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A phylogenetic analysis of the aquatic weevil tribe Bagoini (Coleoptera: Curculionidae) based on morphological characters of adults

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Abstract

Relationships of almost all known Bagoini from the world (Holarctic, Afrotropical and Oriental Regions, and Australia) were analyzed using morphological characters. To define relationships with other Curculionidae and among the species within the tribe, 119 characters were used: 64 of these are genital structures, mainly from the males, where the penis and endophallus are endowed with many complex structures that are apparently unique in Curculionidae. In general, the genital characters appear conservative and tend to resolve relationship at more terminal levels of phylogeny. On the contrary, many external characters are strongly homoplastic, probably secondary modifications associated with their aquatic lifestyle, but which tended to resolve relationships among the lower nodes of the tree. On the basis of this analysis, we confirmed the monophyly of the tribe. Our phylogenetic reconstruction suggests a new taxonomic ordering of the tribe in genera and subgenera. The following taxa, previously considered as synonyms of *Bagous* Germar, 1817, are resurrected as valid taxa: *Hydronomus* Schoenherr, 1825 and *Memptorrhynchus* Iablokoff-Khnzorian, 1960 as genera; *Parabagous* Schilsky, 1907, *Hydronoplus* Fairmaire, 1898 (= *Pseudobagous* Sharp, 1917 **syn. n.**) (**stat. n.**) and *Macropelmus* Dejean, 1821 (= *Pnigodes* LeConte, 1876 **syn. n.**) (**stat. n.**) as subgenera. *Azollaebagous* **gen. n.** and *Hydrillaebagous* **subgen. n.** of *Bagous* are created. Among some genera, especially *Bagous* and its subgenera, we recognize a somewhat large number of species groups, distinguishable mainly by unique character states of the male genitalia. Monophyly of most of these appears well supported. Some of these groups are presently monotypic, but we ascertained that many of them have other representatives not yet described.

Key words: Bagoini, phylogeny, taxonomy, morphology, new taxa, new synonymies

Introduction

Among the approximately 62,000 known weevil species of the world (Oberprieler *et al.* 2007), less than 1% are completely aquatic in their habits. Apart from several species currently included in Brachycerinae: Erirhinini (Oberprieler 2014), a few species belonging to Conoderinae: Ceutorhynchini (Prena *et al.* 2014), and a number of species of Cryptorhynchini: *Tyloderma* Say, 1831 (Wibmer 1981; 1989, as Cryptorhynchinae; Lyal 2014), most aquatic weevils are in the presently monotypic (and *incertae sedis*) tribe Bagoini (Oberprieler *et al.* 2014). The genus *Bagous* Germar, 1817 is distributed world-wide, except for Central and South America (Skuhrovec *et al.* 2011; Oberprieler *et al.* 2014), and is a species-rich and morphologically heterogenous assemblage including 350 described species, 268 of which appear to be possibly valid species (R. Caldara pers. obs.).

A good taxonomic knowledge of Bagoini appears particularly useful for two important reasons. The first is that these species are environmental indicators of fresh water quality, and are susceptible to habitat changes (Sprick 2001). For this reason, unfortunately several of them are threatened or even at risk of extinction. The most important factors causing a relevant decrease in *Bagous* populations are devastation of biotopes/habitats (disposal of small water pools, clearing of ditches, draining of meadows), water pollution (by herbicides, pesticides and nitrogenous compounds), eutrophication and destruction of host-plants (*e.g.*, by motor boats) or their decreasing as a result of competition with anthropogenic plants (e. g. occurrence of green algae) (Sprick 2001; Stals 2008; Skuhrovec *et al.* 2011; Gosik 2013). Moreover, in the monophagous species all factors responsible for the decrease of the host-plants are to be added to those directly affecting the weevils. Given the low dispersion/dispersal capability of the majority of *Bagous* species, many of their populations should be regarded as a relic of the Ice Age, and a possibility of a successful spreading or redistribution seems to be unlikely (Sprick 2001; Skuhrovec *et al.* 2011).

The second reason is that some *Bagous* species have been used as biological control agents against those of their host plants that have been introduced to various countries where they have become invasive. In the U.S.A, the Indian species *B. affinis* Hustache, 1926 and the Australian species *B. hydrillae* O'Brien, 1992 were introduced as biological control agents of *Hydrilla verticillata* (L. f.) Royle (Buckingham 1988; Buckingham & Bennett 1998; O'Brien & Pajni 1989; Wheeler & Center 1997; Center *et al.* 2013), and some Palaearctic species (*B. collignensis* (Herbst, 1797), *B. longitarsis* Thomson, 1868) and Oriental species (*B. geniculatodes* O'Brien, 1995, *B. vicinus* Hustache, 1926) are currently under study to determine their potential as control agents of the invasive *Myriophyllum spicatum* L. (Cock *et al.* 2008). A further study on the Palaearctic species *B. nodulosus* Gyllenhal, 1836 and *B. validus* Rosenhauer, 1847 has also begun in order to assess the potential of these species as control agents of *Butomus umbellatus* L. (Ivo Toševski pers. comm.), an invasive species that colonized rivers and lakes of Eastern Canada and North-eastern U.S.A. during the last century (Gunderson *et al.* 2016).

According to O'Brien & Askevold (1992), monophyly of Bagoini is based on the following character states: (1) scales granulate, moderately to strongly distinctly pitted; (2) rostrum shorter than pronotum; (3) rostrum with distinct well-developed dorsolateral sulcus above scrobe; (4) antennae inserted near apex of rostrum; (5) prosternum with weak rostral canal, its lateral margins low and subparallel; (6) tibiae with dorsal margin distally slightly arcuate; (7) tarsomeres 3 not bilobed, cordate to subcordate; (8) tarsomeres 3 clothed beneath with fine, dense, recumbent to subrecumbent pubescence; (9) dorsal surface of penis body fully sclerotised at least basally. The common ancestor of Bagoini might possess at least some of these characters. However, as long as presently known, no group of Curculionoidea possesses convincing characters allowing to place it as sister group of Bagoini and this is the reason why this tribe is still considered *incertae sedis*.

Historically, Bagoini were long considered as either part of the large subfamily Curculioninae (Reitter 1913; Hoffmann 1954) or else included in Erirhinini (when these were treated as a distinct subfamily: O'Brien & Marshall 1979), always based on general similarities and not on precisely defined characters. Based on the male genitalia, Kuschel (1971) distinguished Bagoinae from "true" Erirhininae, and both Thompson (1992) and Alonso-Zarazaga & Lyal (1999) followed his opinion. The placement of Bagoini in Molytinae by O'Brien *et al.* (1994) was not supported by any detailed synapomorphies, but was again based upon similarities in characters of the genitalia and tibial structure. Oberprieler *et al.* (2007) suggested that Bagoini might be related to the subfamily Brachycerinae, despite having, unlike the latter, a pedal type of aedeagus (one in which, among other features, the penis lacks a distinct dorsal sclerite, or tectum). However, more recently, Oberprieler *et al.* (2014) preferred to treat Bagoini as a tribe *incertae sedis*, emphasizing that the lack of a pedotectal type of aedeagus in Bagoini is not a major issue, since it is possible that a pedal type of aedeagus has evolved more than once. In fact, there are also a number of species included in the erirhinine genera *Echinocnemus* Schoenherr, 1843, *Cryptolarynx* van Schalkwyk, 1966, and *Tanysphyrus* Germar, 1817 that either have a tectum that is so reduced that it is barely distinct, or lack a tectum entirely. Molecular phylogenetic analyses (Marvaldi *et al.* 2002; Hunt *et al.* 2007; McKenna *et al.* 2009; Gunter *et al.* 2015) have as yet not been able to clearly elucidate the taxonomic affinities of *Bagous*, but generally placed it in the “basal” nodes of the phylogram, near the subfamilies Dryophthorinae, Platypodinae and Brachycerinae, and thus among the subfamilies lacking some apparently derived characters. Gillett *et al.* (2014) hypothesized that Bagoinae might be sister to all other Curculionidae, excluding Brachycerinae (including Erirhinini and *Ocladius* Schoenherr, 1825) and Dryophthorinae, which they considered as separated families. Finally, in the catalogue of the Australian weevils, Pullen *et al.* (2014) treated Bagoini as a tribe of Brachycerinae, without any explanation, but probably based on Oberprieler’s belief.

It has been shown that in Bagoini the study of male genitalia is fundamental for identification of species as well as for phylogenetic analysis, whereas many external characters are highly homoplastic (O'Brien & Askevold

1992; Askevold *et al.* 1994; Caldara & O'Brien 1998). From a comprehensive morphological study, especially of the complex structure of the male genitalia, Caldara & O'Brien (1998) concluded that Bagoini, as then delimited, constituted a monophyletic group composed of about 50 monophyletic species groups. For a few of them, distinct generic or subgeneric names had been previously proposed. However, the recognition of such genera or subgenera would require the erection of some 40–50 additional generic and infrageneric taxa, resulting in a very unwieldy classification system. Moreover, an important number of species from Afrotropical, Oriental and East Palaearctic Regions, and from North America were not yet revised. Caldara & O'Brien (1998) therefore proposed not to recognise any supraspecific taxa in Bagoini except for *Bagous* and provisionally decided to treat all clusters of species in this genus as informal species groups. Subsequently, all authors dealing with Bagoini followed this provisional plan (Alonso-Zarazaga & Lyal 1999, Skuhrovec *et al.* 2011, Oberprieler *et al.* 2014).

In the last decades the faunas of Australia (O'Brien & Askevold 1992), Japan (Askevold *et al.* 1994; O'Brien *et al.* 1994, 1995), the Indian subcontinent (O'Brien & Askevold 1995), and the western Palaearctic region (Caldara & O'Brien 1998) were taxonomically revised. On the basis of phylogenetic analyses, seven species groups were identified in Australia (O'Brien & Askevold 1992), and eight in Japan. Some of these groups are endemic to a single region, others have representatives in one or more other regions (Askevold *et al.* 1994; O'Brien *et al.* 1994), and phylograms were published for the species from the last two regions. Relationships among the Indian (O'Brien & Askevold 1995) and the western Palaearctic (Caldara & O'Brien 1998) taxa have also been investigated, and the known species referred to 18 (three endemic) and 24 (15 endemic) species groups respectively. However, phylograms for these taxa were not published in these two papers.

During the last ten years we have had the opportunity to examine the majority of the species described from the regions not yet taxonomically revised, mainly based on type specimens. Therefore, through analyzing more than 220 species of Bagoini, which represent about 85% of the hitherto known species, plus several still undescribed species, we are now able to infer relationships among the members of Bagoini known to occur in the entire Holarctic, Afrotropical and Oriental Regions, and those from Australia and Japan. The goal of the present analysis is to provide a comprehensive phylogenetic framework, which we view as fundamental to the task of creating a plausible taxonomic arrangement of *Bagoini*.

Material and methods

Taxon sampling. The present analysis was based on the study of 138 species previously recognized by O'Brien & Askevold (1992), Askevold *et al.* (1994), O'Brien & Askevold (1995) and Caldara & O'Brien (1998), and belonging to the Australian, Japanese, Indian, and Western Palaearctic faunas, respectively, with the addition of 74 species from the Afrotropical, Oriental, Eastern Palaearctic, and North American Regions. For the updated taxonomy of the Palaearctic species we followed Caldara (2013). We studied type specimens of 222 of the 268 known valid species. In order to test the monophyly of the ingroup (genus *Bagous sensu* Caldara & O'Brien 1998) we included nine other Curculionoidea in our analysis: Brentidae: *Apion frumentarium* (Linnaeus, 1758) (Apioninae: Apionini); Curculionidae: *Notaris scirpi* (Fabricius, 1792) and *Picia sinuatocollis* (Faust, 1885) (Brachycerinae: Erirhinini), *Lissorhoptrus oryzophilus* Kuschel, 1952 and *Tanysphyrus lemnae* (Paykull, 1792) (Brachycerinae: Tanysphyrini), *Curculio nucum* Linnaeus, 1758 (Curculioninae: Curculionini), *Ita crassirostris* Tournier, 1878 (Curculioninae: Itini), *Orthochaetes setiger* (Beck, 1817) (Curculioninae: Styphlini), and *Hylobius abietis* (Linnaeus, 1758) (Molytinae: Molytini). These species were chosen based on the hypothetical affinities previously suggested, and also considering the more recent molecular data on the possible relationships among the Bagoini and other tribes, as discussed above.

In our matrix (Table1) we generally reported the type species of all the genera and subgenera previously described in the Bagoini and the species giving the name to the groups previously proposed for Australian and Japanese species (O'Brien & Askevold 1992; Askevold *et al.* 1994), for the Indian fauna (O'Brien & Askevold 1995) and by Caldara & O'Brien (1998) for the western-Palaearctic species. Species in the non-monotypic groups that showed character states different from those of the name-bearing species of the groups were also added to the study. Species whose character states were identical to those of another species were excluded from the analysis, but they were added to the species list of each species group or taxon and, when necessary, were reported in the discussion of each group.

Phylogenetic analysis—Morphology. Characters were selected based on observable variation among the species that could be parsed into unambiguous discrete states, characters being scored based on direct observation of specimens under the stereomicroscope and photographs of the morphological structures. Genitalia were dissected manually after boiling the entire abdomen in 10% KOH, then were observed in 90% glycerol and illustrated. For terms of weevil characters we followed Lyal (2016). The matrix consists of 119 morphological characters, 55 nongenital and 64 genital, scored for 87 species of Bagoini and 9 species of other Curculionoidea (Table 1). *Apion frumentarium* was used as the root for the phylograms. Equal weight was assigned to all characters and character states. No preliminary polarity assessment was attempted, and all multi-state characters were considered non-additive. Since probabilistic analyses were also implemented, autapomorphic character-states were not excluded from the matrix. The number of characters considered in the present study increased consistently in comparison with those, 54 and 71, used respectively by O'Brien & Askevold (1992) for the Australian species, and Askevold *et al.* (1994) for the joined Australian and Japanese species. In the latter paper the character set used was only a part of a larger set, as yet unpublished, composed of 127 characters, that was developed for the study of the world Bagoini. The numeration in Askevold *et al.* (1994) followed this set of characters, with intervals in the numbered sequence after the exclusion of characters typical to extralimital species. Several of the 127 characters included in the unpublished list were also used here, although variously modified. However, after the inclusion of the supplementary species, some of the characters used by Askevold *et al.* (1994) were excluded from the analysis, since they appeared to vary more or less randomly and/or continuously in clearly unrelated taxa. They are mainly: the body shape, the presence or absence of carinae and sulci on the dorsum of the rostrum, the insertion of the antennae, the shape of the pronotal disc, the longitudinal pronotal sulcus, the shape of the elytral humeri, the presence or absence of tibial denticles, the form of the apodemes of the penis, and the form and direction of the arms of the spiculum ventrale. We added several characters concerning the shape of the antennal funicle and the scrobe, the vestiture of the rostrum and the elytra, and some characters of the genitalia (especially the structure of the sclerites of the endophallus and the shape of the apodemes of the spiculum ventrale), which proved very useful for inferring relationships at genus-rank. However, the general plan of the Bagoini proposed by O'Brien & Askevold (1992) and Askevold *et al.* (1994) was only slightly modified in the present study.

Some particular structures of the penis need a brief explanation: (1) a basal plate, *i.e.*, a proximal extension of the ventral surface of the penis body between the apodemes visible in dorsal view (many species of the *B. bipunctatus*, *B. binodulus* and *B. argillaceus* groups: Figs 5E–F); (2) a dorsal process, projecting from the posterolateral margin of the orifice and concealing it at least in part, fused to the penis body and incapable of rotation or longitudinal articulation (characterising a possibly monophyletic lineage composed of several groups) (Figs 7D–I, 8B–D); (3) a "false" dorsal process, similar to the dorsal process but formed by flexible sclerites (in the *B. biimpressus* group; *e.g.*, *B. geniculatus*: Fig. 7A); (4) a setal brush, *i.e.*, a group of dense long setae usually projecting mesad, often associated with the dorsal process (the *B. brevis*, *B. collignensis* and *B. biimpressus* groups; *e.g.*, *B. geniculatus*: Figs 7E–I); (5) denticles, *i.e.*, fine asperities just discernable under a light microscope and best seen from above, occurring in three locations: on the lateral margin distally of the dorsal process and projecting distad (*e.g.*, the *B. frit* group: Fig. 8C), on the dorsal process on what appears to be the internal surface when the dorsal process is open (*e.g.*, the *B. frit* and *B. transversus* groups: Figs 7F–G, 8C) or in the endophallus, of different sizes, shapes and densities at particular locations (*e.g.*, the *B. bipunctatus* and *B. lutosus* groups); (6) a number of various endophallic sclerites located near the orifice or within the tube (*i.e.*, the part of the body of the penis excluding the orificial portion) or proximally between the apodemes and varying in size, shape and complexity, from the simplest U- to V-shaped (Figs 5A–F, 6C–F) to an ensemble of articulated and fused, cylindrical, clavate to horn-like or flattened, triangular to rectangular to blade-like structures, sometimes with groups of setae intermixed (it is noteworthy that all the species with a dorsal process lack sclerites of the endophallus at its base, between the apodemes, and within the tube of the penis body: Figs 6G–I); (7) the distal and proximal orificial margins, the former generally fairly distinct but the latter typically indistinct, membranous and forming the point of evagination of the endophallus but occasionally distinct and extended into a prominent dorsal sac-supporting sclerite, or concealed in species with a dorsal process; (8) an orificial plate, *i.e.*, a moveable, more or less sclerotised distal extension of the dorsal surface of the penis body covering part of the orifice and varying in size and shape (*e.g.*, the *B. lutosus* and *B. tempestivus* groups), horizontal and directed anteriad in repose when the orifice is closed but vertical when the orifice is open (Figs 6B, 6E); (9) a very unusual ventral process fused directly to the ventral surface of the penis body, incapable of rotation or longitudinal articulation and projecting dorsad (*e.g.*, the *B. cylindricus* group: Fig. 6G).

