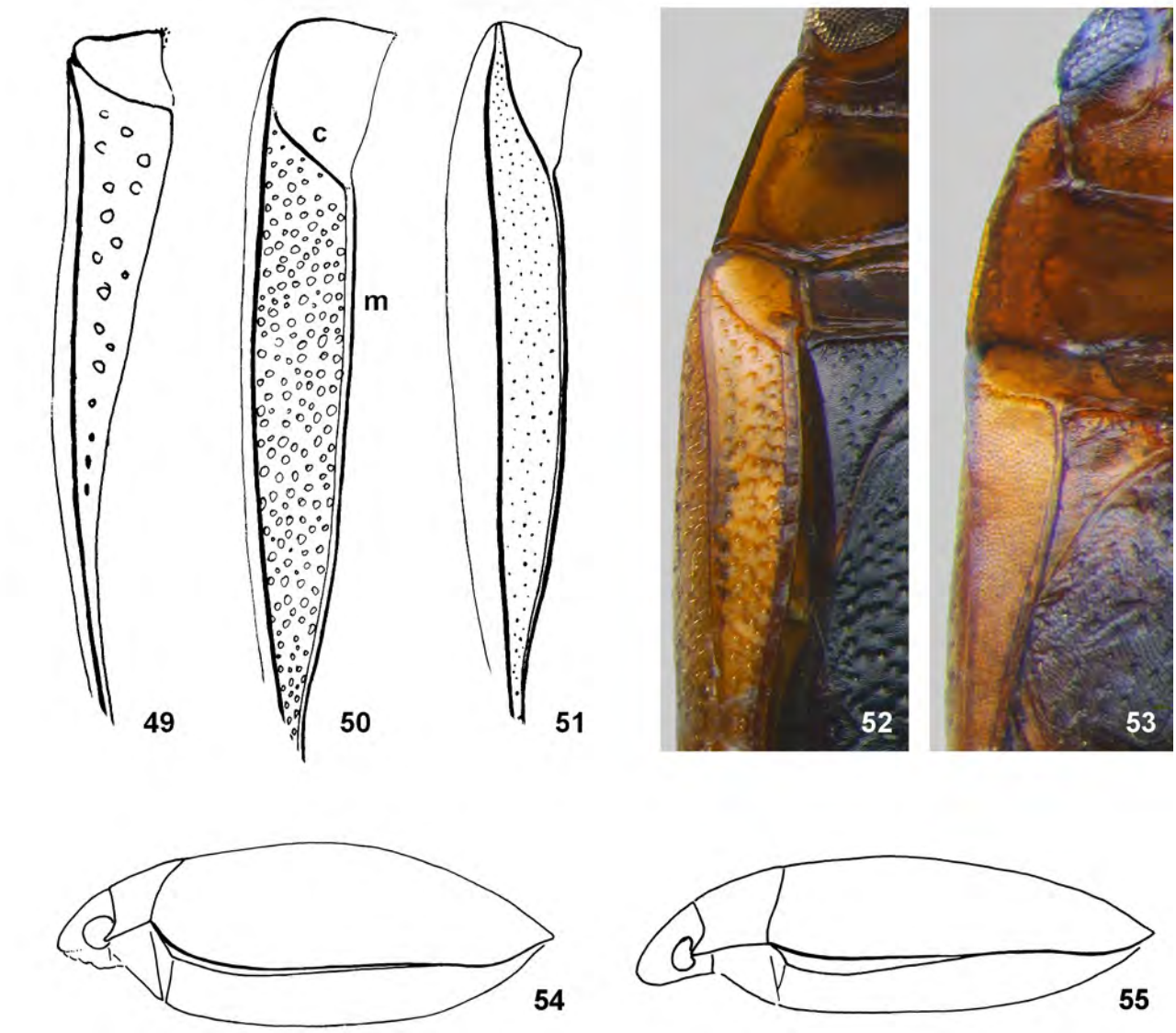
Diagnosis. In the new classification *Hygrotus* is the second of two genera of the tribe Hygrotini. As in *Clemnius* **n. gen**. all species of the genus have two carinae in each antennal cavity (see Figs 4–6).

According to the two main clades in the phylogeny of Hygrotini and several morphological characters, the genus (which corresponds to Clade B in Fig. 1) is subdivided into four clades corresponding to the following four subgenera: clade B1 = subgenus *Coelambus*, clade B2 = subgenus *Hyphoporus*, clade B3 = subgenus *Hygrotus* s. str. and clade B4 = *Leptolambus* **n. subgen.**

Subgenus *Coelambus* Thomson, 1860

Type species: *Dytiscus confluens* Fabricius, 1787: 193, by subsequent designation of Zaitzev (1953: 129).

FIGURES 41–48. Head with details of clypeal rim of (41) *Hygrotus* (*Leptolambus*) *impressopunctatus*, (42) *H*. (*Hyphoporus*) *solieri*, (43) *H*. (s. str.) *guineensis*, (44) *H*. (s. str.) *inaequalis*, (45) idem in lateral view, (46) *H*. (*Coelambus*) *confluens* (the lighter area before the anterior border of the clypeus is the "clypeal stripe"; see Appendix), (47) *H*. (*Leptolambus*) *masculinus* and (48) idem in lateral view.