Parsimony analysis (MP) was performed with TNT 1.1 (Goloboff *et al.* 2008) with a script supplied with the package (aquickie.run). The script provides the maximum parsimony tree, with symmetric resampling and Bremer support; synapomorphies are mapped onto the tree branches. However, the script was slightly modified to increase statistical validity of the analysis: optimal score was set to 1000 replications, instead of 20, and symmetric resampling was set to 1000 replications, instead of 100. Tree statistics were calculated using a TNT script (stats.run) supplied with the package.

The maximum likelihood (ML) tree was inferred with raxmlGUI1.1 (Silvestro & Michalak 2012) using a MarkovK + Γ model. Support values were computed with 1000 bootstrap replications.

Bayesian inference (BI) was performed using MrBayes 3.2 (Ronquist *et al.* 2012). We ran two runs with 4 MCMC chains, each for 1 million generations under a binary MarkovK + Γ model, sampling every 200 generations. The first 25% generations were discarded (burn-in) and convergence was evaluated with the average standard deviation of split frequencies. Goodness of mixing was assessed by looking at the acceptance rate of swaps between adjacent chains, following Ronquist *et al.* (2009).

One of our analyses included only the type species of each genus-rank taxon in the tribe Bagoini, regardless of its present day interpretation as a valid taxon or a synonym (type-species analysis from here on). This was done to ascertain relationships among the genus-rank taxa, as defined by their type-species, and confirm or reject the present day classification. A further analysis included all the taxa in the tribe, and it was carried out in order to give a precise generic attribution to all the species, to delimit the field of morphological variation within each genus, and to recognize cases of uncertainty in the generic placement of some species (all-species analysis from here on). Trees were examined with Figtree 1.4.2 (Rambaut 2014), and graphically enhanced with Photoshop CS3 (Adobe Systems Inc.).

Phylogenetic analysis—mtCOI. The mitochondrial cytochrome oxydase subunit 1 sequences were retrieved from GenBank for all the available *Bagous* species. Eight additional sequences [*B. bagdatensis* Pic, 1904, *B. lutulentus* (Gyllenhal, 1813), *B. robustus* Brisout de Barneville, 1863, *B. exilis* Jacquelin duVal, 1854, *B. monanthiphagus* Stüben, 2010, *B. elegans* (Fabricius, 1801), *B. petro* (Herbst, 1795) and *B. binodulus* (Gyllenhal, 1813)] were provided by P. Stüben and A. Schütte, who recently studied them (Stüben *et al.* 2015). Two more sequences were provided by I. Toševski [*B. nodulosus* (Gyllenhal, 1836) and *B. argillaceus* (Gyllenhal, 1836)]. These ten sequences have been assigned GenBank accession numbers and will be uploaded to GenBank. Sequences of the other Curculionoidea species used for the morphological analysis were also retrieved from GenBank. BI was performed using MrBayes 3.2. Two runs with 4 chains were run for 1 million generations, sampling every 200 generations. The chains were left free to sample all the models of the GTR family using a reversible jump Monte Carlo Markov Chain (MCMC) (Huelsenbeck *et al.* 2004). Heterogeneity of substitution rates among different sites was modeled with a 4 categories discretized Γ distribution and with a proportion of invariable sites. The first 25% of generations were discarded (burn-in) and convergence was evaluated with the average standard deviation of split frequencies. Goodness of mixing was assessed looking at the acceptance rate of swaps between adjacent chains, following Ronquist *et al.* (2009).

We considered a group to be not supported if support values [posterior probability (ps) in BI, bootstrap (bs) % in ML and symmetric resampling (sr) in MP] were below 50%; weakly supported if between 50 and 79%, moderately supported if between 80 and 89%, and strongly supported if values were 90% or higher.

Abbreviations and symbols used in the species lists: AFR=Afrotropical Region; AUS=Australia; NAR=North American Region; ORR=Oriental Region; PAL=Palaearctic Region.

Species labeled with an * were used in the phylogenetic analysis based on morphology. The small number in apices before the species name in the checklists of each taxon and species group identifies the species that had the same sequence of character states. These species were therefore grouped in the matrix under a single species, that is labeled with an *. Species labeled with § were used in the phylogenetic analysis based on mtCOI.

List of characters

The characters with the numbers used by Askevold *et al.* (1994) in the previous most comprehensive phylogenetic study, including Australian and Japanese species, are reported in parentheses.

External structures

char. 1. Body length (rostrum excluded) (char. 76 in Askevold *et al.* 1994).
 0. >2.2 mm.
 1. <2.0 mm.

char. 2. Scales, structure (char. 77 in Askevold *et al.* 1994, modified).
 0. all flat, not pitted.
 1. partly not pitted and partly pitted.
 2. all pitted.

char. 3. If char. 2≠0, type of pitted scales.
 0. with several pits (Figs 1E, 2C).
 1. with a single pit (Fig. 2B).

char. 4. Rostrum, length (char. 78 in Askevold *et al.* 1994, modified).
 0. long to moderately short (length/width > 4).
 1. distinctly short (length/width < 3).

char. 5. Rostrum, sexual dimorphism in cross-section.
 0. no dimorphism.
 1. subquadrate in male, cylindrical in female.

char. 6. Rostrum, dorsal surface at point of antennal insertion (char. 82, in Askevold *et al.* 1994).
 0. flat to regularly convex (Figs 1A, 1C).
 1. distinctly angulate (Fig. 1D).

char. 7. Rostrum, curvature of ventral margin in lateral view.
 0. moderately curved (Fig. 1D).
 1. strongly curved (Fig. 1B).
 2. straight.

char. 8. Rostrum, dorsal apical third.
 0. more or less uniformly convex (Fig. 1H).
 1. flattened (Figs 1B, 1D, 1F).

char. 9. Rostrum, apex.
 0. laterally not carinate.
 1. laterally carinate (Fig. 1F).

char. 10. Rostrum, suprascrobal sulcus (char. 80 in Askevold *et al.* 1994).
 0. absent.
 1. present, more or less distinct (Figs 1C–D).

char. 11. Rostrum, apical lateral and dorsal setae.
 0. absent or very few (Fig. 1A).
 1. numerous (Fig. 1B).

char. 12. Rostrum, setae and/or scales at middle 1/3 of ventral margin.
 0. sparse.
 1. numerous.
 2. very numerous, arranged in a dense fringe (Figs 1C, 2D).

char. 13. Rostrum, setae at basal 2/3 of rostrum, laterally.
0. irregularly spaced.
1. with row of regularly spaced setae along entire lateral margin close to ventral margin (Fig. 1F).

char. 14. Scrobe, vestiture.
0. glabrous (Figs 1B–C).
1. squamose (Fig. 1A).

char. 15. Scrobe in dorsal view, visibility.
0. at most visible at antennal insertion (Fig. 1F).
1. visible for entire length (Fig. 1G).

char. 16. Scrobe in lateral view, direction.
0. oblique to length of rostrum.
1. parallel to length of rostrum (Figs 1A–B).

char. 17. If char. 16=1, extension of scrobe.
0. reaching eye (Figs 1B, 1D).
1. not reaching eye (Fig. 1A).

char. 18. Antennal scape, insertion.
0. lateral (Fig. 1H).
1. laterodorsal (Figs 1E–G).

char. 19. Antennae, funicle.
0. with 7 segments.
1. with 6 segments.

char. 20. If char. 19=0, length of seventh funicular segment.
0. transverse (Fig. 2D).
1. at least as long as wide (Fig. 2E).

char. 21. If char. 19=0, width of seventh funicular segment in relation to sixth funicular segment.
0. wider than sixth.
1. nearly as wide as sixth (Figs 2D,–E).

char. 22. Antennae, sixth funicular segment.
0. with pubescence as dense as on segments 1–5.
1. with pubescence denser than on segments 1–5.

char. 23. Antennal club structure.
0. more or less uniformly pubescent (Fig. 2D).
1. glabrous (Fig. 2E).

char. 24. Forehead between eyes, median depression.
0. not sulcate nor foveate (Figs 1E–F, 1H).
1. sulcate or foveate (Fig. 1G).

char. 25. Upper margin of eye.
0. at a level under that of the forehead.
1. at a level slightly over that of the forehead.

char. 26. Pronotum, length.
0. Pronotum 0.85x or less as long as broad.
1. Pronotum 0.90x or more as long as broad.

char. 27. Pronotum, sides.
0. without tubercles (Fig. 2B).
1. with prominent tubercle (Fig. 2A).

char. 28. Pronotal disc, vestiture.
0. without scales emarginate at apex.
1. with sublunate scales, distinctly emarginate at apex.

char. 29. Basal portion of pronotum.
0. covered with more or less round scales.
1. broadly covered with plumose scales (Fig. 2C).

char. 30. Prosternal-postocular lobe area.
0. ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin (Figs 3A, 3B, 3D).
1. ventrally distinct, moderately to markedly raised, forming discontinuity with anterior prosternal margin and with anterior point of lateral margin of rostral canal (Fig. 3C).

char. 31. Prosternum, rostral canal (char. 103 in Askevold *et al.* 1994).
0. absent (Fig. 3A, 3D).
1. weak (Fig. 3B).
2. deep (Fig. 3C).

char. 32. Prosternum, basal transverse ridge.
0. absent.
1. weak.
2. distinct (Fig. 3D).

char. 33. If char. 31≠0, prosternum, postero-lateral margins of rostral canal (char. 104 in Askevold *et al.* 1994).
0. barely raised.
1. sharply raised, markedly rounded or subacute just in front of coxae (Fig. 3C).
2. strongly acute and projecting posterad over procoxae.

char. 34. Elytra, shape.
0. rectangular (Fig. 4C).
1. subquadrate (Fig. 4A).

char. 35. Base of elytral intervals.
0. squamulate.
1. glabrous (Fig. 2C).

char. 36. Declivital callus of fifth elytral interval (char. 116 in Askevold *et al.* 1994).
0. absent (Figs 3E, 4A).
1. present, although sometimes barely developed (Figs 3F–G, 4C).

char. 37. Elytra, posterior declivity in lateral view.
0. moderate, <60 degrees (Fig. 4D).
1. strong, at least 75 degrees (Fig. 4B).

char. 38. Apex of elytron.
0. convex, but not acuminate.
1. moderately acuminate.
2. very strongly acuminate (Fig. 3F).
char. 39. Vestiture of elytral intervals, vittate pattern.
0. absent.
1. present to apex (Fig. 3F).
2. present only in basal 2/3.

char. 40. Vestiture of elytra, semicircular white fascia at posterior third.
0. absent (Figs 4C–D).
1. present (Figs 4A–B).

char. 41. Arrangement of scales of elytral intervals (char. 106 in Askevold *et al.* 1994).
0. irregularly arranged, each interval with more than two rows of tightly fitting scales.
1. arranged in regular pairs, side by side, each interval with two, individually distinct rows of round scales.

char. 42. Elytral strial punctures.
0. small (Figs 3E–F).
1. large, from one third to more than a half of interval width (Fig. 2H).

char. 43. Abdomen, punctures (more clearly visible after removal of scales).
0. small (Fig. 4H).
1. large (Fig. 4G).

char. 44. Ventrite 5, impression.
0. without median impression.
1. with shallow to moderately shallow median impression (Fig. 4F).
2. with median impression with weakly carinate margin (Fig. 4E).

char. 45. If char. 44=2, ventrite 5, median impression with carinate margin.
0. without setae.
1. bearing row of long setae (Fig. 4E).

char. 46. Ventrite 5, sides.
0. without pit with setae.
1. with a pit with 1–4 pairs of setae (Fig. 4F).

char. 47. Tibiae, swimming hairs (char. 121 in Askevold *et al.* 1994).
0. Tibiae with bristles of inner margin of moderate length, not longer than diameter of tibia (Figs 3H–I).
1. Tibiae with long fine swimming hairs, many of them much longer than diameter of tibia (Fig. 3J).

char. 48. Tibiae, outer margin (character especially visible on hind tibiae in lateral view).
0. straight or nearly so toward apex (Figs 3–I).
1. slightly to strongly arcuate toward apex (Fig. 3J).

char. 49. Tibiae, inner margin (char. 123 in Askevold *et al.* 1994).
0. from base to point of arcuation, slightly to markedly arcuate, inner margin appearing somewhat sinuate (Figs 3H, 3I).
1. with outer and inner margin more or less parallel to apex (Fig. 3J).

char. 50. Tibiae, inner margin.
0. without large submedian tooth (Fig. 3J).
1. with large submedian tooth (Fig. 3I).

char. 51. Tarsomere 2, shape (char. 125 in Askevold *et al.* 1994, modified).
0. weakly to distinctly longer than wide (Fig. 2G).
1. distinctly transverse (Fig. 2F).

char. 52. Tarsomere 3, shape (char. 125 in Askevold *et al.* 1994, modified).
0. completely bilobed.
1. not bilobed (Fig. 2G), at most very broadly cordate (Fig. 2F).

char. 53. Tarsomere 3, pubescence (char. 126 in Askevold *et al.* 1994).
0. clothed beneath with dense, erect pubescence.
1. clothed beneath with fine to coarse, dense, recumbent to subrecumbent pubescence (Fig. 3H).
2. subglabrous beneath, with few long setae (Fig. 3J).

char. 54. Apical margin of female tergite VII, thickness.
0. relatively thin.
1. thickened.

char. 55. Apical margin of female tergite VII, shape.
0. rounded to bluntly rounded.
1. truncate to slightly emarginate.
2. deeply emarginate.

MALE GENITAL CHARACTERS

char. 56. Aedeagus.
0. of pedotectal type (with tectum).
1. of pedal type (without tectum).

char. 57. Penis body, length.
0. length / width > 4 (Figs 6F–G, 8C–D).
1. length / width < 3 (Figs 5A–B).

char. 58. Penis body in cross-section (char. 52 in Askevold *et al.* 1994).
0. cylindrical to subcylindrical.
1. T-shaped, the sides deeply compressed in basal two thirds and almost meeting at midline.

char. 59. Penis body, apex.
0. rounded to more or less acute, but not sagittate (Fig. 7F).
1. more or less sagittate (Figs 6H, 7E).

char. 60. Penis body, apex.
0. without long pili.
1. with long pili (Fig. 5D).

char. 61. Penis body, apical part (char. 36 in Askevold *et al.* 1994).
0. symmetrical.
1. asymmetrically deflected to left (Fig. 8C).

char. 62. Penis body, dorsally (char. 42 in Askevold *et al.* 1994).

0. without longitudinal furrows.

1. with dorsolateral, longitudinal furrows, one on each side, forming acute, raised margin extending from behind orifice to midlength or further, and dorsal surface markedly convex but depressed below level of lateral margin.

char. 63. Penis body, dorsal surface.

0. sclerotized.

1. with sclerotized area greatly reduced and present only as a narrow basal bridge (Fig. 5H).

char. 64. Penis body, dorsal surface at base (char. 27 in Askevold *et al.* 1994).

0. more or less emarginate (Fig. 6G).

1. truncate (Fig. 6C).

char. 65. Penis body, shape ventrolaterally (char. 31 in Askevold *et al.* 1994).

0. uniformly rounded, without oval lobe.

1. with oval lobe in apical third (Fig. 7B).

char. 66. Penis body, lateral margin laterad and distad of orifice.

0. smooth.

1. denticulate (Fig. 8C).

char. 67. Penis body, sides.

0. completely sclerotized.

1. partly membranous (Fig. 8A).

char. 68. Penis body, shape ventrally (char. 26 in Askevold *et al.* 1994).

0. uniformly rounded.

1. triangular in cross-section, at about median region.

char. 69. Penis body, ventrobasally (in lateral view).

0. with ventral outline continuous to base.

1. with ventrobasal notch (Fig. 6D).

char. 70. Penis body, ventrobasal margin (char. 29 in Askevold *et al.* 1994).

0. not extending posteriorly (Fig. 5B).

1. with short, ventrobasal plate extending between apodemes, not forming an acute median point visible from above (Fig. 5F).

2. with short, ventrobasal plate extending between apodemes, forming an acute median point visible from above (Fig. 5E).

char. 71. Penis body, shape ventrobasally (char. 30 in Askevold *et al.* 1994).

0. uniformly rounded.

1. ventrobasal area medially depressed, ventrolaterally slightly costate at base.

2. ventrobasal area medially depressed, ventrolaterally distinctly bicarinate from apodeme to about one-third of length of penis body.

char. 72. Penis body, ventral longitudinal furrow.

0. ventrally convex to nearly flattened.

1. with subapical, ventral depression extending toward base and forming shallow to prominent sulcus.

char. 73. Penis body, orifice (char. 16 in Askevold *et al.* 1994, modified).

0. without long setal brush.

1. with long setal brush (Fig. 7H).

char. 74. Penis body, laminar orificial lateral sclerites.
0. absent.
1. present although in some species only distinguishable at apical portion (Figs 5A–B, 5E, 5G, 6A, 6C).
char. 75. If char. 74=1, position of orificial lateral sclerites.
0. flat in more or less same level.
1. obliquely uniformly raised.
2. raised and basally recurved upwards.

char. 76. If char. 74=1, lateral margin of orificial lateral sclerites.
0. not reaching anterior margin of orifice (Figs 5E–F).
1. reaching anterior margin of orifice (Fig. 6A).

char. 77. If char. 74=1, attachment of orificial lateral sclerites apically.
0. apex not attached to sides of penis body (Fig. 6C).
1. apically attached to sides of penis body (Fig. 7A).

char. 78. If char. 74=1, movement of orificial lateral sclerites.
0. immovable.
1. distinctly laterally movable (Fig. 7A).

char. 79. Penis body, horizontal dorsal plate of orifice.
0. absent.
1. bell-shaped (Fig. 5C).
2. heart-shaped (Fig. 7C).
3. oval (Fig. 6B).
4. elongate-rectangular (Fig. 6E).

char. 80. If char. 79≠0, movement of dorsal plate over orifice of penis body.
0. immovable (Figs 5C, 7C).
1. movable (Figs 6B, 6E).

char. 81. If char. 79≠0, sclerite of dorsal plate over orifice of penis body.
0. without median sclerite rising from orificial sclerites.
1. with orificial margin rising to form submedian elongate sac-supporting sclerite (Figs 6B, 6E).

char. 82. Penis body, median orificial sclerites, shape (char. 1 in Askevold *et al.* 1994, modified).
0. absent.
1. with U-shaped, hooked process (Fig. 7B).
2. with U-shaped, hemispherical sclerite.
3. with upturned Y-shaped process (Fig. 6F).

char. 83. Penis body, sclerite of dorsal area of orifice (char. 8 in Askevold *et al.* 1994).
0. orifice without lateral sclerite.
1. orifice with lateral, transverse vertical sclerite (Fig. 7D).

char. 84. Sclerites complex within tube of penis body, shape.
0. absent.
1. with a pair of submedian, subapical sclerites well separated from each other (Figs 5E, 6C).
2. with a pair of submedian, subapical sclerites posteriorly joined (Fig. 6H).
3. with a pair of submedian, subbasal sclerites well separated from each other.