FIGURES 49–55. (49–53): Epipleuron with oblique epipleural carina and genicular fossa of: (49) *Clemnius* (s. str.) *berneri*, (50) *Hygrotus* (*Leptolambus*) *polonicus polonicus*, (51) *H.* (*Coelambus*) *caspius*, (52) *H.* (*Leptolambus*) *impressopunctatus* and (53) *Rhithrodytes agnus*; epipleural carina (c) and inner margin of epipleuron (m) including angle mentioned in diagnoses of subgenera. **(54–55):** Elytral margin in lateral view of: (54) *H.* (*Coelambus*) *caspius* (strongly ascending to shoulder) and (55) *Clemnius* (s. str.) *berneri* (moderately ascending to shoulder) (Figs 52 and 53 are reproduced from Fery 2013 and from Fery 2016 with the permissions of F. Gusenleitner, Linz, Austria, and G. Foster, Ayr, UK, respectively).

The subgenus *Coelambus* contains eight Palaearctic and one Nearctic species (*Hygrotus* (*C.*) *punctilineatus* (Fall, 1919)).

Diagnosis. Body shape moderately to elongate oval (TL/MW ca. 1.7–2.0); small to medium sized species (TL 3.0–4.5 mm) (see Fig. 9 for *H.* (*Coelambus*) *confluens*). Head with anterior clypeal margin truncate and slightly emarginated, border not produced forwards; bead absent. Antennomeres simple, not broadened. Elytra with margin in lateral view strongly ascending to shoulder (see Fig. 54 for *H.* (*Coelambus*) *caspius* (Wehncke, 1875)); epipleuron comparably narrow, narrower than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably wide angle (< ca. 150°; similar to Fig. 51). Elytra light yellowish (more yellowish brown in *H.* (*Coelambus*) *ahmeti* Hájek, Fery & Erman, 2005), distinctly vittate (in some species/individuals vittae strongly reduced in anterior half). Venter usually black, but females of some species (e.g. *H.* (*Coelambus*) *pallidulus*) with abdomen at least in part yellow or brownish. Last abdominal ventrite without deep depression.

Aedeagus with median lobe elongate, very slender (distal half very thin in lateral view), symmetric or almost symmetric (e.g. in *H.* (*Coelambus*) *enneagrammus* (Ahrens, 1833), and *H.* (*Coelambus*) *confluens*; see Figs 23 and

24). Parameres with condylar process rather long and forming an almost right angle with distal part (Figs. 37 and 38 for *H.* (*Coelambus*) *enneagrammus* and *H.* (*Coelambus*) *confluens*, respectively). Male metatarsal claws of equal length.

Distribution. Mainly Palaearctic, with one species in Canada and northern USA (*Hygrotus* (*Coelambus*) *punctilineatus*).

Main habitat types. The subgenus includes species typical of both lentic and lotic habitats, with varied salinity tolerance going from freshwater to hypersaline.

Subgenus *Hyphoporus* Sharp, 1880 n. stat.

Type species: *Hydroporus solieri* Aubé, 1838: 554, by monotypy.

The subgenus *Hyphoporus* contains 19 species distributed in the Oriental and Palaearctic regions (see Fig. 2 and Table 1).

Diagnosis. Body shape short oval (TL/MW ca. 1.6–1.7), rather globose; small to medium sized species (TL 3.5–5.6 mm) (see Fig. 18 for *H.* (*Hyphoporus*) *solieri*). Head with anterior clypeal margin truncate, straight or slightly emarginated, border not produced forwards; bead continuous, middle part narrowed in most species (see Fig. 42 for *H.* (*Hyphoporus*) *solieri*); (except *H.* (*Hyphoporus*) *bengalensis* (Severin, 1890) with continuous bead). Antennomeres simple, not broadened. Elytra with margin in lateral view moderately ascending to shoulder (similar to Fig. 55); epipleuron comparably broad, broader than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably small angle (< ca. 135°; similar to Fig. 50). Elytra with interrupted vittae or dotted (in some species very darkened); venter black or brown. Last abdominal ventrite without deep depression. Aedeagus with median lobe robust, asymmetric (see Fig. 28 for *Hygrotus* (*Hyphoporus*) *tonkinensis* (Régimbart, 1899); in *H. bengalensis* median lobe more or less symmetric; see Vazirani 1969 for several further figures); parameres with condylar process of diverse length, forming an obtuse angle with distal part (see Fig. 40 for *H.* (*Hyphoporus*) *tonkinensis*). Male metatarsal claws of equal length.

Distribution. Palaearctic and Oriental, from Iran to India and south-east Asia; one species–*H.* (*Hyphoporus*) *solieri*–from Iran to the Arabian Peninsula and Egypt.