4. with two pairs of subapical sclerites: a submedian pair, with sclerites adpressed together and a sublateral pair, with sclerites posteriorly joined (Fig. 6I).
5. with two pairs of subapical sclerites: a submedian pair, with sclerites well separated from each other and a sublateral pair, posteriorly joined (Fig. 6G).

char. 85. If char. 84=5, penis body, ventrally.
0. without sclerites fused to ventral portion.
1. with a median sclerite fused to ventral portion and not movable (Fig. 6G).

char. 86. If char. 84=1, shape of submedian sclerites.
0. subtriangular with point at apex (Fig. 6C).
1. subtriangular with point at base (Fig. 5E).

char. 87. Spicules and denticles within tube of penis body.
0. absent or distributed more or less uniformly, not forming large, concentrated areas.
1. with a pair of lateral concentrations of numerous fine denticles (Fig. 5F).
2. with a pair of lateral concentrations of sparse large denticles.

char. 88. Sclerite complex within tube of penis body (char. 2 in Askevold *et al.* 1994).
0. not entwined by spicules.
1. entwined by many very small spicules (Fig. 6E).

char. 89. Subbasal spicules of endophallus (char. 2 in Askevold *et al.* 1994, modified).
0. absent or very fine and distributed more or less uniformly, not forming concentrated areas.
1. with subbasal pair of dense concentrations of fine elongate spicules (Fig. 6A).
2. with many large spicules (Fig. 5C).

char. 90. Basal sclerites of endophallus.
0. absent.
1. with two pairs of subclavate sclerites variously articulated (Fig. 5C, 5D).
2. with two elongate curved sclerites (Fig. 5B).
3. with two overlapped plates (Fig. 5A).
4 with two pairs of flat sclerites (Fig. 5E).
5 with axe-shaped sclerite.
6. with hook-shaped sclerite.

char. 91. Base of endophallus, spiculate sacule (char. 2 in Askevold *et al.* 1994).
0. absent.
1. with sacule containing elongate, curved spicules forming dark, somewhat paired mass (Fig. 6A).
2. with sacule containing elongate, curved spicules uniformly arranged.

char. 92. Median setal brush behind orifice of penis body.
0. absent.
1. situated at base of subapical sclerites (Fig. 7A).
2. situated on anterior surface of dorsal process (for dorsal process see char. 93) (Figs 7E, 7G–I, 8B–C).
3. situated on ventral surface of dorsal process (for dorsal process see char. 93).

char. 93. Post-orificial area of penis body ("dorsal process") (char. 14 in Askevold *et al.* 1994).
0. absent.
1. with immovable sclerotized process arising from and attached to each postero-lateral angle of orifice (Figs 7D–G, 8B–D).

char. 94. If char. 93=1, dorsal process, apex.
0. not directed basad.
1. directed basad.

char. 95. If char. 93=1, dorsal process in lateral view.
0. without sclerotized subtriangular plate behind dorsal process.
1. with sclerotized subtriangular plate behind dorsal process.

char. 96. If char. 93=1, dorsal process laterally.
0. not semicircular.
1. semicircular, with anterior concavity (Figs 7E, 8B, 8D).

char. 97. If char. 93=1, penis body (char. 44 in Askevold *et al.* 1994, modified).
0. widest just after dorsal process.
1. widest in front of dorsal process (Figs 7F, 7I, 8B–D).

char. 98. If char. 93=1, dorsal process, direction.
0. directed more or less vertically (Fig. 7G).
1. almost horizontal, directed apicad (Fig. 8D).

char. 99. If char. 93=1, dorsal surface of penis body, behind dorsal process (char. 15 in Askevold *et al.* 1994).
0. convex.
1. with broad depression (Fig. 8D).

char. 100. If char. 93=1, inner surface of dorsal process (char. 17 in Askevold *et al.* 1994).
0. lacking denticles (Fig. 7E).
1. covered with dense area of denticles (Fig. 7F, 8C detail).

char. 101. If char. 93=1, dorsal process.
0. without lateral wings.
1. with lateral wings (Fig. 8B).

char. 102. If char. 93=1, lateral margin of penis body at base of dorsal process (char. 19 in Askevold *et al.* 1994).
0. simple.
1. with subapical lateral incision (Fig. 7G).

char. 103. If char. 93=1, lateral margin of penis body behind dorsal process.
0. moderately rounded.
1. acute (Fig. 7E).

char. 104. If char. 93=1, sides of penis body behind dorsal process.
0. rectilinear to slightly curvilinear.
1. distinctly swollen.

char. 105. If char. 93=1, sublateral margin of penis body behind dorsal process (char. 20 in Askevold *et al.* 1994, modified).
0. without denticles.
1. denticulate (Fig. 8C).

char. 106. If char. 93=1, sublateral margin of penis body behind dorsal process (char. 20 in Askevold *et al.* 1994, modified).
0. dorsally uniformly rounded behind dorsal process.
1. with dorsal, sublateral, carinate ridge bordering median depression behind dorsal process (Fig. 7I).
2. with dorsal, sublateral, carinate, V-shaped ridge bordering median depression behind dorsal process (Fig. 8C).

char. 107. If char. 93=1, shape of penis body immediately proximad of dorsal process.

0. more or less parallel-sided at midlength (Fig. 7E).
1. markedly constricted immediately proximad of dorsal process (Fig. 7F).

char. 108. If char. 93=1, lateral margin of penis body behind dorsal process.
0. rounded.
1. markedly carinate behind dorsal process, surface ventral to carina markedly excavate, dorsal surface mesad of carina markedly depressed.

char. 109. If char. 93=1, dorsal surface of penis body, medially, behind dorsal process.
0. more or less uniformly convex.
1. more or less markedly raised, forming acute, longitudinal, median carina.

char. 110. Penis apodemes, length.
0. long, slender, usually at least one-half as long as penis body (Figs 5A–H, 6A).
1. short, at most one-third as long as penis body (Figs 6B–C, 6F–G, 8B–C).
2. extremely short, almost obliterated.

char. 111. Tegmen, parameroid lobes.
0. distinct.
1. very short.
2. absent.

FEMALE GENITAL CHARACTERS

char. 112. Arms of spiculum ventrale, direction (char. 61 in Askevold *et al.* 1994).
0. with inner margins divergent or subparallel to apex.
1. with inner margins strongly convergent, joined at ca. midlength.

char. 113. Arms of spiculum ventrale, apical setae.
0. short (Figs 8E–F).
1. long (Fig. 8H).

char. 114. Apodemes of spiculum ventrale, shape.
0. parallel, subparallel or contiguous for most of length (Y-shaped) (Fig. 8E, 8H).
1. very broadly and arcuately divergent from base (U-shaped) (Fig. 8G).
2. fully bifurcated, arising laterally on plate of sternite (Fig. 8F).

char. 115. Insertion of spermathecal gland.
0. attached on ramus at apex of body, generally with ramus protruding slightly past body.
1. attached on body, anteapically.

char. 116. Bursa, sclerites.
0. absent.
1. present (Fig. 8I).

char. 117. Gonocoxite, stylus.
0. present, distinct (Fig. 8K).
1. absent (Fig. 8J).

char. 118. Gonocoxite.
0. rectilinear.
1. sinuate.

char. 119. Gonocoxite.
0. at most with a few setae (Fig 8K).
1. densely setose (Fig. 8J).

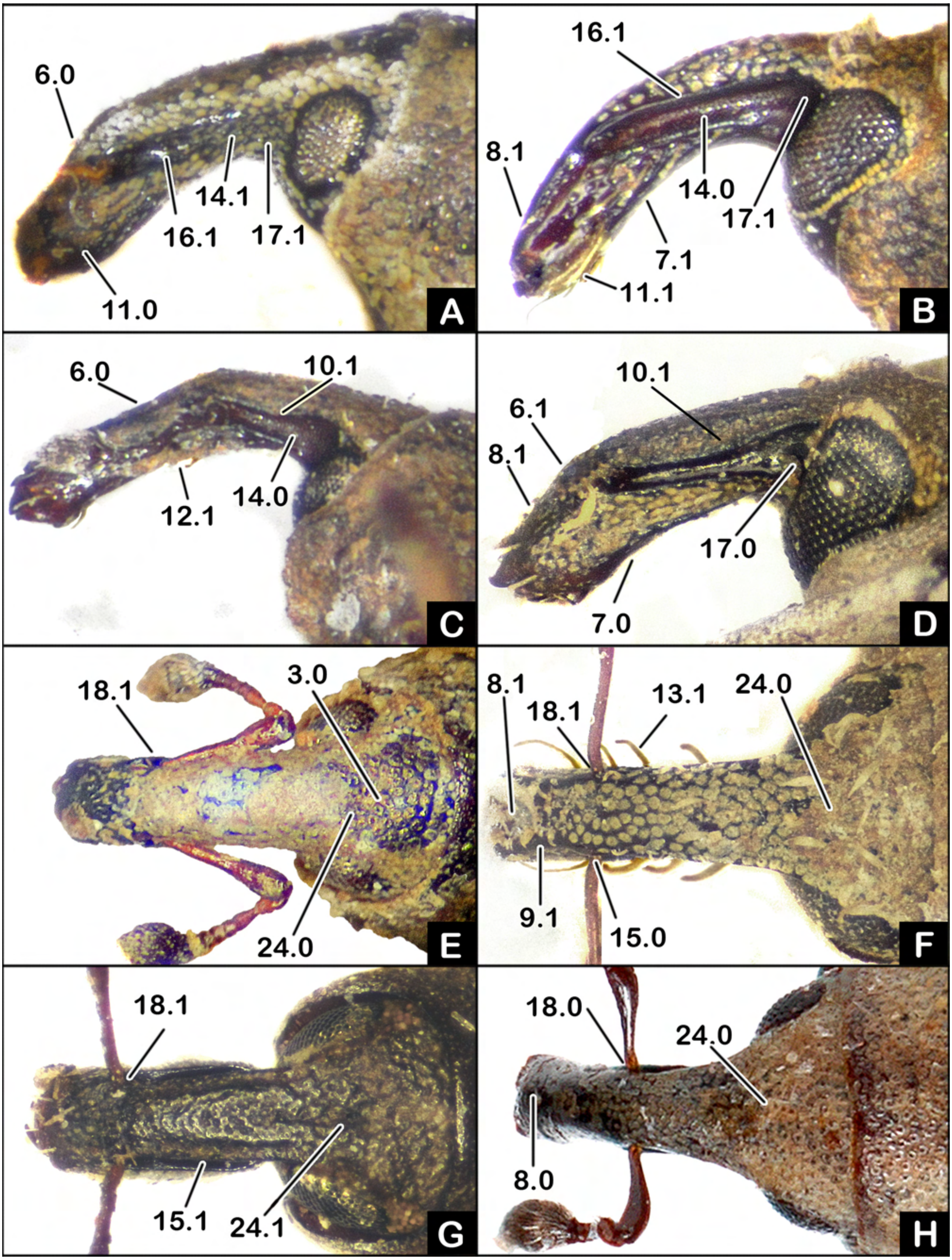

FIGURE 1. Rostrum in lateral view of (A) *Hydronomus alismatis*; (B) *Memptorrhynchus crispus*; (C*) Bagous* (*Parabagous*) *guttatus*; (D) *Bagous* (*Hydronoplus*) *longulus*. Rostrum in dorsal view of (E) *Hydronomus alismatis*; (F) *Memptorrhynchus crispus*; (G) *Bagous* (*Hydronoplus*) *longulus*; (H) *Bagous* (*Macropelmus*) *tubulus*. Not at the same scale. Scale references are not reported in this and following figures since the illustrations are only meant to show the characters used for the phylogenetic inference.

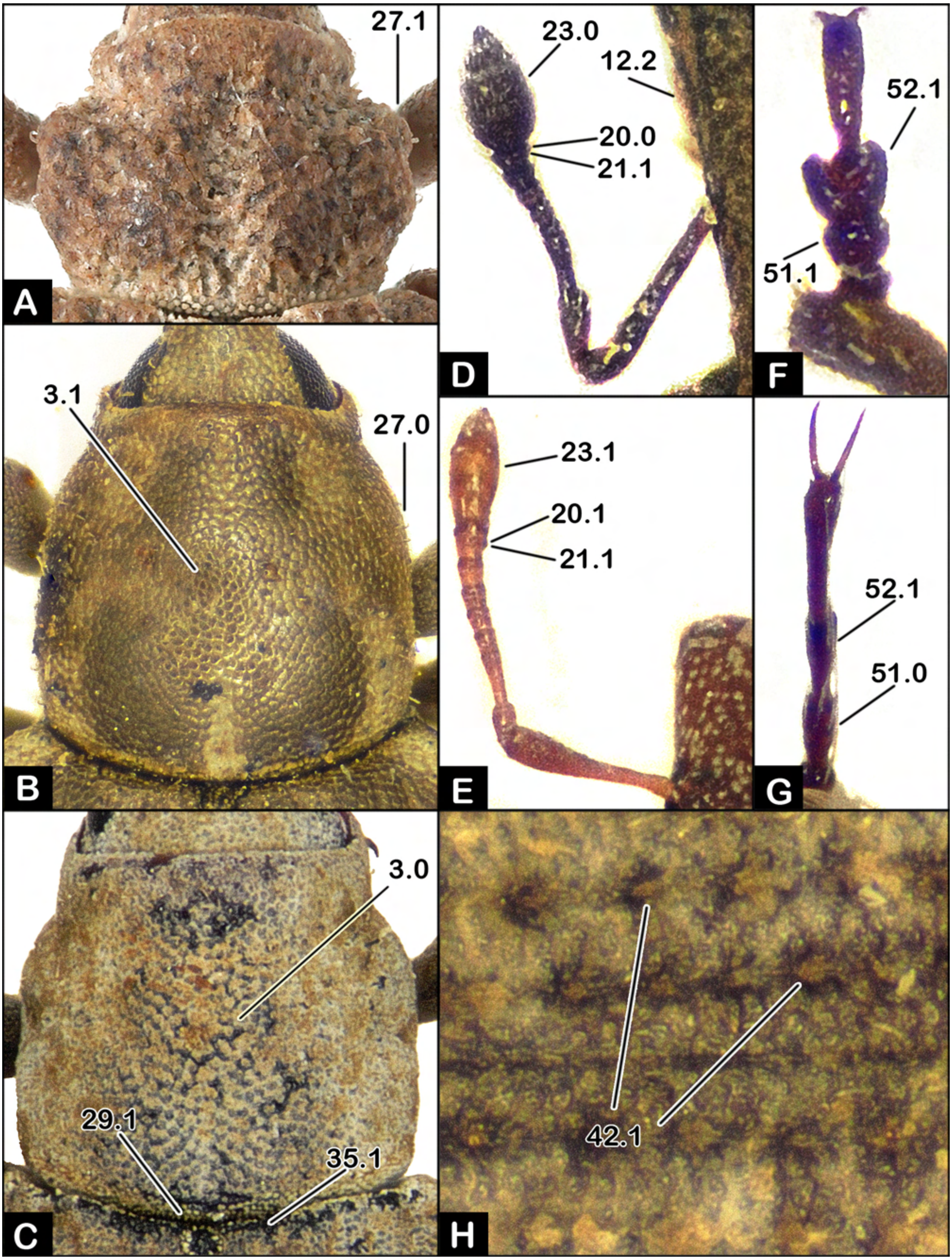

FIGURE 2. Pronotum of (A) *Bagous* (*Macropelmus*) *setosus*; (B) *Bagous* (*Macropelmus*) *argillaceus*; (C) *Bagous* (*Bagous*) *binodulus*. Antenna of (D) *Bagous* (*Parabagous*) *guttatus*; (E) *Bagous* (*Macropelmus*) *geniculatus*. Fore tarsus of (F) *Bagous* (*Parabagous*) *guttatus*; (G) *Bagous* (*Macropelmus*) *trapae*. Detail of elytra of (H) *Bagous* (*Macropelmus*) *limosus*. Not at the same scale.

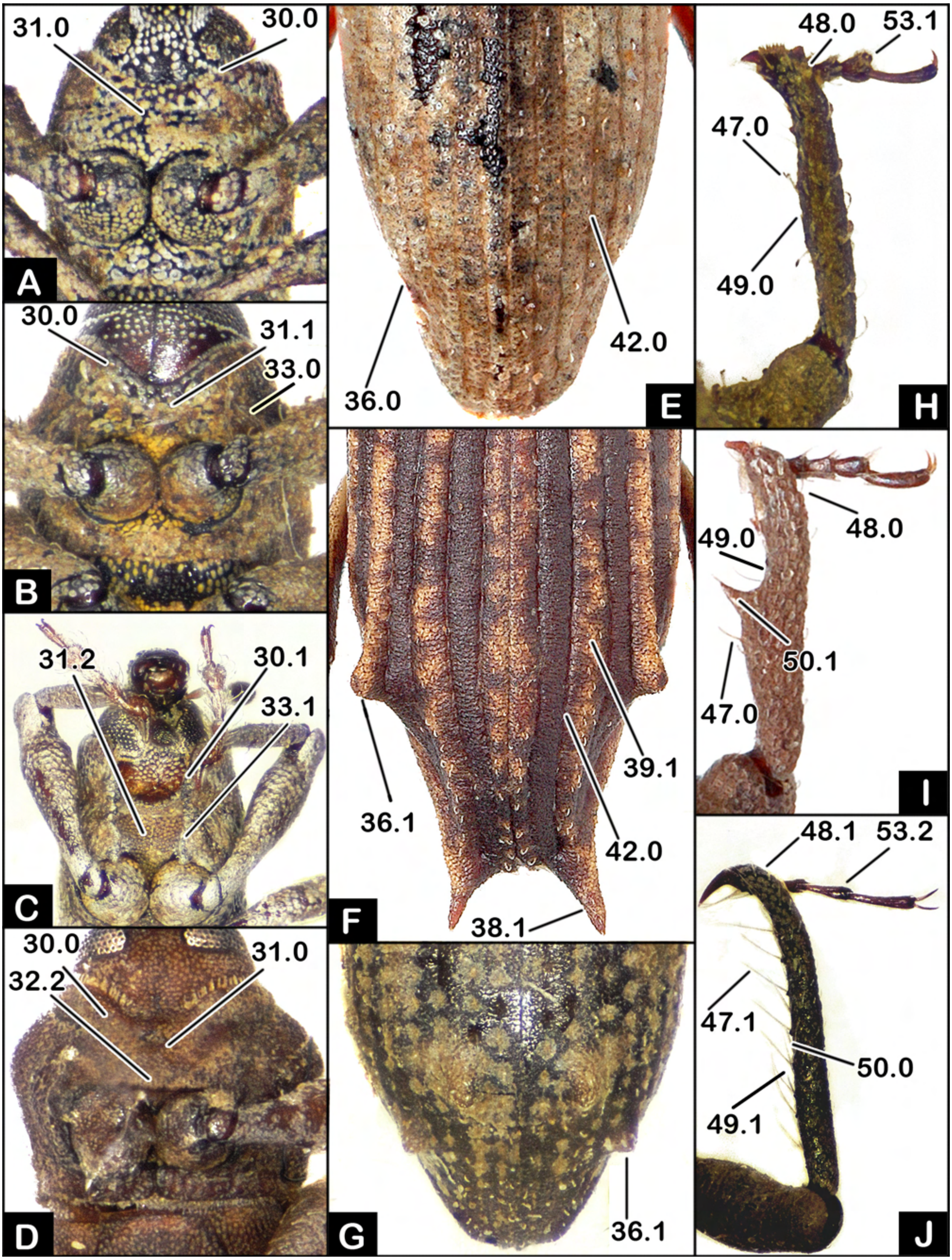

FIGURE 3. Prosternum of (A) *Hydronomus alismatis*; (B) *Memptorrhynchus crispus*: (C) *Bagous* (*Hydronoplus*) *longulus*; (D) *Bagous* (*Macropelmus*) *geniculatus*. Elytra of (E) *Bagous* (*Macropelmus*) *tubulus*; (F) *Bagous* (*Macropelmus*) *elegans*; (G) *Bagous* (*Macropelmus*) *trapae*. Anterior leg of (H) *Memptorrhynchus crispus*; (I) *Bagous* (*Macropelmus*) *fragosus*; (J) *Bagous* (*Macropelmus*) *trapae*. Not at the same scale.

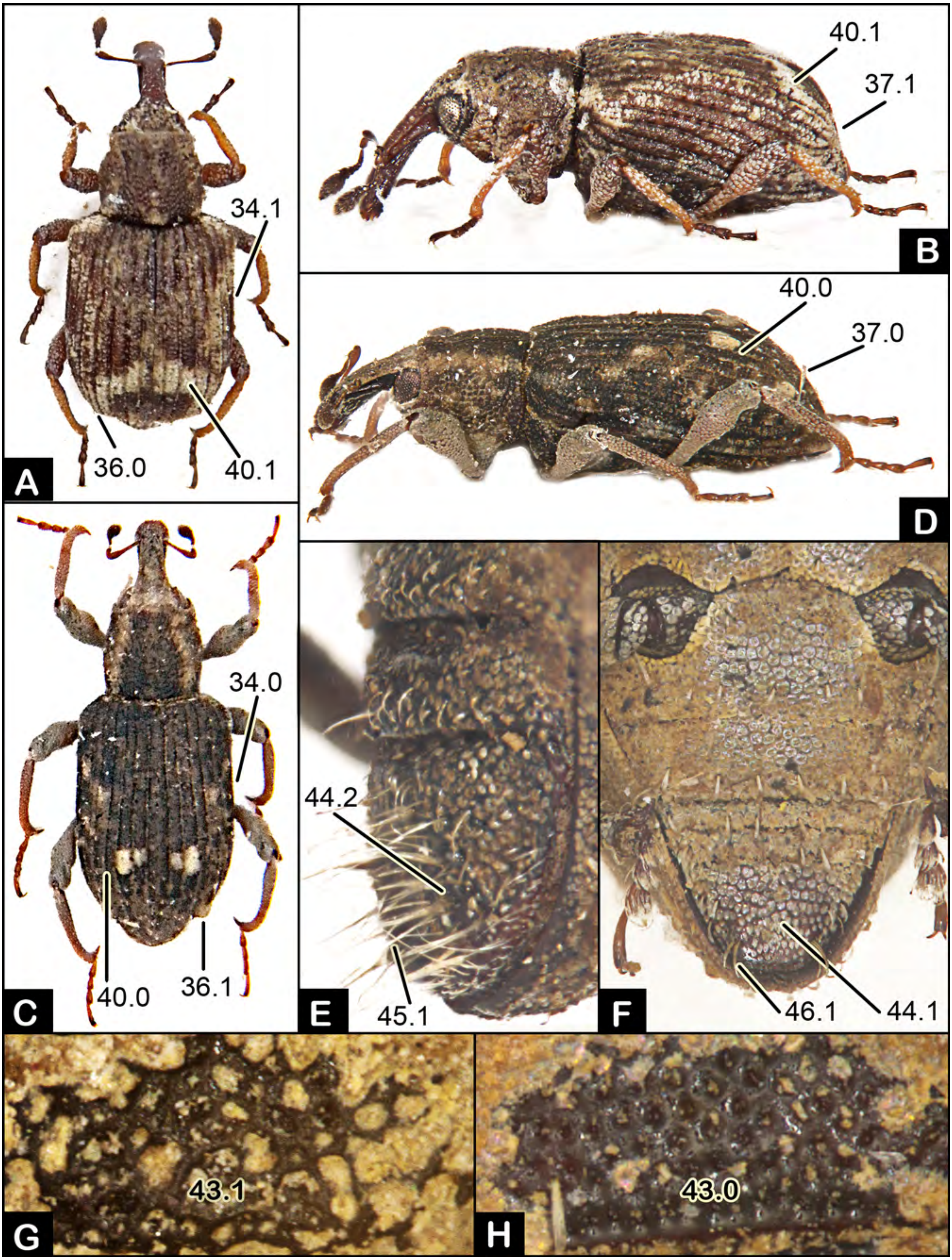

FIGURE 4. Habitus of *Azollaebagous clarencensis*, in (A) dorsal and (B) lateral view; *Bagous* (*Hydrillaebagous*) *hydrillae*, in (C) dorsal and (D) lateral view. Venter of (E) *Bagous* (*Bagous*) *binodulus*; (F) *Memptorrhynchus crispus*. Detail of ventrite 1 after removal of scales of (G) *Bagous* (*Macropelmus*) *affaber*; (H) *Bagous* (*Macropelmus*) *collignensis*. Not at the same scale.

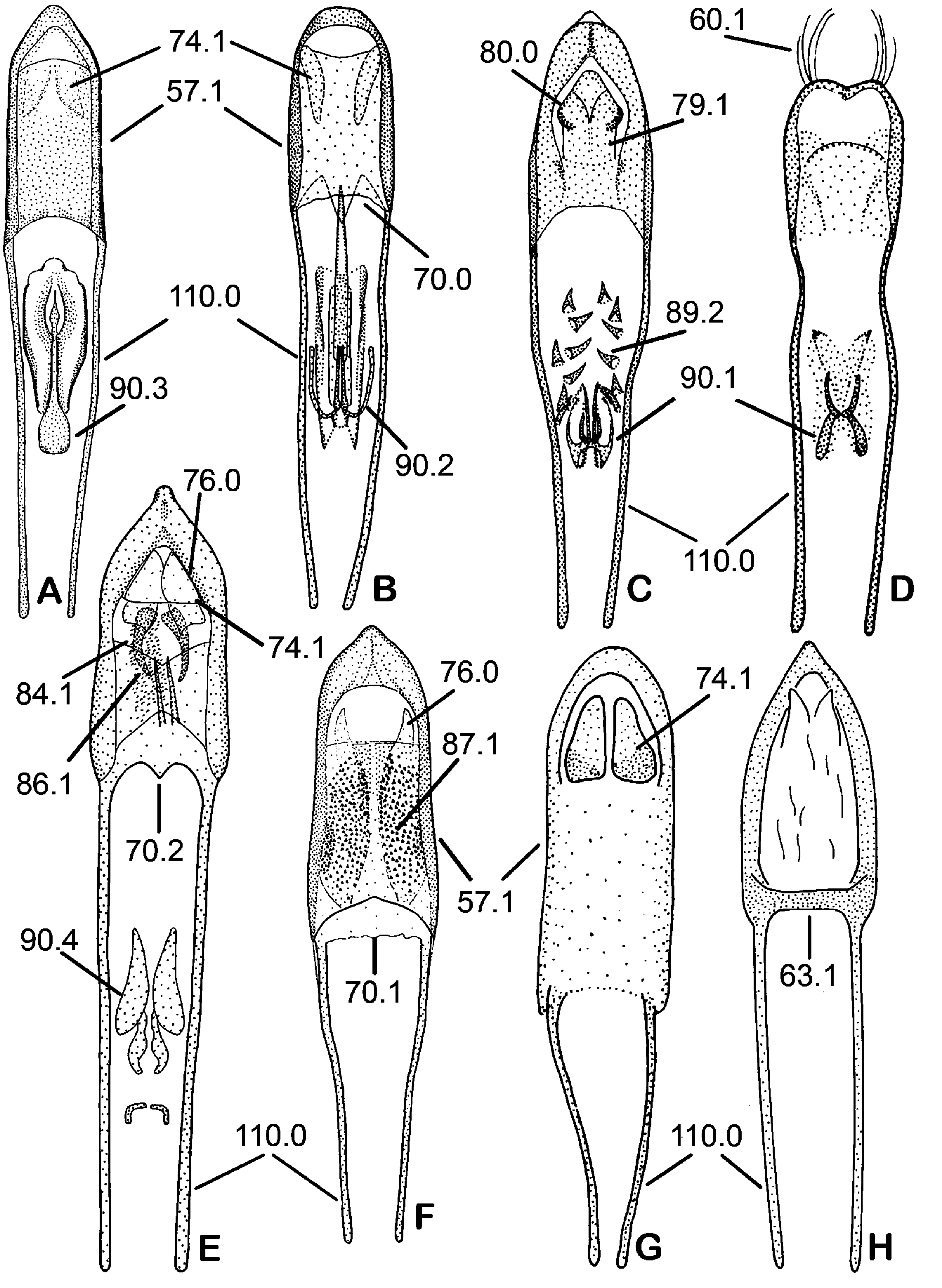

FIGURE 5. Penis in dorsal view of (A) *Hydronomus alismatis*; (B) *Memptorrhynchus brevipennis*; (C) *Bagous* (*Parabagous*) *costulatus*; (D) *Bagous* (*Parabagous*) *longirostris*; (E) *Bagous* (*Bagous*) *binodulus*; (F) *Bagous* (*Bagous*) *robustus*; (G) *Azollaebagous clarencensis*; (H) *Bagous* (*Bagous*) *josephi*. Not at the same scale.

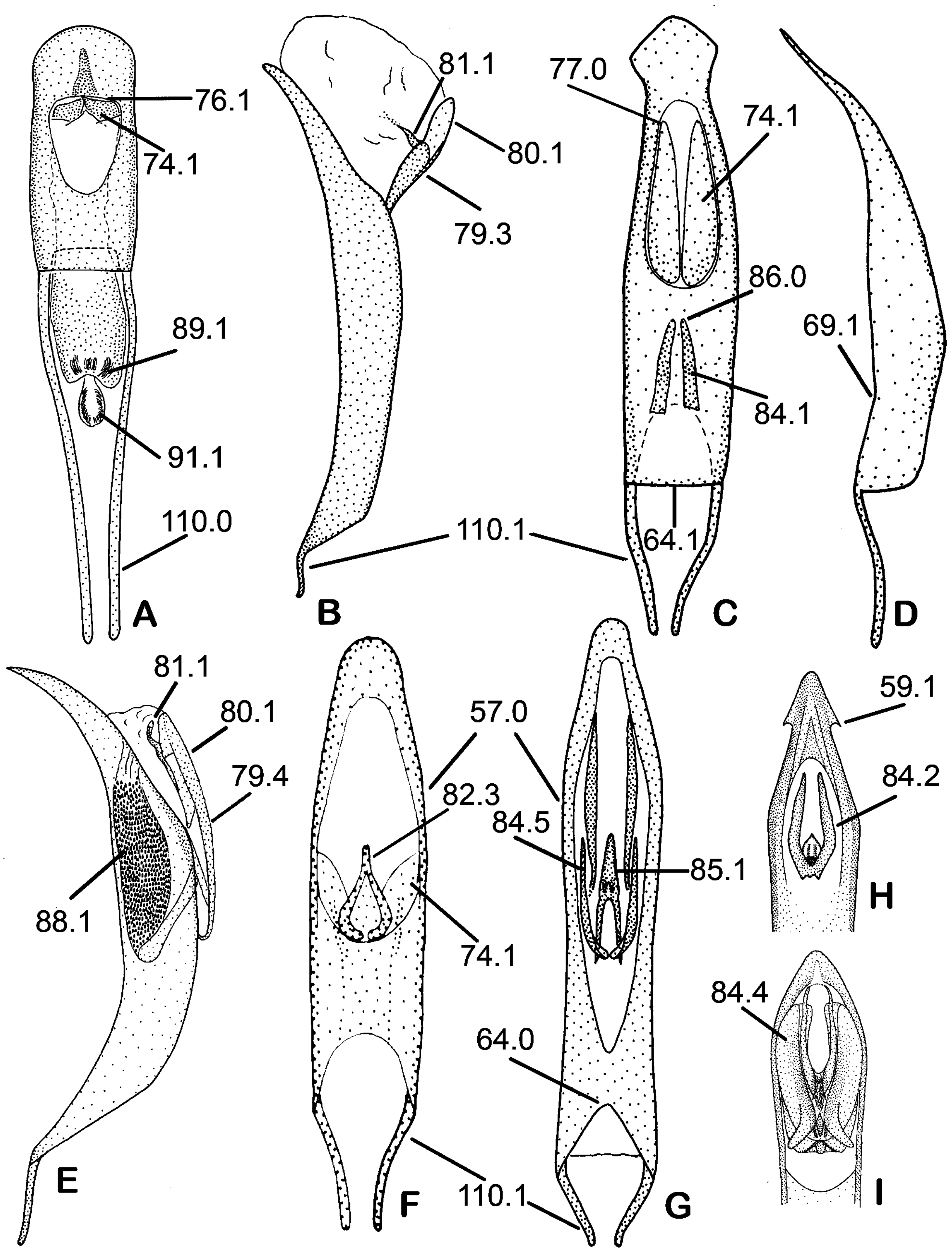

FIGURE 6. Penis in dorsal and lateral view of (A) *Bagous* (*Hydrillaebagous*) *hydrillae*; (B) *Bagous* (*Macropelmus*) *tempestivus*; (C and D) *Bagous* (*Macropelmus*) *affaber*; (E) *Bagous* (*Macropelmus*) *lutosus*; (F) *Bagous* (*Macropelmus*) *exilis*; (G) *Bagous* (*Macropelmus*) *cylindricus*; (H) *Bagous* (*Macropelmus*) *dieckmanni*; (I) *Bagous* (*Macropelmus*) *peregrinus*. Not at the same scale.