Main habitat types. There is no information on the habitat of most of the species of the subgenus, although they are likely to be mostly associated with freshwater environments. However, it shall be mentioned that Hájek (2006: 48) illustrated a rest-pool in a wadi (Pir Sohrab, Iran) where he has collected *H.* (*Hyphoporus*) *aper* (Sharp, 1882) together with *Neptosternus circumductus* Régimbart, 1899.

Subgenus *Hygrotus* Stephens, 1828

Type species: *Dytiscus inaequalis* Fabricius, 1777: 239, by subsequent designation of Curtis (1835: pl. 531).

Herophydrus Sharp, 1880: cxlviii; type species: *Hydroporus hyphydroides* Perris, 1864: 277 (= *Herophydrus guineensis* (Aubé 1838: 455)), by monotypy. **n. syn.**

Dryephorus Guignot, 1950: 150; type species: *Coelambus nodieri* Régimbart, 1895: 37, by original designation of Guignot (1950: 150). **n. syn.**

Heroceras Guignot, 1950: 150; type species: *Herophydrus descarpentriesi* Peschet, 1923: 176, by original designation of Guignot (1950: 150). **n. syn.**

The newly defined subgenus *Hygrotus* s. str. includes six species previously included in the former subgenus *Hygrotus* s. str., the single species of former genus *Heroceras* (*H. descarpentriesi*) and all 44 species (one of them bitypic) of the former genus *Herophydrus* (see Fig. 2 and Table 1).

Diagnosis. Body shape short oval to moderately elongate oval (TL/MW ca. 1.7–1.8); species of former *Hygrotus* s. str. and *Heroceras* small (TL 2.8–3.6 mm) (see Fig. 8 for *H.* (s. str.) *inaequalis* and Fig. 17 for *H.* (s. str.) *descarpentriesi*) and species of former *Herophydrus* small to large (TL 2.6–7.4 mm) (see Fig. 16 for *H.* (s. str.) *guineensis*). Head of species of former *Hygrotus* with anterior clypeal margin evenly and semicircularly rounded, border produced forwards and with complete bead (see Figs 44 and 45 for *H.* (s. str.) *inaequalis*); species of former

Herophydrus and *Heroceras* with anterior clypeal margin truncate, straight or slightly emarginated, border not produced forwards; bead present, but in many species narrowed in medial part (see Fig. 43 for *H.* (s. str.) *guineensis*), in others medially obsolete or widely reduced except before eyes (cf. Appendix). Antennomeres simple, not broadened except in *H.* (s. str.) *descarpentriesi*, with antennomeres of both sexes, but especially males, strongly dilated (Fig. 17). Elytra with margin in lateral view rather strongly ascending to shoulder (similar to Fig. 54); epipleuron comparably broad, broader than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably small angle (< ca. 135°; similar to Fig. 49). Elytral pattern diverse (vittate, dotted or uniform); venter black or brown. Last abdominal ventrite without deep depression.

Aedeagus with median lobe robust, distal part very diverse in ventral view, more or less symmetric (see Figs 22 and 27 for *H.* (s. str.) *inaequalis* and *H.* (s. str.) *guineensis*) or at most slightly asymmetric in some former *Herophydrus* (see figures in Biström & Nilsson 2002); parameres with condylar process generally short, forming an obtuse angle with distal part (see Fig. 32 and 39 for *H.* (s. str.) *inaequalis* and *H.* (s. str.) *guineensis*). Male metatarsal claws of equal length.

Distribution. Palaearctic, Nearctic, Ethiopian and Oriental. Species of the former subgenus *Hygrotus* (the *H.* (*Hygrotus*) *inaequalis*-group in Fig. 2) are distributed in Europe, northern Africa, Asia and northern America (reaching northern Mexico); species of former *Herophydrus* occur mainly in Africa, with five species in the Palaearctic, one (*H.* (s. str.) *musicus*) reaching the Oriental region and *H.* (s. str.) *morandi* (Guignot, 1952) known from Cambodia only; *H.* (s. str.) *descarpentriesi* is endemic to mountainous regions in south-eastern Madagascar.

Main habitat types. The subgenus includes species typical of lentic and lotic freshwater environments; some species can be found in inland mineralised or coastal brackish waters, such as for example *H.* (s. str.) *musicus* (Millán *et al*. 2006). The latter species can also be found in mineral and thermal spring-pools (pers. communication by J. Hájek, Prague, Czech Republic). The habitat of most African species of the subgenus is poorly known.

Subgenus *Leptolambus* n. subgen.

Type species: *Dytiscus impressopunctatus* Schaller, 1783: 312, by present designation.

The subgenus includes 51 species (one of them bitypic), all previously included in the former subgenus *Coelambus* (see Fig. 2 and Table 1). Notes: *Coelambus hudsonicus* Fall, 1919 is treated by us as junior subjective synonym of *Hygrotus* (*Leptolambus*) *novemlineatus* (Stephens, 1829) (according to Nilsson & Hájek 2017a). We are aware that some authors (e.g. Foster *et al.* 2016) accepted subspecific rank for this taxon and others (e.g. Alarie *et al.* 1999) specific rank, but all without giving any justification for their proceeding.