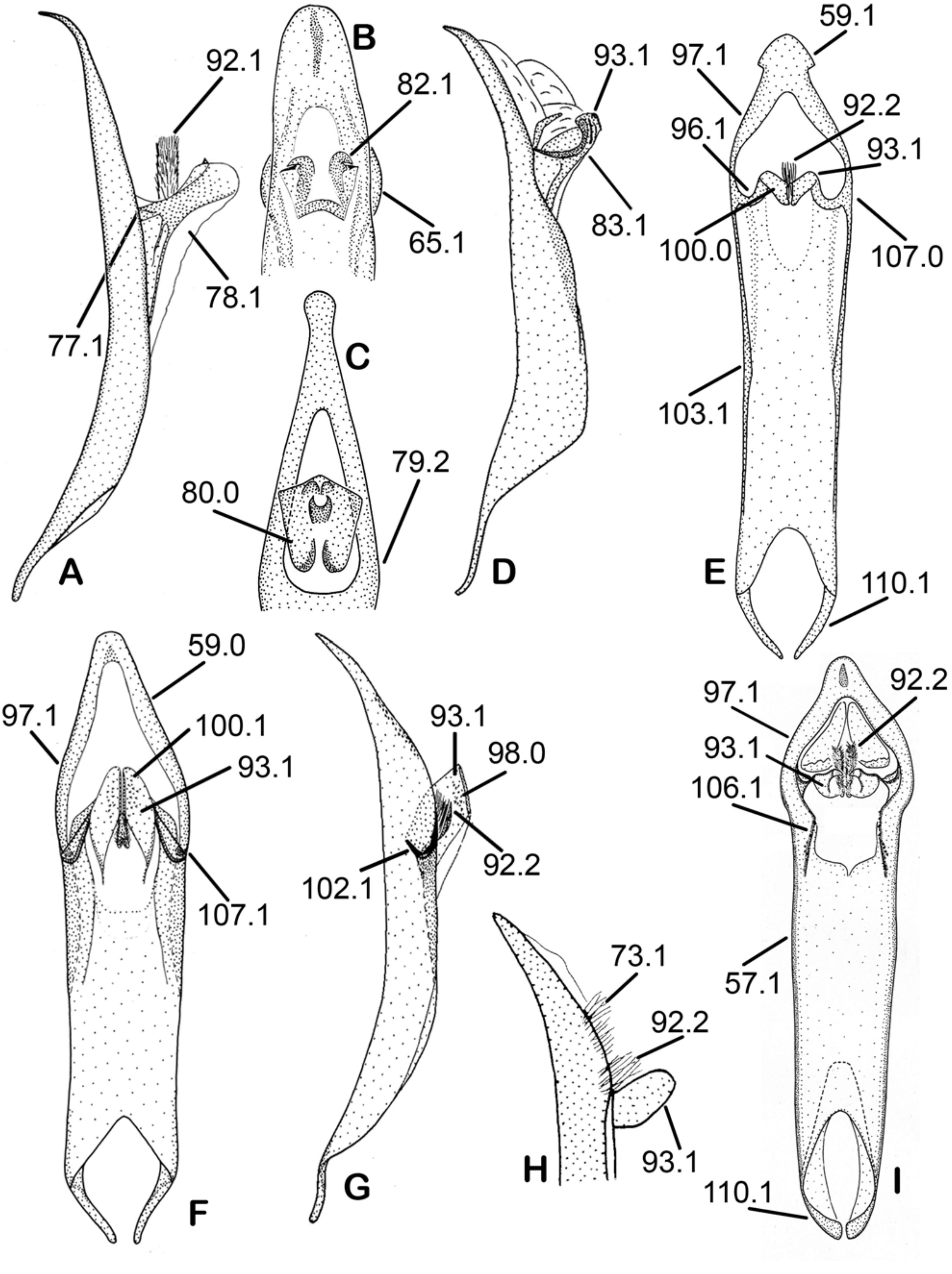

FIGURE 7. Penis in dorsal and lateral view of (A) *Bagous* (*Macropelmus*) *geniculatus*; (B) *Bagous* (*Macropelmus*) *humeridens*; (C) *Bagous* (*Macropelmus*) *tuberculatus*; (D) *Bagous* (*Macropelmus*) *nodulosus*; (E) *Bagous* (*Macropelmus*) *collignensis*; (F and G) *Bagous* (*Macropelmus*) *limosus*; (H) *Bagous* (*Macropelmus*) *humeralis*; (I) *Bagous* (*Macropelmus*) *adelaidae*. Not at the same scale.

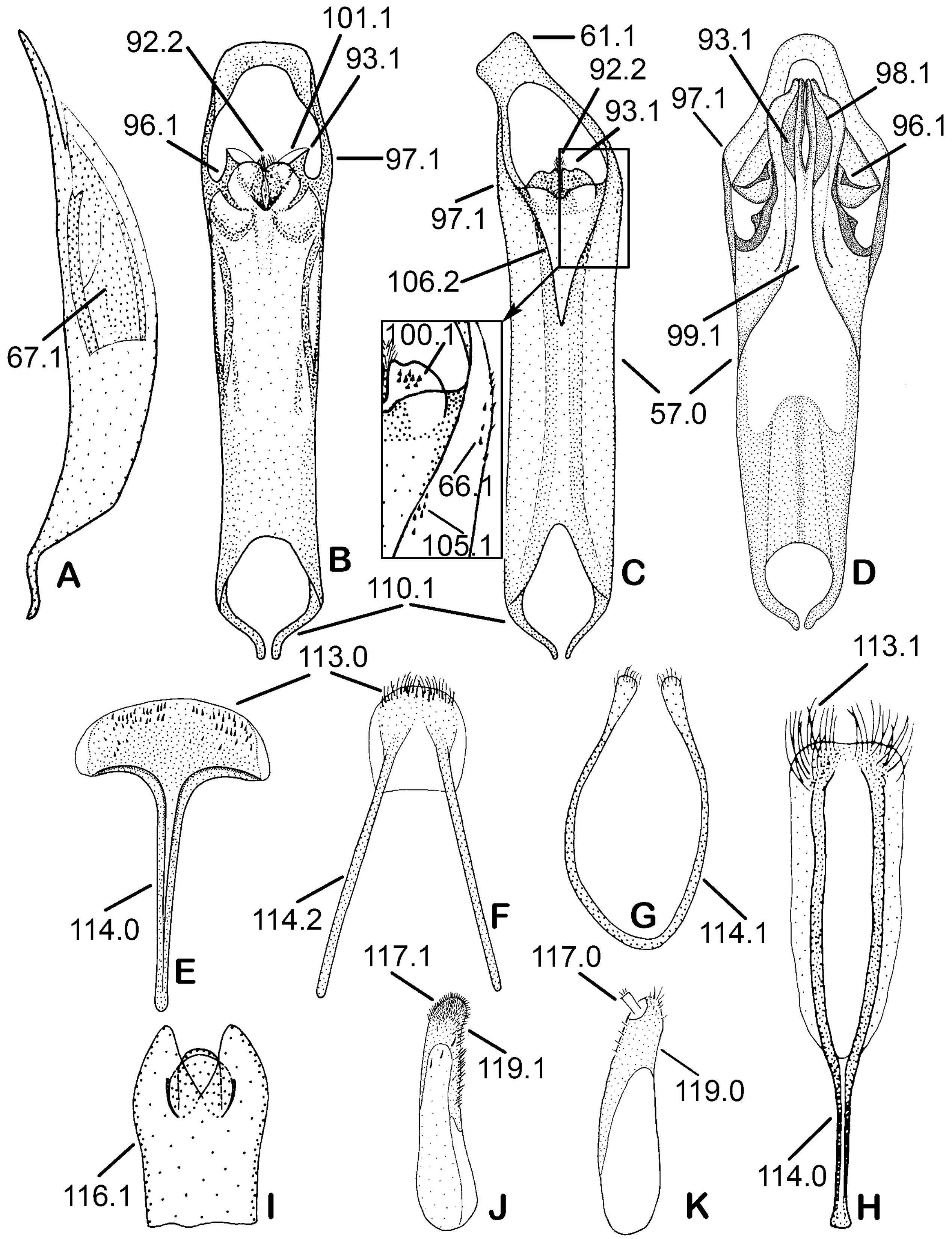

FIGURE 8. Penis in dorsal and lateral view of (A) *Bagous* (*Macropelmus*) *subruber*; (B) *Bagous* (*Macropelmus*) *brevis*; (C) *Bagous* (*Macropelmus*) *frit*, with detail of the small teeth; (D) *Bagous* (*Macropelmus*) *trapae*. Spiculum ventrale of (E) *Bagous* (*Bagous*) *quadrimaculatus*; (F) *Memptorrhynchus brevipennis*; (G) *Bagous* (*Parabagous*) *chevrolati*; (H) *Bagous* (*Macropelmus*) *elegans*. Sclerites of bursa copulatrix of (I) *Bagous* (*Parabagous*) *chevrolati*. Gonocoxa of (I) *Bagous* (*Bagous*) *nympheae*; (J) *Bagous* (*Macropelmus*) *laevigatus*. Not at the same scale.

Results

Morphological analysis (Figs 9–10). The topologies found with BI, ML and MP (Figs 9, 10) were congruent for the clades with higher statistical support. In cases of non-congruence among the methods we gave preference to the BI, since it is considered to outperform parsimony (Wright & Hillis 2014).

All-species analysis (Fig. 9). The tribe Bagoini proved to be monophyletic, with high support (maximal support in BI, 94% bs in ML and 95% sr in MP, Bremer support 4). Within this clade, *Hydronomus alismatis* was sister to the other species of the tribe. These clustered in three monophyletic groups, here considered at genus rank: *Memptorrhynchus* Iablokoff-Khnzorian, 1960 (*M. crispus* and *M. brevipennis*), *Azollaebagous* new genus, described herein (*A. contrarius* and *A. pygmaeodes*) and *Bagous*. The first two taxa had maximal or very strong support in all analyses, whereas *Bagous* had almost maximal support only in BI, but was only weakly supported in ML and MP (respectively, 65% bs and 63% sr, Bremer support 1). Within *Bagous*, some clades had good statistical support: *Bagous* subgen. *Hydronoplus* was fully supported in all analyses; *Bagous* subg. *Parabagous* was fully supported in BI and strongly supported in ML and MP (96% bs and sr, Bremer support 4); *Bagous* subg. *Hydrillaebagous* new subgenus, described herein, was almost fully supported in BI (99% pp), and weakly supported in ML (73% bs) and MP (63% sr, Bremer support 2); several other species clustered in a monophyletic group, *Bagous* subg. *Macropelmus*, that had 62% pp in BI, and was present, albeit lacking significant statistical support, also in ML and MP. The remaining species fell in a polytomy. Among these last species is also *B. binodulus*, the type species of the genus. For practical reasons, we include all these species in *Bagous* subgenus *Bagous*, being well aware that this might not be a natural taxon.

Type-species analyses (Fig. 10). Results were very similar, with some differences in the support values. In particular, the genus *Bagous* had stronger support (BI: 99% pp, ML: 78% bs, MP= 72% sr, Bremer support 3), as well as *Bagous* subgenus *Macropelmus* (BI: 97% pp, ML: 84% bs, MP: 61% sr), whereas the genus *Hydronomus* as sister to all the other genera was not statistically supported (BI: 50% pp, lower than 50% bs and sr in, respectively, ML and MP).

Mitochondrial cytochrome oxidase I analysis (Fig. 12). The species of Bagoini of which mtCOI was available were all part of the genus *Bagous* as defined by the morphological analysis. Two monophyletic units were defined, that are congruent with two of the clades recognized by the morphological analysis (species of the otherclades were not available for the molecular study). One of these was strongly supported (97% pp) and included species that are part of the subgenus *Macropelmus*. The second clade, corresponding to the subgenus *Bagous* s. str., was weakly supported also in the mtCOI analysis (with the same support as found in the morphological all-species analysis, 62% pp). Within these two clades, some monophyletic units were differentiated. In the subgenus *Macropelmus*, one of these included *B. limosus*, *B. frit*, *B. collignensis* and *B. longitarsis*, with almost maximal support. The first two species, "basal" to the sister group comprising *B. collignensis* and *B. longitarsis,* clustered together also in the morphological analysis, in a weakly supported clade (69% pp). A second monophylum, with a moderate support (81% pp) incorporates *B. tempestivus*, *B. monanthiphagus* and *B. exilis*. Two more units were evidenced, one, weakly supported, joined *B nodulosus* with *B. argillaceus* and *B. elegans*, whereas *B. petro* resulted in a single unit. Relationships among these four monophyletic units were not statistically supported. Within the *Bagous* s. str. clade, two monophyletic units were distinguished. One of these, maximally supported, included *B. binodulus*, *B. lutulentus*, *B. robustus* and *B. glabrirostris*. The second unit, only weakly supported (60% pp), included *B. subcarinatus* and *B. bagdatensis*.

Even though a wider set of species would be required, and the study was exclusively carried out on a single mitochondrial gene, the congruence of the resulting topologies for the available species between morphology and mtCOI sequences suggests that the signals that build the trees are strong and unequivocal, and we are thus confident of the credibility of the suggested relationships among the taxa of the tribe Bagoini.

Discussion

The aim of this study was to infer phylogenetic relationships within the Bagoini. Apparent relationships among the other Curculionoidea, as indicated by the topology of the trees, shall not be considered as suggestive of any true relationship, and will not be discussed here.

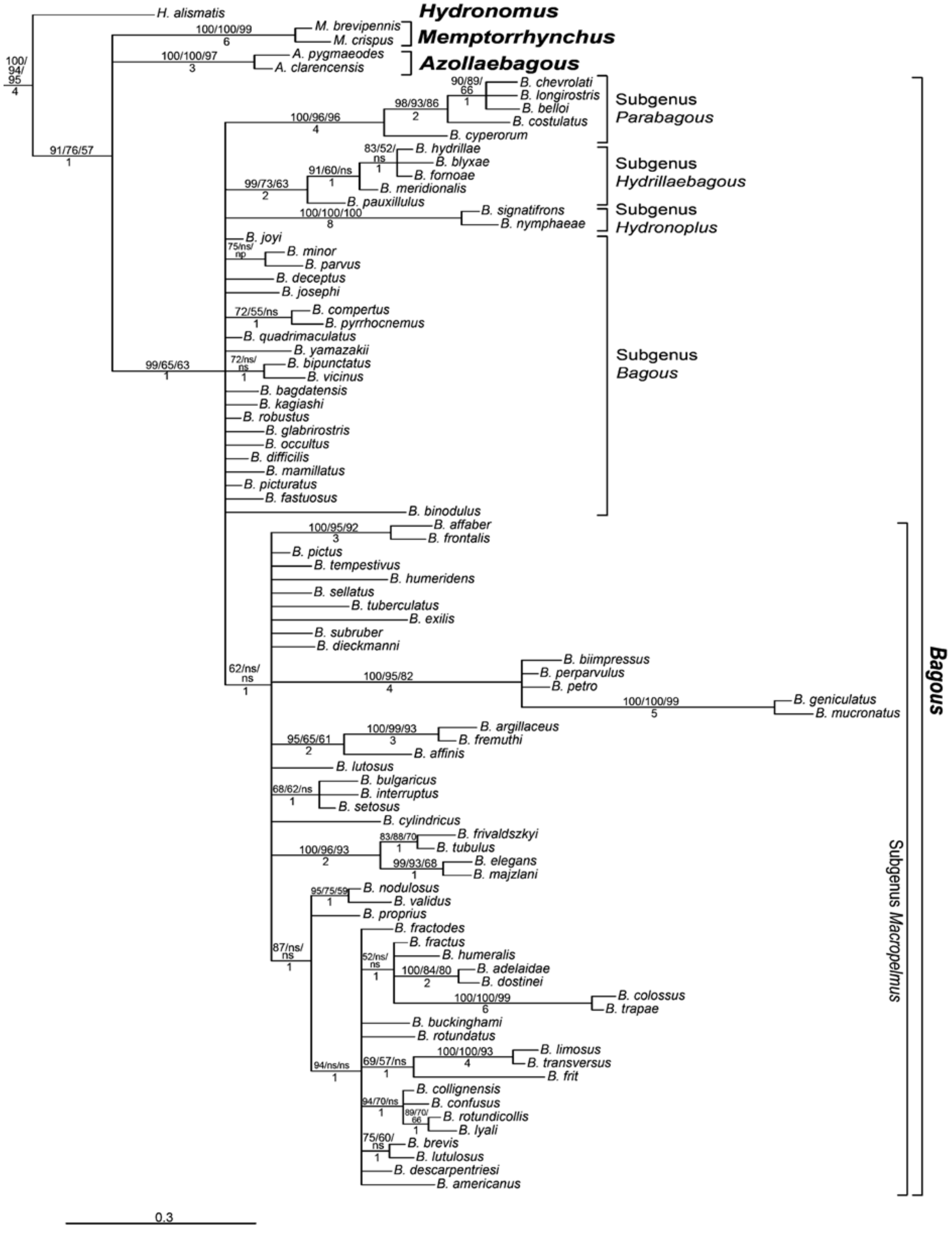

FIGURE 9. Morphological analysis—all species. Bayesian consensus tree (50% majority rule). Numbers above branches: support values, in percentage, in the following order: posterior probability (BI) / bootstrap value (ML) / symmetric resampling (MP); 'ns' means that the group was present, but its support was < 50%; 'np' means that the group was not present. Number below branches: Bremer support in the MP analysis. Scale bar unit: expected changes of state per character. MP analysis: length 261, consistency index = 0.61, retention index = 0.83. Outgroup taxa not reported to increase readability of the Bagoini clade.