Diagnosis. Body shape moderately to elongate oval (TL/MW ca. 1.75–2.05); small to medium sized species (TL 2.7–5.8 mm) (see Figs 13–15 for *H.* (*Leptolambus*) *impressopunctatus*, *H.* (*Leptolambus*) *orthogrammus* (Sharp, 1882) and *H.* (*Leptolambus*) *obscureplagiatus* (Fall, 1919)). Head with anterior clypeal margin truncate and emarginated (see Fig. 41 for *H.* (*Leptolambus*) *impressopunctatus*); in some species medially at least less curved than near eyes (see Fig. 47 for *H.* (*Leptolambus*) *masculinus*); border not produced forwards and bead absent (except in *H.* (*Leptolambus*) *masculinus* and *H.* (*Leptolambus*) *salinarius*; cf. Appendix). Antennomeres simple, not broadened. In most species elytral margin in lateral view somewhat less ascending to shoulder than in Fig. 54; in species of Anderson's (1976) group III (*H.* (*Leptolambus*) *bruesi* (Fall, 1928), *H.* (*Leptolambus*) *compar* (Fall, 1919), *H.* (*Leptolambus*) *nigrescens* (Fall, 1919), *H.* (*Leptolambus*) *dissimilis* (Gemminger & Harold, 1868), and *H.* (*Leptolambus*) *turbidus* (LeConte, 1855)) margin only moderately ascending (similar to Fig. 55); in most species epipleuron comparably broad, broader than mesotibia distally; carina meeting inner margin of epipleuron forming a comparably small angle (ca. 135°; similar to Fig. 50 or Fig. 52). In four species of Anderson's (1983) group IV (*H.* (*Leptolambus*) *diversipes* (Leech, 1966), *H.* (*Leptolambus*) *fontinalis* Leech, 1966, *H.* (*Leptolambus*) *pedalis* (Fall, 1901), and *H.* (*Leptolambus*) *thermarum* (Darlington, 1928)) epipleuron narrower and carina meeting inner margin of epipleuron forming a comparably wide angle (> ca. 150°; similar to Fig. 51). In *H.* (*Leptolambus*) *curvipes* (Leech, 1938) (belonging also to group IV in Anderson 1983) epipleuron slightly broader and carina meeting inner margin of epipleuron forming an angle of ca. 140°; however, in these five species of Anderson's (1983) group IV elytral margin not as strongly ascending as in species of newly defined subgenus *Coelambus* (see Fig. 54 for *H.* (*Coelambus*) *caspius*). Elytra pattern diverse (vittate, diffuse-vittate or "cloudlike") (see Anderson

1983; see also Fig. 15 of *H.* (*Leptolambus*) *obscureplagiatus* as an example for diffuse-vittate or "cloudlike" elytral pattern); venter black. Last abdominal ventrite without deep depression.

Aedeagus with shape of median lobe diverse, from robust to very slender; symmetric in ventral view (see Figs 25 and 26 for *H*. (*Leptolambus*) *parallellogrammus* (Ahrens, 1812), and *H*. (*Leptolambus*) *impressopunctatus*). Species of *H*. (*Leptolambus*) *saginatus*-group (see Fig. 2) with distal part of parameres strap-like and condylar process also forming an almost right angle with distal part (see Fig. 33 for *H*. (*Leptolambus*) *fresnedai* (Fery, 1992)). Species of *H*. (*Leptolambus*) *parallellogrammus*-group (see Fig. 2) with parameres more or less triangular and condylar process indistinct and not forming an angle with distal part (see Fig. 35 for *H*. (*Leptolambus*) *parallellogrammus*). Other species with distal part of parameres triangular or broadly strap-like and condylar process forming an almost right angle with distal part (see Fig 34 for *H*. (*Leptolambus*) *impressopunctatus*) or with very unusually shaped parameres (see Fig. 36 for *H*. (*Leptolambus*) *nubilus*; cf. also fig. 7B in Anderson 1976 for *H*. (*Leptolambus*) *dissimilis*). Male metatarsal claws of equal length except in species of *H*. (*Leptolambus*) *saginatus*-group (only four species of all Hygrotini with metatarsal claws of unequal length).

Etymology. From Greek λεπτός (= leptos = narrow) and "lambus" in reference to *Coelambus*. The gender of the generic name is masculine.

Distribution. The subgenus is divided into two main clades, one with mostly Palaearctic distribution except for the Holarctic *H*. (*Leptolambus*) *impressopunctatus* and the Nearctic *H*. (*Leptolambus*) *picatus* (Kirby, 1837), and a second with mostly Nearctic species, except for *H*. (*Leptolambus*) *marklini* (Gyllenhal, 1813), *H.* (*Leptolambus*) *novemlineatus*, and *H*. (*Leptolambus*) *unguicularis* (Crotch, 1874) which are Holarctic. Some species of the Nearctic clade reach northern Mexico: *H*. (*Leptolambus*) *fraternus* (LeConte, 1852), *H.* (*Leptolambus*) *lutescens* (LeConte, 1852), *H.* (*Leptolambus*) *nubilus*, and *H*. (*Leptolambus*) *wardii* (Clark, 1862). *Hygrotus* (*Leptolambus*) *nubilus* was recently recorded from Hawaii, where it has likely been introduced (see Fery & Challet 2015).