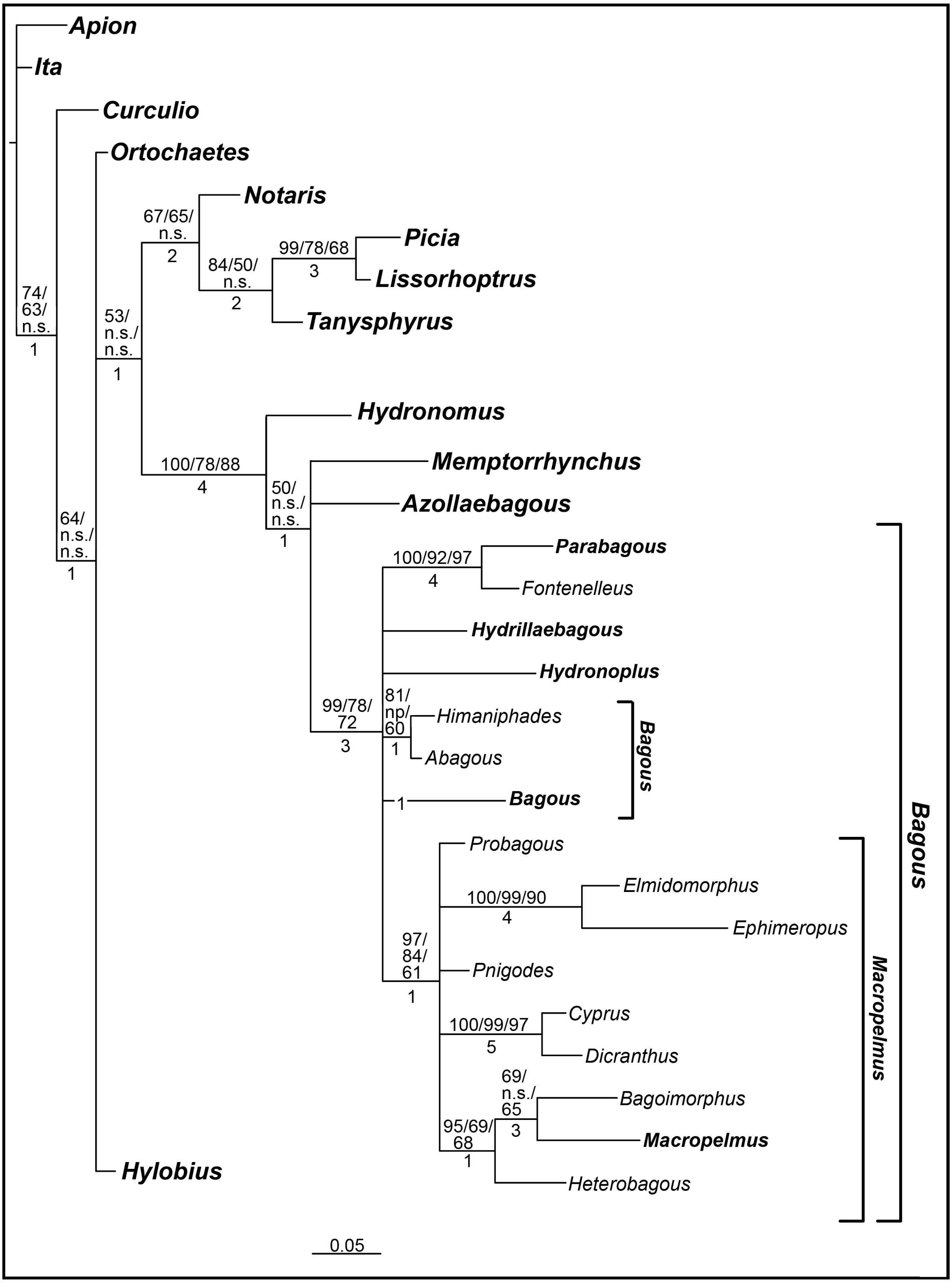

FIGURE 10. Morphological analysis—type species only. Bayesian consensus tree (50% majority rule). Taxa in **bold** font: valid taxa recognized in the present work; larger font: genera, smaller font: subgenera. Taxa in regular font: synonyms in the present work. Numbers above branches: support values, in percentage, in the following order: posterior probability (BI) / bootstrap value (ML) / symmetric resampling (MP); 'ns' means that the group was present, but its support was < 50%; 'np' means that the group was not present. Number below branches: Bremer support in the MP analysis. Scale bar unit: expected changes of state per character. MP analysis: length 146, consistency index = 0.70, retention index = 0.78.

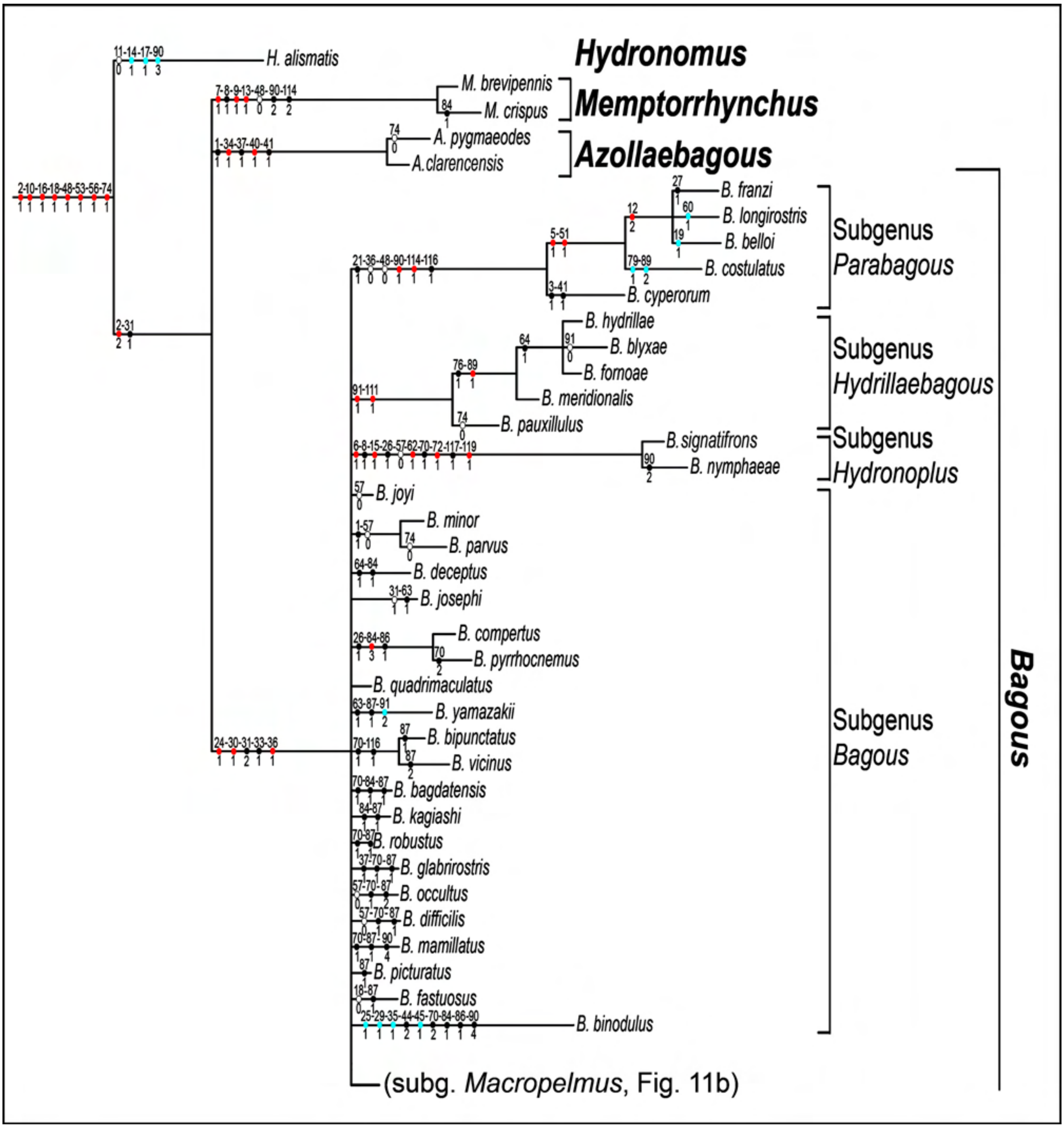

FIGURE 11a–b. Morphological analysis. Synapomorphies and autapomorphies plotted on the Bayesian consensus tree. Numbers above branches refer to the character, numbers below branches refer to the state of the character. Red dots: synapomorphies unique for the clade. Blue dots: autapomorphies unique for the species. Black dots: synapomorphies and autapomorphies not unique for the clade or species. White dots: reversals. Outgroup taxa not reported to increase readability of the Bagoini clade.

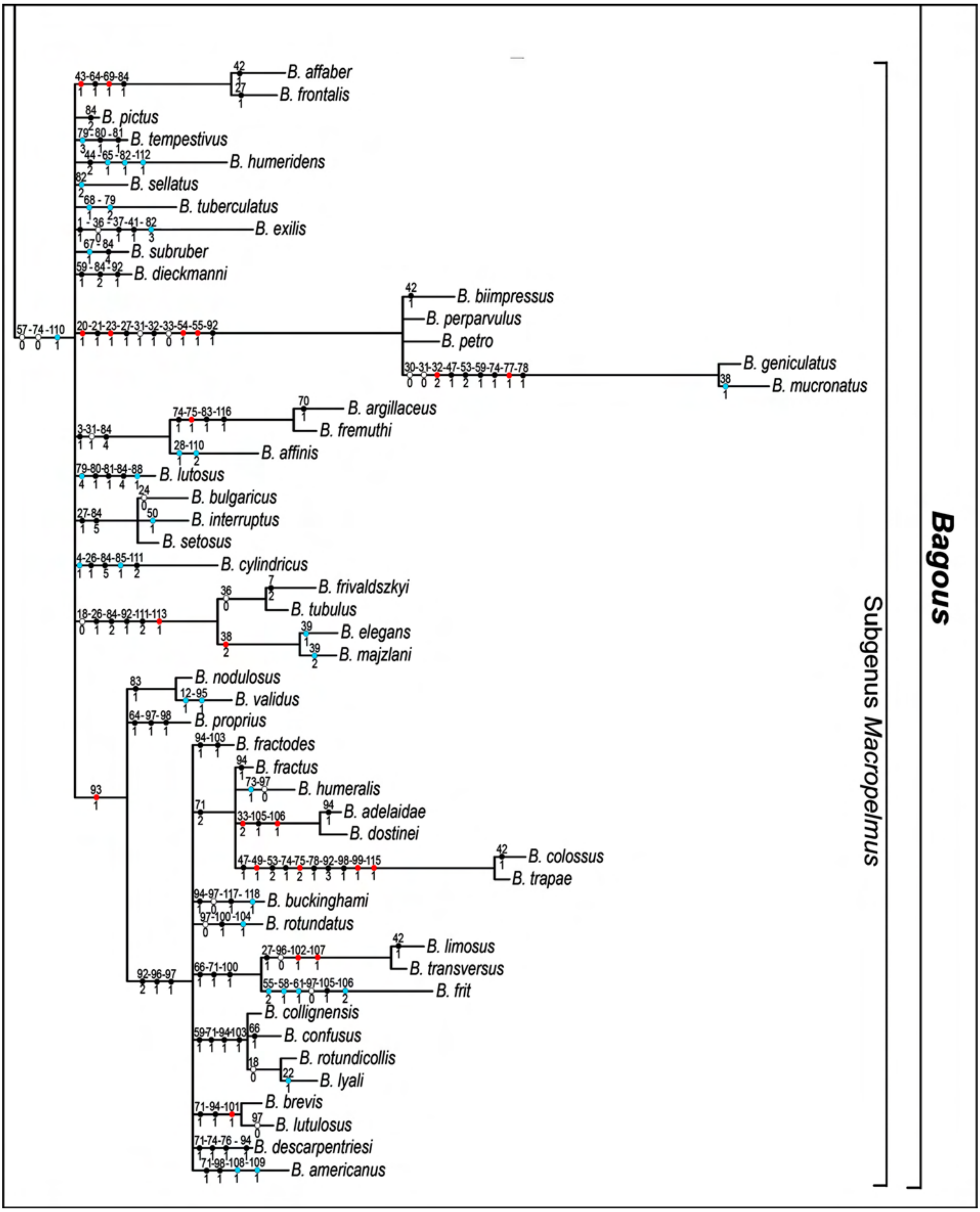

FIGURE 11b. (Continued)

Morphological characters. Among the character states included in 119 characters here considered, almost 100 were uniquely present in a single clade (Figs 11a, b). Several parallel character states were present, but, as indicated by the high retention index, in many cases they were synapomorphic for species in different clades.

The Bagoini classification. In the phylogenetic analyses based on the morphological matrix (Table 1) the Bagoini are here assembled in four genera: *Hydronomus*, *Memptorrhynchus, Azollaebagous* **new genus** and *Bagous*. Inside the genus *Bagous*, five subgenera are recognized: *Bagous, Parabagous, Macropelmus, Hydronoplus* and *Hydrillaebagous* **new subgenus**.

The genus *Bagous*. The genus *Bagous* is recognized as being composed of five subgenera, morphologically mainly differentiated by characters of the male genitalia. Four of these subgenera correspond to more or less strongly supported clades, whereas the nominal subgenus appears to be an assemblage of the species that are not part of the four supported subgenera. A further analysis exclusively dealing with the species in the subgenus *Bagous*, based on a wider availability of molecular data, and on morphological characters specifically chosen to evaluate similarities and differences among these species, might allow us to achieve a more complete view of their reciprocal affinities. The subgenus *Macropelmus* is the largest subgenus and includes all the species sharing the shortening of the penis apodemes. Support for its monophyly in the all-species analysis is quite low due to a number of parallel character states present in some of the species that are shared with species of other subgenera. Even still, we find the shortening of the penis apodemes to be of great importance and consider this subgenus to be a natural group. This is confirmed by the higher support that is obtained in the type-species analysis (Fig. 12). In the molecular analysis, the species characterized by the shortening of the penis body apodemes also clustered in a distinct clade. According to our reconstruction (Fig. 9), all the species having a dorsal process on the penis body form a monophyletic clade. The presence of a more or less complex tuft of setae arranged medially at the base of the sclerites or the dorsal process is another character that is typical of many of the species of this subgenus.

Species-groups. Within some of the subgenera, we defined species groups. In some cases, these groups correspond to a phylogenetic clade, in other cases holophyly is uncertain or not supported and the groups may be paraphyletic or correspond to an evolutionary grade. However, the informal category represented by species-groups has been used consistently for decades in the classification of Bagoini (O'Brien & Askevold 1992, Askevold *et al.* 1994, Caldara & O'Brien 1998). Even though it has no nomenclatural significance, it is useful for an easier recognition of morphologically similar species, and these are the reasons why we decided to maintain its usage.

Almost all species-groups previously proposed were maintained, a few had to be upgraded to the rank of subgenus or genus, others were lumped together in a single group, a few more were created for species that formed a supported clade.

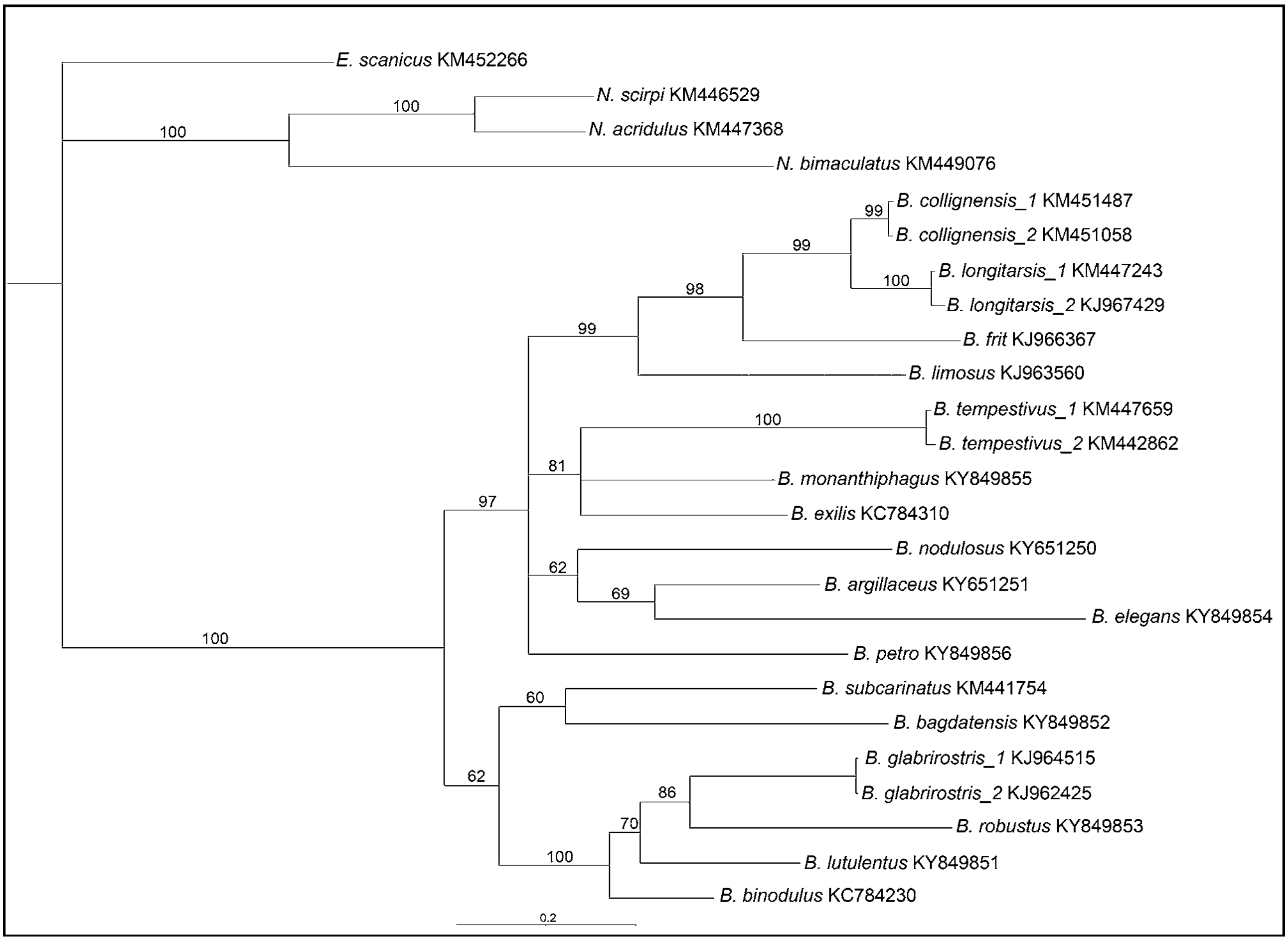

FIGURE 12. Mitochondrial cytochrome oxidase I analysis. Bayesian consensus tree (50% majority rule). Codes after the species name are GenBank Accession Numbers. Scale bar unit: expected substitutions per site.

The large number of groups inside *Macropelmus*, some of which are monospecific, accommodates species sharing a particular shape of the sclerites and the presence of sclerotized structures or carinae and sulci along the body of the penis. Some of these species-groups are so well differentiated that previously they had even been recognized as distinct genera.

The addition to the analyses of 74 species from Afrotropical, Oriental and North American faunas increased only marginally the number of species groups, since most species were easily attributed to already recognized groups. However, this was not always possible since we preferred to maintain a certain uniformity of evaluation. A few new groups were therefore created here: the *B. fractodes*, *B. americanus*, *B. humeralis*, and *B. descarpentriesi* groups, which are composed of only one or two species.

Recently Gosik (2013) proposed a phylogenetic tree of 14 Palaearctic Bagoini using character states of preimmaginal stages. Although based on very few species, the topology of the tree proposed by Gosik (2013) confirms *Bagous alismatis* (*Hydronomus alismatis* in the present paper) as the sister taxon to all other Bagoini. Some of the relationships which we found by using the adult characters, such as that between *B. tubulus* and *B. elegans*, are also confirmed.

We hope we have succeded in setting down herein a basic knowledge of the phylogenetic relationships among the taxa that compose the tribe of the Bagoini. The analysis of more species, including some yet undescribed, and the availability of the mtCOI sequences for a broader number of species will contribute to clarifying some of the presently uncertain points and possibly will allow us to derive stronger support for some of the weaker nodes, and increase congruence among the various analyses.

Taxonomy

Tribe Bagoini

Type genus: *Bagous* Germar, 1817

Diagnosis. Most scales of both dorsal and ventral vestiture granulate, moderately to distinctly pitted, not hydrofuge except at point of articulation, usually with waterproof coating. Rostrum with lateral and dorsal apical setae numerous (except *Hydronomus*). Scrobe in lateral view completely visible, parallel to length of rostrum (char. 16.1). Insertion of antennal scape usually laterodorsal (except *B. tubulus* group, *B. rotundicollis*, *B. fastosus*) (char. 18.1). Segment 7 of antennal funicle wider than segment 6 (except *Bagous* subgen. *Parabagous* and *B. biimpressus* group). Rostrum with suprascrobal sulcus, more or less distinct (char. 10.1). Forehead between eyes usually sulcate or foveate (except *Hydronomus*, *Memptorrhynchus* and a few other unrelated species). Postocular lobe ventrally distinct, somewhat to markedly raised, forming discontinuity with anterior prosternal margin and with anterior point of lateral margin of rostral canal (except *Hydronomus*, *Memptorrhynchus*, *Azollaebagous*, and *B. geniculatus* and related species). Prosternal canal weak to deep, rarely absent (in *Hydronomus* and *B. geniculatus* and related species). Side margins of prosternum usually sharply raised, markedly rounded or acute just in front of coxae (except *Memptorrhynchus*, *Azollaebagous*). Tibiae with outer margin distally slightly to strongly arcuate (char. 48.1) (except *Memptorrhynchus* and *Bagous* subgen. *Parabagous*). Tarsomere 3 not completely bilobed, at most broadly cordate to subcordate, often sublinear to elongate-linear. Tarsomere 3 clothed beneath with fine to coarse, dense, recumbent to subrecumbent pubescence (char. 53.1). Ventrite 5 with a shallow median impression (char. 44.1) and with a lateral pit with 1–4 pairs of setae (char. 46.1). Aedeagus of pedal type (without tectum) (char. 56.1), with dorsal surface of penis body usually fully sclerotised except in orificial area, usually with numerous basal or apical more or less complex sclerites. Laminar orificial lateral sclerites present although sometimes only distinguishable at apical portion (char. 74.1) (modified in most species with dorsal process). Penis with long to very short apodemes.

Remarks. The species belonging to this tribe share seven synapomorphies (char. 10.1, 16.1, 18.1, 48.1, 53.1, 56.1, 74.1). According to Oberprieler (2014) the Bagoini seem to have relationships with both the tribes Erirhinini, in particular the *Echinocnemus* assemblage *sensu* Oberprieler, and Tanysphyrini. The Bagoini and *Lissorhoptrus* + *Picia* + *Tanysphyrus* share the vestiture of the body formed at least in part by more or less pitted scales (char. 2.1), ventrite 5 with a median impression (char. 44.1) and with a lateral pit with 1–4 pairs of setae (char. 46.1), whereas Bagoini and *Lissorhoptrus* + *Picia* share the tarsomere 2 longer than wide (char. 51.0) and tarsomere 3 not bilobed (char. 52.1). However, these two last characters appear clearly adaptive and therefore possibly misleading.

Genus *Hydronomus* Schoenherr, 1825 resurrected name

Hydronomus Schoenherr, 1825: c.583 (type species: *Curculio alismatis* Marsham, 1802). Tournier 1874: 103. Schilsky 1907: D. Sharp 1917a: 31. Solari 1930: 46. Hustache 1930: 236. Klima 1934: 127. Hoffmann 1954: 711, 713. Dieckmann 1983: 351, 373. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Diagnosis. Scales subgranulate to granulate, moderately pitted except for ventrites 3–5 (char. 2.1). Rostrum with very few lateral and dorsal apical setae (char. 11.0). Scrobe not reaching eye (char. 17.1) and squamose (char. 14.1). Forehead between eyes not sulcate nor foveate (char. 24.0). Postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin (char. 30.0). Prosternal canal absent (char. 31.0). Elytra lacking declivital calli (char. 36.0). Tibiae arcuate at apical outer margin (char. 48.1); inner margin of tibiae lacking denticles. Penis with long apodemes (char. 110.0). Endophallus with basal sclerite complex formed by overlapped plates (char. 90.3).

Remarks. In the all-species analysis the genus is sister to all the other Bagoini with a strong support in BI (91% pp), and a lower support in ML and MP (respectively, 76% bs and 57% sr). In the type-species analysis the genus was not supported as sister to the remaining taxa of the tribe (BI: 50% pp, ML and MP lower than 50%). This incongruence was probably determined by the fact that *Hydronomus* is monotypic, whereas the other genera have a large number of species, sharing the character states differentiating them from *Hydronomus*. In the all-species analysis this resulted in a much stronger support for the clade encompassing the other genera of the tribe. *Hydronomus* shares with the other Bagoini several characters, such as the pitted scales, shape of the body, legs, and male and female genitalia. It differs from them by the absence of a prosternal canal and of pitted scales on some ventrites. Four unequivocal character states characterize *Hydronomus* (char. 11.0, 14.1, 17.1, 90.3) in respect to the other Bagoini: scrobe not reaching eyes and squamose (an apparently plesiomorphic state), rostrum with very few lateral and dorsal apical setae, endophallus with basal sclerite complex formed by overlapped plates.
This genus is presently composed only of the type species. However, we have an undescribed Chinese taxon belonging to this genus and differing from *H. alismatis* by the shape of the body of the penis and the basal sclerites.

Species included. **PAL:** **Hydronomus alismatis* (Marsham, 1802).

Genus *Memptorrhynchus* Iablokoff-Khnzorian, 1960 resurrected name

Memptorrhynchus Iablokoff-Khnzorian, 1960: 253 [type species: *Memptorrhynchus ripicola* Iablokoff-Khnzorian, 1960 (= *Bagous brevipennis* Kirsch, 1878)]. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Diagnosis. Body broad-oval and robust. Rostrum unusually flattened at apex (char. 8.1), with lateral plica (char. 9.1); curvature of ventral margin in lateral view strong (char. 7.1), at basal 2/3 with row of sparse, regularly spaced setae along lateral margin close to ventral margin (char. 13.1). Forehead between eyes not sulcate nor foveate (char. 24.0). Pronotal disc moderately to strongly transversely convex. Postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin (char. 30.0). Prosternal canal weak (char. 31.0). Side margins of prosternum not clearly raised (char. 33.0). Elytra with setae on odd-numbered intervals surrounded by rosette of scales of same color; declivital callus absent (char. 36.0). Outer margin of tibiae, especially on hind tibiae, straight or nearly so toward apex (in lateral view) (char. 48.0); tibiae denticulate along inner margin, sometimes with denticles stouter and more numerous on midtibiae; tarsi short, tarsomere 3 cordate. Penis with long apodemes (char. 110.0). Endophallus with basal sclerite complex formed by elongate curved sclerites (char. 90.2). Apodemes of spiculum ventrale fully bifurcated, arising laterally on plate of sternite, apparently forming two straight rods with arms (char. 114.2).

Remarks. Monophyly of the species referred to this genus was supported in all analyses.

Memptorrhynchus is characterized by the poorly developed, barely distinguishable prosternal canal, the tibiae almost straight to apex along the outer margin, the tarsi short with tarsomere 3 broadly cordate, and the male genitalia which present certain similarities with those of *Hydronomus* (*i.e.*, the features of the sclerite complex at the base of the endophallus). This is a homogeneous group and its species show six synapomorphies (char. 7.1, 8.1, 9.1, 13.1, 90.2, 114.2) in nongenital characters (rostrum strongly curved and with flat apex with lateral carinae, and with row of lateral setae) as well as genital morphology (shape of the penis and especially of the spiculum ventrale with apodemes strongly divergent and arising laterally on plate). The bulk of this group is present in the Afrotropical region with three extralimital species (two Indian and one Palaearctic).

Species included: **AFR:** [1]*Memptorrhynchus bergensis* (Marshall, 1953) **n. comb.**, [1]*M. crassus* (Hoffmann, 1968) **n. comb.**, *[1]*M. crispus* (Faust, 1899) **n. comb.**, [1]*M. gaillardi* (Hustache, 1936) **n. comb.**, [1]*M. polysignatus* (Hoffmann, 1968) **n. comb.**, [1]*M. vafer* (Marshall, 1958) **n. comb.**; **ORR:** [1]*M. luteitarsis* (Hustache, 1926) **n. comb.**, [1]*M. ovoideus* (Hustache, 1926) **n. comb.**; **PAL:** *[2]*M. brevipennis* (Kirsch, 1878) **n. comb.**

Genus *Azollaebagous* gen. n.

(Figs 4A–B, 5G)

Type species: *Bagous clarencensis* Blackburn, 1894.
Gender: masculine.

Diagnosis. Body very small in size, 2.0 mm or less in length (rostrum excluded) (char. 1.1). Postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin (char. 30.0). Prosternal canal weak (char. 31.1). Side margins of prosternum barely raised (char. 33.1). Elytra subquadrate (char. 34.1), with posterior declivity in lateral view strong at 75 degrees (char. 37.1); declivital callus absent (char. 36.0); scales of elytral intervals arranged in regular pairs (char. 41.1); vestiture with a semicircular white stripe at posterior third (char. 40.1). Tibiae with slightly arcuate apices (char. 48.1). Penis with long apodemes (char. 110.0) and with endophallus generally lacking sclerites.

Description. Body short and broad-oval, very small in size, 2.0 mm or less in length (rostrum excluded), densely clothed with hydrofuge pitted scales. Rostrum in female usually distinctly longer than in male. Antennae with 7-segmented funicle, usually inserted at midlength. Forehead between eyes foveate. Pronotum moderately transverse, with sides weakly rounded, disc moderately to strongly transversely convex. Postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin. Prosternal canal weak, with side margins weak. Elytra slightly longer than wide, with humeri subquadrately rounded, with parallel sides, posterior declivity in lateral view strong at 75 degrees, lacking callosities; scales of elytral intervals arranged in regular pairs, side by side, each interval with two individually distinct rows of round scales; vestiture with a semicircular white stripe at posterior third. Tibiae with slightly arcuate apices, lacking distinct denticles and with setae very short and indistinct; tarsi short, with tarsomere 3 broad and slightly cordate, clothed beneath with fine, dense, recumbent pubescence. Penis with long apodemes and with endophallus generally lacking sclerites. Apodemes of spiculum ventrale straight, long, parallel.

Remarks. This genus is associated with *Azolla* and easily identified by five apomorphies (char. 1.1, 34.1, 37.1, 40.1, 41.1), all in nongenital characters: body very small in size, elytra subquadrate with posterior declivity strong and with a semicircular stripe of white scales at posterior third, elytral interstriae covered with two regular rows of scales (homoplastic with other species of *Bagous*). *Azollaebagous* was maximally supported in BI and ML and strongly supported in MP (97% sr, Bremer support 3).This genus shares with *Memptorrhynchus* the almost indistinct prosternal canal and the tarsi short, with broad cordate tarsomere 3.

Etymology. The name is composed by the joining of the name *Azolla* to the name *Bagous* highlighting that all the species of this new genus appear to live on *Azolla*, a genus of the water fern plant family Azollaceae.

Species included. **AUS:** *[1]*Azollaebagous clarenciensis* (Blackburn, 1894) **n. comb.**; **ORR:** [2]*A. alexanderi* (O'Brien, 1995) **n. comb.**, [1]*A. contrarius* (O'Brien, 1995) **n. comb.**, [1]*A. pygmaeus* (Voss, 1960) **n. comb.**; **PAL:** *[2]*A. pygmaeodes* (O'Brien & Morimoto, 1995) **n. comb.**

Genus *Bagous* Germar, 1817

Diagnosis. Forehead between eyes sulcate or foveate (char. 24.1); postocular lobes well-developed (char. 30.1); prosternum with deep rostral canal (char. 31.2) and with postero-lateral margins of rostral canal sharply raised (char. 33.2) (except for the *B. biimpressus* group of the subgen. *Macropelmus*); elytral interval 5 usually with declivital callus obtuse to acute, poorly to well-developed (char. 36.1, absent in subgenus *Parabagous* and in *B. exilis, B. frivaldszkyi* and *B. tubulus*). Tarsomere 3 cordate to linear; penis body ventrally membranous to fully sclerotized, usually with numerous basal or apical, more or less complex sclerites, with long to very short apodemes.

Remarks. In the all-species analysis the genus was almost maximally supported in BI (99% pp) but only weakly supported in ML (65% bs) and MP (63 % sr, Bremer support 1); in the type-species analysis its support in ML and MP was stronger (respectively, 78% bs and 72% sr, Bremer support 3).

Infrageneric classification of the genus *Bagous* is controversial. As already discussed, three large complexes of species are maximally, or nearly maximally supported: subgenera *Parabagous, Hydronoplus* and *Hydrillaebagous* **new subgenus**. The subgenus *Macropelmus* represents a further clade that includes a very large number of species sharing the shortening of the penis apodemes,. All other species, including *B. binodulus*, the type species of the genus, fall in a polytomy. The species available for the molecular analysis clustered in clades that match their placement in the topology of the BI reconstruction based on the morphological analysis. The type-species analysis produced the same pattern but with a further group (including *Himaniphades* and *Abagous*) that was not present in ML and had only low support. In accordance with the all-species analysis, we refer it to the subgenus *Bagous* as a species-group (*B. bipunctatus* group).

Subgenus *Bagous* Germar, 1817

Bagous Germar, 1817, Germar, 1817: 340 (type species: *Rhynchaenus binodulus* Gyllenhal, 1813). Brisout de Barneville 1863: 491. Tournier 1874: 103. Schilsky 1907: D. Hustache 1930: 205. Neresheimer & Wagner 1930: 261. Klima 1934: 110. Hoffmann 1954: 712, 714. Dieckmann 1964: 88; 1983: 352. O'Brien & Wibmer 1982: 92. O'Brien & Askevold 1992: 338; 1995: 12. O'Brien *et al.* 1994: 8. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Abagous Sharp, 1917a: 27 (type species: *Rhynchaenus lutulentus* Gyllenhal, 1813). Hoffmann 1954: 717, 740 (subgen. of *Bagous*). Dieckmann 1983: 354, 369 (subgen. of *Bagous*). Caldara 2013: 172.

Himeniphades Kôno, 1934: 245 (type species: *Himeniphades bipunctatus* Kôno, 1934). Caldara 2013: 172.

Diagnosis. Penis body usually widest at base, thence slightly tapered at least in basal 2/3, sometimes with short, ventrobasal plate extending between apodemes (char. 70.1 and 70.2) and with endophallus within tube of penis body with a pair of lateral concentrations of numerous fine denticles or sparse large denticles (char. 87.1 and 87.2). Penis apodemes long (char. 110.0).

Remarks. This subgenus includes all the species that are not part of the other subgenera. Some of the species of this subgenus can be referred to some well characterized species-groups, while the remaining species are morphologically quite heterogeneous, sharing only a single genital character.

Seven species belonging to the subgenus *Bagous* were available for the mtCOI analysis, and they clustered in a different clade from the species belonging to subgenus *Macropelmus*, with weak support (62% pp). Within this clade, two monophyletic groups were distinguished, that match only in part the composition of the morphological species groups.

1. *Bagous josephi* group

Diagnosis. Prosternal canal weak (char. 31.1). Sclerotization of ventral surface of penis body broadly membranous. Sclerotized area of dorsal surface of penis body greatly reduced and present only as a narrow basal bridge (char. 63.1). Endophallus lacking sclerites.

Remarks. Monospecific. Some characters of the penis, such as the almost completely membranous dorsal surface of the body and the complete absence of sclerites in the endophallus, are uncommon in the Bagoini.

Species included. **AUS:** **Bagous josephi* O'Brien, 1992.

2. *Bagous compertus* group

Diagnosis. Body elongate-cylindrical. Pronotum 0.90x or more as long as broad (char. 26.1); with more or less distinctly carinate basal margin across middle one-fourth to one-half. Sclerite complex within tube of penis body with pair of submedian, subapical sclerites well separated (char. 84.3). Submedian sclerites subtriangular with point at base (char. 86.1). Ventral surface of penis body broadly membranous.

Remarks. The species of this group are characterized by a long series of external and genital characters, shared with other not closely related or completely unrelated groups, except for one of them (char. 84.3) unique for this group. *B. pyrrhocnemus* and *B. pyrrhocnemodes* differ from the other species of the group by the ventrobasal margin of the penis body with short, ventrobasal plate extending between apodemes and forming an acute median point, visible from above (char. 70.2), This structure is shared with *B. binodulus*, to which the BI analysis suggests a relationship (49% pp). This group is weakly supported in BI (72% pp) and ML (55% bs). It is presently composed of five Indian species, extensively treated and keyed by O'Brien & Askevold (1995).

Species included. **ORR:** *[1]*Bagous compertus* Faust, 1888, [1]*B. limnophilae* O'Brien, 1995, [1]*B. nigrinus* O'Brien, 1995, [2]*B. pyrrhocnemodes* O'Brien, 1995, *[2]*B. pyrrhocnemus* O'Brien, 1995.

3. *Bagous binodulus* group

Diagnosis. Upper margin of eye at a level slightly higher than the forehead (char. 25.1). Glabrous, smooth and shining area over eyes and at base of interval 1 (char. 35.1). Basal portion of pronotum broadly covered with plumose scales (char. 29.1). Basal margin of elytra slightly to markedly costate from scutellum to, or almost to, humerus. Ventrite 5 with median impression with carinate margin (char. 44.2) bearing a row of long setae (char. 45.1). Ventrobasal margin of penis body with short, ventrobasal plate extending between apodemes and forming an acute median point, visible from above (char. 70.2). Sclerite complex within tube of penis body with a pair of submedian, subapical well-separated sclerites (char. 84.1). Submedian sclerites subtriangular with a point at base (char. 86.1). Basal sclerite complex of two pairs of flat sclerites (char. 90.4).