Main habitat types. Many species of this subgenus are found in mostly lentic freshwaters, but several in the Nearctic clade, as well as the species of the *H*. (*Leptolambus*) *parallellogrammus*-group, can tolerate from slightly saline to hypersaline waters (Villastrigo *et al*., in press). The subgenus includes the most salt-tolerant species of the tribe, *H*. (*Leptolambus*) *salinarius* and *H*. (*Leptolambus*) *masculinus*.

Discussion

The phylogenetic results of Villastrigo *et al*. (in press) revealed the need of a thorough systematic rearrangement of the tribe Hygrotini. The close relationships between the former *Hygrotus*, *Herophydrus* and *Heroceras* had already been previously noted by several authors (see the Introduction and the Appendix), and suggested by the incomplete molecular and morphological phylogenies available prior to our study (Miller 2001; Biström & Nilsson 2002; Ribera *et al*. 2002, 2008; Alarie & Michat 2007; Abellán *et* al. 2013; Miller & Bergsten 2014).

Species of *Hyphoporus* have always been considered to be related to species of *Herophydrus*, from which they differ mainly by the male genital shape (e.g. Biström & Nilsson 2002; Miller & Bergsten 2016). We opted for maintaining *Hyphoporus* as a valid subgenus, not only based on our phylogenetic results, but also due to the distinctiveness of their male genitalia. It is, however, possible that in further analyses with a more complete sampling *Hyphoporus* proves to be a derived clade within the wider subgenus *Hygrotus* s. str.

Hygrotus descarpentriesi, formerly considered in its own genus *Heroceras*, is a morphologically very deviating species when compared with its closest relatives from Madagascar as resolved in the molecular phylogeny (Fig. 1). The habitus is more elongated, the elytral surface is smooth in the male and reticulated (although not matt) in the female (a character not found in any other Malagasy species of *Hygrotus*), the clypeal bead is almost absent (see the Appendix), and–the most apparent character–both sexes, but especially the males, have strongly dilated antennae. The latter character is present occasionally in other groups of Dytiscidae (e.g. in the genera *Agabus* Leach, 1817, *Limbodessus* Guignot, 1939, *Hydrovatus*, *Rhithrodytes*, *Exocelina* Broun, 1886, *Lioporeus* Guignot, 1950, and others; see e.g. Miller & Bergsten 2016 for some examples and Fig. 17), but still exceptional within Hygrotini. Despite all these peculiarities, *H.* (s. str.) *descarpentriesi* was originally described in *Herophydrus*, and found at least to be related to this genus by the morphological phylogenetic analysis of Biström & Nilsson (2002).

The most unexpected result of the phylogeny was the division of Hygrotini into two clades (A and B in Fig. 1), the former (our *Clemnius* **n. gen.**) including a small number of species previously considered belonging in part to former subgenus *Hygrotus* s. str. and in part to former subgenus *Coelambus*. The species of *Clemnius* **n. gen**. had never been suggested to be closely related to each other within Hygrotini. They all share some likely plesiomorphic characters of body shape and colouration. Most of them are also similar in terms of male genitalia shape, which is in general simpler and more similar to those of other related tribes of Hydroporinae.

Of the two subgenera recognised within *Clemnius* **n. gen**., *Cyclopius* **n. subgen.** is well characterised by the special morphology of the male last abdominal ventrite, but we could not recognise any clear unambiguous synapomorphy for *Clemnius* **n. subgen.** The relationships within the latter are still poorly defined, and need further morphological and molecular studies to be clarified.

Although a formal biogeographic analysis is out of the scope of our paper, it is interesting to note that most of the recognised clades have a well-defined distribution within one of the main biogeographic regions:

- *Clemnius* **n. gen.** is Nearctic with the only exception of one species, the widespread Palaearctic *Clemnius* (s. str.) *decoratus* (see Nilsson & Hájek 2017a, b).
- Subgenus *Coelambus* is almost exclusively Palaearctic, with only one exception, the Nearctic *C. punctilineatus*. However, this species is extremely similar to the Palaearctic species *C. nigrolineatus* (Steven, 1808) (this has not been recognised before), including the shape of the male protarsal claws. Their male and female genitalia show only some slight differences and their general shape could be considered virtually identical. Additionally, females of both species have the upper side dull. It is thus most likely that *C. punctilineatus* has very recently colonised the Nearctic region from a Palaearctic ancestor.
- Subgenus *Hygrotus* s. str., as here defined, is largely of Afrotropical distribution (and likely origin), with only some species reaching the southern Palaearctic region and a small clade–the *H*. (s. str.) *inaequalis*-group–in the Palaearctic and Nearctic regions (Fig. 2).
- Subgenus *Hyphoporus* is mostly Oriental, with some species reaching the Palaearctic region in China (Yunnan), Afghanistan, northern India (Uttar Pradesh), Pakistan and in the west until Iran and Egypt.
- Subgenus *Leptolambus* **n. subgen.** is divided into two clades, one mostly Palaearctic and one mostly Nearctic (see above and Fig. 2). Only some northern species of *Leptolambus* **n. subgen.** have likely recently expanded their geographic range to the whole Holarctic, and three species have a discordant distribution: *H.* (*Leptolambus*) *picatus* is a Nearctic species in the Palaearctic clade, and *H.* (*Leptolambus*) *polonicus* (Aubé, 1842) and *H.* (*Leptolambus*) *zigetangco* Fery, 2003 are Palaearctic species likely to be in the Nearctic clade (see Fig. 2), although for the last two species there are no molecular data and thus their phylogenetic position is uncertain.

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APPENDIX

Note: The generic and subgeneric names cited in the Appendix are those of the new classification unless stated otherwise.

Detailed description of the clypeus in Hygrotini.

The presence and the shape of the clypeal bead (often also called "clypeal rim" or "raised clypeal margin") are used by many authors to separate genera or subgenera within the tribe Hygrotini, mainly the former subgenus *Hygrotus* from former subgenus *Coelambus* and both from the former genera *Herophydrus* and *Hyphoporus* (see Table 1 for the authors and dates of all taxa mentioned here, as well as their past and new classification). Unfortunately, a determination is not always reliable or even impossible because the respective character states are not well recognisable in several species or are present in species which due to other characters, both morphological and molecular, should better be included in another genus or subgenus. Thus, the usefulness of the "clypeal bead" has been debated since long time. This clypeal bead is present in more than half of all members of Hygrotini, and varies considerably in shape. Although in the light of the results of the molecular phylogeny it is clear that the clypeal bead is a highly labile character, without much phylogenetic significance, a detailed description of its structure is necessary to understand the historical classification of Hygrotini, and it can nevertheless have some usefulness to identify some groups of species.

Former subgenera *Hygrotus* and *Coelambus*

The more common character state in members of the former subgenus *Coelambus* as recognised prior to this study (Nilsson & Hájek 2017a, b) is the absence of a clypeal bead (as in e.g. *H.* (*Coelambus*) *confluens,* Fig. 46, and *H.* (*Leptolambus*) *impressopunctatus*, Fig. 41). The anterior part of the clypeus descends anteriad more or less evenly or in a slightly convex shape to the labrum (see Figs 5e and 6e). In almost all species of former *Coelambus* the anterior margin of the clypeus is bordered (directly before reaching/contacting the labrum) with a very narrow rim, which we here call the "clypeal line" (see Fig. 5d for *H.* (*Leptolambus*) *impressopunctatus* and Fig. 6d for *H*. (s. str.) *inaequalis*; see also below for more details). A rather broad transverse band posterior to this line (reaching more or less until the clypeal grooves) is often somewhat less reticulate (and thus more shiny) and more sparsely and finely punctured than the rest of the clypeus posterior to this band (e.g. recognisable "under the arrows" in Fig. 5 for *H*. (*Leptolambus*) *impressopunctatus*). Thus, this band might be interpreted as a separate part of the clypeus and—also due to the depressed clypeal grooves posterior to the band—can appear as if it was somewhat vaulted (although it is not), which might be interpreted as a (flat) bead. The structure of this band can vary considerably even among specimens of the same population of a species—in one specimen the band can appear as a flat bead, in another one found at the same locality the illusion of a bead is lacking. In all these typical members of the former subgenus *Coelambus* the anterior border of the clypeus (where it reaches/contacts the labrum) and that "clypeal line" (if present) can be recognised when the clypeus is viewed perpendicularly. Additionally, in this view it can be recognised that the anterior border of the clypeus of all these species of former subgenus *Coelambus* is not evenly rounded, but truncate and somewhat emarginated.

In members of the former subgenus *Hygrotus* the anterior border of the clypeus is evenly rounded in perpendicular view (see Fig. 44 for *H*. (s. str.) *inaequalis*). Additionally, the clypeus does not descend directly to the labrum, but is strongly and almost sharply produced forwards (see Figs. 6 and 45 for *H*. (s. str.) *inaequalis*), so that it reaches so far over the labrum that the real anterior border of the clypeus (where it reaches/contacts the labrum) cannot be recognised when the clypeus is viewed perpendicularly, as the anteriorly produced part of the clypeus covers most of the labrum and in particular the "clypeal line" (if that line is present at all). This is the reason why in species of the former subgenus *Hygrotus* it is necessary to differentiate between the anterior border of the clypeus and its anterior end, the latter being situated posterior (!) to the former. Short behind and parallel to its evenly curved anterior border the clypeus is depressed over the entire distance between the eyes; this depression is anteriorly delimited by a more or less sharp line (see Fig. 44 for *H*. (s. str.) *inaequalis*). That is why between this line and the anterior border an evenly curved "clypeal" bead is formed which has more or less the same width over its entire length.

There are two species of the former subgenus *Coelambus* that have a clypeus with almost exactly the same structure as the species of former subgenus *Hygrotus*, something that has confused generations of dytiscid specialists: *Hygrotus* (*Leptolambus*) *salinarius* and *H.* (*L.*) *masculinus* (see Figs 47 and 48 for *H*. (*L.*) *masculinus*). However, in contrast to members of the former subgenus *Hygrotus*, these two species have the anterior border of the clypeus truncate (in several specimens of *H.* (*L.*) *masculinus* at least less curved centrally than near the eyes) and also somewhat emarginated in *H.* (*L.*) *salinarius*—being in this respect typical *Hygrotus* (*Coelambus*) and not *Hygrotus* s. str.

Former genera *Hyphoporus* and *Herophydrus*

Members of former genera *Herophydrus* and *Hyphoporus* have a different structure of the anterior part of the clypeus. Whilst all former *Hyphoporus* have a complete clypeal bead which is mostly narrowed medially (see Fig. 42 for *Hygrotus* (*Hyphoporus*) *solieri*), in former *Herophydrus* some species have a complete bead, some a medially shortly interrupted bead (see Fig. 43 for *Hygrotus* (s. str.) *guineensis*) as well as others with a medially broadly interrupted bead and *Hygrotus* (s. str.) *rohani* (Peschet, 1924) with a hardly delimited bead (cf. Biström & Nilsson 2002). In those species with incomplete bead, the situation in the middle of the clypeal border is similar to that in typical *Hygrotus* (*Leptolambus*)—the anterior part of the clypeus descends anteriad more or less evenly or in a slightly convex shape to the labrum and the labrum as well as an eventual "clypeal line" are not hidden by the anterior part of the clypeus. Left and right of the bead interruption, the clypeus is widely vaulted and sometimes slightly produced forwards, however never as strongly produced as in former subgenus *Hygrotus*. The two parts of the bead are backwards either delimited by a more or less distinct line or by an anteriorly rather sharply delimited depression (as in the *inaequalis*-group of *Hygrotus* s. str.).

In members of subgenus *Hyphoporus* and those of former genus *Herophydrus* with complete bead, the anterior border of the clypeus is medially also widely vaulted and thus a little produced anteriorly. This is why in perpendicular view an eventually existing "clypeal line" and a very small posterior part of the labrum are covered by the vaulted anterior border of the clypeus. It must, however, be emphasised that these structures are totally different from those in members of former subgenus *Hygrotus*—in all these species the clypeus is by far not as strongly and not as sharply produced forwards as in the latter. Additionally, the bead or its two lateral parts are considerably broader left and right of the middle, whilst it is of more or less of equal width over its entire length in members of the former subgenus *Hygrotus*.

Species of former *Herophydrus* and *Hyphoporus* have the anterior margin of the clypeus truncate and emarginated in perpendicular view (see Fig. 43 for *guineensis*; in some species, however, this emargination is only rather indistinct), but we must concede that we have not been able to study all species and must rely in part on the figures given in Biström & Nilsson (2002).

The separation of former *Herophydrus* from *Hyphoporus* by morphological characters has been debated since long time (see e.g. Guignot 1950: 149, Vazirani 1969: 203–205, Biström & Nilsson 2002: 20–21). We did not find any satisfying solution for this problem and believe that a final classification can only be given once the molecular data of all species of these two genera are known. So far we must refer on what was given by Vazirani (1969: 204) in his key to these two genera, but add some exceptions.

According to Guignot (1950: 149; more or less repeated by Vazirani 1969: 204) in former genus *Herophydrus* the punctation of the head reaches an imaginary line connecting the hind margins of the eyes, but on a small band posterior to this line (on the vertex) this punctation is absent or at most replaced by a few much smaller punctures. In former genus *Hyphoporus* the punctation of the head reaches distinctly beyond this imaginary line and is not replaced by finer punctation. Additionally, both authors note that in *Herophydrus* the median lobe is (more or less) symmetric and in *Hyphoporus* it is not. On the other hand, Guignot (1959: 339) himself conceded that "lack of punctation in that band on the vertex" [our translation from French] does not really hold in *H.* (s. str.) *musicus* and *H.* (s. str.) *rufus*, and we must concede that we were not able to use this character for reliable identifications.

In what refers to the symmetry of the median lobe we want to underline that *Hygrotus* (*Hyphoporus*) *bengalensis* has a more or less symmetric median lobe, and on the other hand that many former *Herophydrus* have a median lobe which is at least not strictly symmetric (as can be appreciated e.g. in some figures in Biström & Nilsson 2002).

Former genus *Heroceras*

Hygrotus (s. str.) *descarpentriesi* is a species not well represented in collections; thus, some of the very few descriptions in the literature may not rely on careful studies of specimens. It is more or less known as a "*Herophydrus* with widened antennae"

(cf. Guignot 1950: 150 and Pederzani 1995: 35). Guignot (1959: 372) provided for this species: "Tête bourrelet clypéal ininterrompu, ..." [= head with clypeal bead not interrupted ...] and "... bourrelet clypéal peu marqué ..." [= ... clypeal bead not well marked ...]. Miller & Bergsten (2016: 204) gave "... having the anterior clypeal margin broadly bordered."

We have studied one male and one female syntype of this species (coll. Peschet, MNHN; see Fig. 17), one additional female from the coll. Guignot (MNHN), and several further specimens collected recently by one of us (M.M.). To our great surprise, at first glance we were not able to detect any distinct clypeal bead. Only when adequately illuminated it was possible to see that in the female syntype the clypeus is very slightly vaulted before the anterior margin. In the male syntype a few transversely stretched punctures indicate a posterior margin of a bead—however, only on the right side of the clypeus. In particular, there are absolutely no traces of a bead recognisable before the eyes. The latter observation is surprising, because even *H.* (s. str.) *nodieri*, with a very broadly interrupted clypeal bead, shows laterally distinct rests of a bead next to the eyes. Similar observations were made with the recently collected material. Additionally, we want to state that only a small posterior part of the labrum is covered by the vaulted anterior border of the clypeus—this being in contrast to Biström & Nilsson (2002: 18, 19) who stated labrum "not visible from above". On the other hand, our observation that the clypeal bead is practically lacking in former *Heroceras* is supported by Biström & Nilsson (2002: 18, 19, table 1) who gave the anterior margin of the clypeus (character 1 on p. 18) with state 0 (= without bead). These authors, however, did not comment this feature.

It shall be mentioned here that the almost total lack of a medial clypeal bead was the reason for Guignot (1950) to create his subgenus *Dryephorus* of genus *Herophydrus*. Similarly, other species of former *Herophydrus* show only rests of a bead before each eye, such as *Hygrotus* (s. str.) *heros* (Sharp, 1882) (cf. Zimmermann 1919: 150). Although in a different subgenus, *Hygrotus* (*Leptolambus*) *polonicus polonicus* (Aub, 1842) and its subspecies *sahlbergi* (Sharp, 1882) have the clypeus anteriorly somewhat vaulted (cf. Zimmermann 1930: 96). Zimmermann (1919: 150) claimed that also *Hygrotus* (*Leptolambus*) *unguicularis* might be ranged under *Hygrotus* s. str. "... wegen der feinen, aber wenigstens in der Mitte deutlichen Clypeusrandung ..." [= because of the fine, but at least medially distinct beading]. We have studied numerous specimens of *H. unguicularis* and can state that Zimmermann (1919) must have been misguided: most probably he mixed up what in Hygrotini is usually called clypeal "bead" (and which is rather broad) with what we call here "clypeal line".

Falkenström (1933: 12) noted that on the one hand *Hygrotus* (s. str.) *versicolor* (Schaller, 1783) should be ranged in *Herophydrus* due to the shape of the clypeal border (meaning a medially reduced width of the clypeal bead), but on the other hand refused this classification.

The "clypeal stripe"

As mentioned above, in many species of Hygrotini, and in particular in species of former subgenus *Coelambus*, the anterior border of the clypeus is provided with a "clypeal line". This line is in some species rather distinct, in others irregularly interrupted and in some not recognisable or absent. The distinctness of this line seems to show also some individual variation within a species. Balfour-Browne (1934: 150) pointed to a special feature of *Hygrotus* (*Coelambus*) *confluens*: at the base of the labrum, before the anterior border of the clypeus there is a flat, transverse stripe which is rather shiny, not reticulate, provided with only a very few punctures, broadest in middle and evenly tapering to the sides (Fig. 46). We interpret this "clypeal stripe" as a broadened "clypeal line". Such stripe can be also found in *H.* (*C.*) *pallidulus*, *H.* (*C.*) *caspius*, *H.* (*C.*) *pectoralis* (Motschulsky, 1860) (stripe very thin), *H.* (*C.*) *nigrolineatus*, *H.* (*C.*) *punctilineatus*, *H.* (*C.*) *enneagrammus* and in *H.* (*C.*) *flaviventris* (Motschulsky, 1860), but in all latter species this stripe is by far not as broad as in *H.* (*C.*) *confluens* and often difficult to observe, as it is strongly reduced to almost a simple line slightly broader medially than laterally. In *H.* (*C.*) *ahmeti* this "clypeal stripe" is in fact reduced to a line of more or less even width. We have found such medially very slightly broadened stripe/line also in a few other species, such as *H.* (*Leptolambus*) *marklini*, *H.* (*L.*). *fraternus*, *H.* (*L.*). *patruelis* (LeConte, 1855), and *H.* (*L.*). *pedalis*.

Finally, we want to emphasise, that this "clypeal stripe" is by no means homologous to the "clypeal bead" found in species of former *Herophydrus*, *Hyphoporus* and subgenus *Hygrotus*.