Remarks. This group is composed of a single Palaearctic species, *i.e.*, the type species of the genus *Bagous*, which bears several striking nongenital as well as genital autapomorphic characters unique in the Bagoini. The penis shares certain general features with those of the species of the *B. bipunctatus* group. The presence of a basal plate of the penis body extending between apodemes is shared between the two groups, but a similar structure appears also in the subgenus *Hydronoplus*.

Species included. **PAL:** [§]**Bagous binodulus* (Herbst, 1795).

4. *Bagous quadrimaculatus* group

Diagnosis. Pronotum with more or less distinctly carinate basal margin across middle one-fourth to one-half. Basal margin of elytra swollen, slightly to markedly costate from scutellum to, or almost to, humerus. Sclerotization of ventral surface of penis body broadly membranous. Endophallus lacking sclerites.

Remarks. This monospecific group includes a species from the Indian subcontinent well characterized by a series of homoplastic characters. Habitus and shape of the male genitalia seem more similar to those of the species of the *B. compertus* group.

Species included. **ORR:** **Bagous quadrimaculatus* O'Brien, 1995.

5. *Bagous bipunctatus* group

Diagnosis. Tube of penis body with a pair of lateral concentrations of more or less numerous, fine to large, mostly acute denticles (char. 87.1). Ventrobasal margin of penis body with short, ventrobasal plate extending between apodemes, therefore visible from above (excluding *B. kagiashi* and *B. picturatus* from Japan) (char. 70.1).

Remarks. The species presently included in this large widespread group are defined by one distinctive character of the endophallus, which consists of a pair of regions with distinctly concentrated and usually minute (rarely large) denticles toward the apex. Otherwise the group is heterogeneous in external structure such as tarsal shape and tibial curvature and dentition. Among the species of the complex, the females of *B. bipunctatus* and *B. puncticollis* possess a bursa with sclerites more or less bilobed and convex (as in unrelated species like those of the *B. argillaceus* group) (char. 116.2). Monophyly of this group is suggested also by the phylogenetic analysis, its species being included in a clade, although not statistically supported (44% pp). It is distributed worldwide except for Australia.

Species included. **AFR:** [4]*Bagous coenosus* Gyllenhal, 1836, *[3]*B. fastosus* Hartmann, 1904, [4]*B. madecassus* Fairmaire, 1897, [4]*B. quadrinodulosus* Hustache, 1932. **NAR:** [2]*B. californicus* LeConte, 1876, [2]*B. chandleri* Tanner, 1943, [2]*B. dietzi* Tanner, 1954, [2]*B. floridanus* Tanner, 1943, [5]*B. lunatoides* O'Brien, 1979, [2]*B. lunatus* Blatchley, 1916, *[10]*B. mamillatus* Say, 1831, [2]*B. obliquus* LeConte, 1876, [2]*B. planatus* LeConte, 1876, [2]*B. puritanus* Blatchley, 1916, [2]*B. restrictus* LeConte, 1876, [7]*B. tuberosus* (Tanner, 1943). **ORR:** *[7]*B. difficilis* O'Brien, 1995, *[8]*B. vicinus* Hustache, 1926. **PAL:** [2]*B. amurensis* Egorov & Gratshev, 1990, §*[4]*B. bagdatensis* Pic, 1904, *[1]*B. bipunctatus* (Kôno, 1934), §[2]*B. glabrirostris* (Herbst, 1795), *[9]*B. kagiashi* Chujo & Morimoto, 1959, §[2]*B. lutulentus* (Gyllenhal, 1813), *[6]*B. occultus* O'Brien, 1995, [2]*B. olcesei* Tournier, 1874, *[5]*B. picturatus* Egorov & Gratshev, 1990, [1]*B. puncticollis* Boheman, 1845, §*[2]*B. robustus* Brisout de Barneville, 1863, [2]*B. spiculatus* O'Brien & Morimoto, 1994, §[2]*B. subcarinatus* Gyllenhal, 1836, [2]*B. subcordatus* O'Brien & Morimoto, 1994, *[11]*B. yamazakii* O'Brien & Morimoto, 1995.

6. *Bagous parvus* group

Diagnosis. Body very small, less (char. 1.1) or at most just longer than 2.0 mm. Penis body at least 4 times longer than wide (char. 57.0).

Remarks. The three species that we refer to this group were previously placed in the *B. pygmaeus* group (Askevold *et al.* 1994; O'Brien *et al.* 1994; O'Brien & Askevold 1995), but are now referred to the genus *Azollaebagous*. The differences from this genus are the strongly developed postocular lobes, the more pronounced prosteral canal, the more elongate elytra with less marked posterior declivity, and lack of curved whitish band at apical third of elytra. This group is weakly supported in BI (75% pp).

Species included. **ORR:** *[1]*B. joyi* O'Brien, 1995, *[2]*B. parvus* O'Brien, 1995. **PAL:** *[3]*B. minor* O'Brien & Morimoto, 1995.

7. *Bagous deceptus* group

Diagnosis. Body very small, at most just longer than 2.0 mm. Penis body with dorsal surface at base truncate (char. 64.1). Sclerites complex within tube of penis body with a pair of submedian, subapical sclerites well separated from each other (char. 84.1).

Remarks. The single species included in this group was previously included in the *B. pygmaeus* group (Askevold *et al.* 1994; O'Brien *et al.* 1994; O'Brien & Askevold 1995). It differs from all these species, however, by the shape of the penis and the presence of a pair of sclerites in the endophallus.

Species included. **ORR:** **B. deceptus* O'Brien, 1995.

Subgenus *Hydronoplus* Fairmaire, 1898 stat. nov.

Hydronoplus Fairmaire, 1898: 243 (type species: *Hydronoplus signatifrons* Fairmaire, 1898). Klima 1934: 129. Alonso-Zarazaga & Lyal 1999: 88. Oberprieler *et al.* 2014: 456.

Pseudobagous Sharp, 1917a: 27 (type species: *Bagous longulus* Gyllenhal, 1836). Alonso-Zarazaga & Lyal 1999: 88. Oberprieler *et al.* 2014: 456; **syn. n.**

Diagnosis. Body elongate-cylindrical. Rostrum flattened at apex (char. 8.1) and with dorsal surface at point of antennal insertion distinctly angulate (char. 6.1). Scrobe in dorsal view visible for its entire length (char. 15.1). Forehead with tuberculate elevation along margin of eye. Pronotum 0.90x or more as long as broad (char. 26.1). Pronotum with more or less distinctly carinate basal margin across middle one-fourth to one-half. Basal margin of elytra swollen, slightly to markedly costate from scutellum to, or almost to, humerus. Penis body long (char. 57.0). Ventrobasal margin of penis body with short plate extending between apodemes, and therefore visible from above (char. 70.1). Penis body with subapical, ventral depression extending toward base and forming shallow to prominent sulcus (char. 72.1); with dorsolateral, longitudinal furrows, one on each side, forming an acute, raised margin that extends from behind orifice to midlength or further, and dorsal surface markedly convex but depressed below level of lateral margin (char. 62.1). Gonocoxite lacking stylus (char. 117.1), densely setose (char. 119.1).

Remarks. This subgenus is fully supported in all analyses and is one of the most easily distinguishable groups in the Bagoini. Fairmaire (1898) and Sharp (1917a) created the new genera *Hydronoplus* (here downgraded to subgenus) and *Pseudobagous* (here synonymized with *Hydronoplus*) for *B. signatifrons* and *B. longulus*, respectively. *Hydronoplus* is characterized by nine apomorphies, four in external morphology and five in the shape of male and female genitalia, and includes six Afrotropical species and one Indian species. Since the character-states sequence was identical in the type species of *Hydronoplus* and *Pseudobagous*, only the former appears in the type-species tree (Fig. 10).

Species included. **AFR:** [1]*Bagous junodi* (Sharp, 1917), [1]*B. longulus* Gyllenhal, 1836, [1]*B. micaceus* Hustache, 1924, [1]*B. promontorii* Marshall, 1906, [1]*B. pilitarsis* Hustache, 1923, *[1]*B. signatifrons* (Fairmaire, 1898). **ORR:** *[2]*B. nymphaeae* Faust, 1888.

Subgenus *Hydrillaebagous* subgen. n.

(Figs 4C–D, 6A)

Type species: *Bagous hydrillae* O'Brien, 1992.
Gender: masculine.

Diagnosis. Endophallus with subbasal pair of dense concentrations of fine, elongate spicules (excluding *B. pauxillulus*) (char. 89.1). Base of endophallus with sacule containing elongate, curved spicules forming dark, somewhat paired masses (excluding *B. blyxae* and *B. matthewsi*) (char. 91.1). Penis body at apex with distinct broad lip. Tegmen with very short parameroid lobes (char. 111.1).

Description. Rostrum moderately short, with antennae inserted subapically. Prosternal canal well-developed, with acutely raised lateral margins. Elytra with humeri obliquely angulate, slightly produced, with declivital callus of interval 5 small, antedeclivital callus of interval 3 absent, odd-numbered intervals slightly convex. Tibiae with apices slightly to markedly arcuate, with setae and denticles prominent or not; tarsi moderately short and sublinear, usually with tarsomere 3 slightly broader than tarsomere 2, and clothed beneath with recumbent, dense, fine pubescence. Penis body at apex with distinct broad lip, with lateral margin of orificial sclerites reaching anterior margin of orifice, with endophallus usually with subbasal pair of dense concentrations of fine, elongate spicules; base of endophallus usually with sacule containing elongate, curved spicules forming dark, somewhat paired masses. Apodemes long. Tegmen with very short parameroid lobes.

Remarks. Monophyly of this subgenus, represented by many Australian species and one Indian species, was almost maximally supported in BI (99% pp), and weakly supported in ML (73% bs) and MP (63% sr). Morphologically, it shows synapomorphies of the male genitalia (char. 91.1 and 111.1). In *B. matthewsi* and *B. blyxae* the ventral surface of the penis body is broadly membranous (as in other unrelated groups) and in *B. ramamurthyi* the pronotum has a distinctly carinate basal margin across middle one-fourth to one-half, a character state shared with many other species of *Bagous*. All the species of this new subgenus appear to live on *Hydrilla*, a genus of the plant family Hydrocharitaceae. Among other bagoines with known biology, only *B. affinis* of the *B. argillaceus* group lives on this genus of plants.

Etymology. The name is composed by the joining of the name *Hydrilla* to the name *Bagous* highlighting the name of the genus of the host plants.

Species included. **AUS:** [1]*Bagous australasiae* Blackburn, 1894, *[2]*B. blyxae* O'Brien, 1992, [2]*B. blyxodes* O'Brien, 1992, [1]*B. brittoni* O'Brien, 1992, [1]*B. callosus* O'Brien, 1992, [1]*B. dubius* O'Brien, 1992, [1]*B. femoralis* O'Brien, 1992, *[4]*B. fornoae* O'Brien, 1992, [1]*B. infrequens* O'Brien, 1992, *[1]*B. hydrillae* O'Brien, 1992, [2]*B. matthewsi* O'Brien, 1992, [4]*B. meridionalis* O'Brien, 1992, [1]*B. occiduus* O'Brien, 1992, *[3]*B. pauxillulus* O'Brien, 1992, [1]*B. propinquus* O'Brien, 1992, [1]*B. proximus* O'Brien, 1992, [1]*B. purcelli* O'Brien, 1992, [4]*B. rieki* O'Brien, 1992, [1] *B. tarsalis* O'Brien, 1992. **ORR:** [1]*B. ramamurthyi* O'Brien, 1995.

Subgenus *Parabagous* Schilsky, 1907 resurrected name

Bagous subgen. *Parabagous* Schilsky, 1907: N (type species: *Bagous chevrolati* Tournier, 1874). Klima 1934: 111. Hustache 1930: 206. Hoffmann 1954: 716, 722. González 1971: 5. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999. 88. Caldara 2013: 172.

Fontenelleus Hoffmann, 1962: 120 (type species: *Bagous cyperorum* Peyerimhoff, 1929). Caldara & O'Brien 1998: 137 (*Fontenellus* err.). Alonso-Zarazaga & Lyal 1999. 88. Caldara 2013: 172.

Diagnosis. Antenna with segment 7 of funicle nearly as wide as segment 6 (char. 21.0) and distinctly separated from club (except for *B. belloi* with 6 funicular segments). Forehead neither sulcate nor foveate (char. 24.0), with tuberculate elevation along margin of eye (excluding some species). Vestiture of odd-numbered elytral intervals generally tesselate, with alternate rectangles of dark and pale scales; setae of odd-numbered elytral intervals surrounded usually by rosette of scales of same color. Elytra lacking declivital callosities (char. 36.0). Metasternum distinctly shorter than ventrite 1. Tibiae stout, with inner margin weakly bisinuate, lacking denticles and with several moderately short bristles; outer margin of tibiae, especially on hind tibiae, straight or nearly so toward apex (in lateral view) (char. 48.0). Tarsi short, with tarsomere 3 subcordate. Basal sclerite complex with two pairs of subclavate sclerites variously articulated (char. 90.1). Sclerotization of ventral surface of penis body broadly membranous. Apodemes of spiculum ventrale very broadly and arcuately divergent from base (U-shaped) (char. 114.1). Bursa with digitate sclerotized structure (char. 116.1).

Remarks. This subgenus was fully supported in BI and strongly supported in ML and MP (96% bs and sr). The species belonging to this subgenus share four synapomorphies: shape of funicular segment 7 (char. 21.0), features of the sclerite complex at the base of the endophallus of the penis (char. 90.1), shape of the spiculum ventrale (char. 114.1) and the sclerite complex of the bursa (char. 116.1). Some strongly modified external features (*i.e.*, short and robust legs, scale vestiture, long elytral setae) might be related to the biology of these species, which is generally poorly known. These species appear to be more strictly associated with the soil than aquatic habitats. Specimens with known data were collected either in desert or forested habitats, from lowland to high altitude, usually by sifting soil and debris far from permanent aquatic pools.

We refer three groups to this subgenus.

1. *Bagous chevrolati* group

Diagnosis. Rostrum with dense fringe of seta-like scales in median 1/3 along ventral margin (char. 12.2). Pronotum with more or less rounded sides, with more or less distinct apical constriction, more or less deeply punctured with intervals between punctures more or less granulose. Elytra more or less elongate, with odd elytral intervals covered with recumbent or erect, short or long setae.

Remarks. The species of this group are characterized by one synapomorphy (char. 12.2): the dense fringe of setalike scales along the ventral margin of the rostrum. *B. chevrolati* differs from the other species by the presence of a sclerite complex within the tube of the penis body that has a pair of submedian, subapical sclerites well separated from each other (char. 84.1). *B. belloi* is unique within Bagoini in having 6 funicular segments (char. 19.1), and *B. longirostris* is unique in having the penis body with long pili at the apex (char. 60.1).

Species included. **PAL:** [1]*Bagous anatolicus* Caldara & O'Brien, 1998, [1]*B. andalusiacus* González, 1971 *[3]*B. belloi* Caldara & O'Brien, 1998, *[1]*B. chevrolati* Tournier, 1874, [1]*B. corsicanus* Hoffmann, 1936, [1]*B. cosiensis* Caldara & O'Brien, 1998, [1]*B. elongatus* Pic, 1896, [1]*B. epirotes* Caldara & O'Brien, 1998, [1]*B. franzi* González, 1971, [1]*B. freti* Caldara & O'Brien, 1998, [1]*B. gracilentus* Desbrochers des Loges, 1896, [1]*B. guttatus* Desbrochers des Loges, 1896, [1]*B. ibericus* González, 1971, [1]*B. libanicus* Desbrochers des Loges, 1896, *[2]*B. longirostris* Vitale, 1904, [1]*B. lyauteyi* Hoffmann, 1952, [1]*B. marocanus* Hustache, 1923, [1]*B. osellai* Caldara & O'Brien, 1998, [1]*B. rudicollis* Desbrochers des Loges, 1896.

2. *Bagous costulatus* group

Diagnosis. Penis body with broad horizontal plate over orifice (char. 79.1). Endophallus at base with many large spicules (char. 89.2).

Remarks. This group differs from the *B. chevrolati* group by two character states in the male genitalia (char. 79.1 and 89.2).

Species included. **PAL:** **Bagous costulatus* Perris, 1870, *B. sabellai* Caldara & O'Brien, 1998.

3. *Bagous cyperorum* group

Diagnosis. Integument completely hidden by finely pitted, almost smooth (char. 3.1) whitish scales, which on elytral intervals are polygonal and arranged in double rows (char. 41.1). Area over eye tuberculate. Rostrum in cross section cylindrical and equal in length in both sexes (char. 5.0). Tarsomere 3 subcordate, not wider than tarsomere 2.

Remarks. This monospecific group differs from all other Bagoini by the features of the elytral vestiture; within the subgenus *Parabagous* it is characterised by the larger size, the sexually monomorphic rostrum, and the different shape of the tarsi. In all analyses this group was sister to the other species of *Parabagous*, with generally strong support.

Species included. **PAL:** **Bagous cyperorum* Peyerimhoff, 1929.

Subgenus *Macropelmus* Dejean, 1821 stat.n.

Macropelmus Dejean, 1821: 89 (type species: *Curculio frit* Herbst, 1795). Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Cyprus Schoenherr, 1825: c. 585 [type species: *Curculio cylindrus* Paykull, 1800 (= *Bagous tubulus* Caldara & O'Brien, 1994)]. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Lyprus Schoenherr, 1826: 288 [type species: *Curculio cylindrus* Paykull, 1800 (= *Bagous tubulus* Caldara & O'Brien, 1994)]. Schoenherr 1836: 536. Schilsky 1907: D (subgen. of *Bagous*). Sharp 1917b: 103. Hustache 1930: 206 (subgen. of *Bagous*). Hoffmann 1954: 716, 721 (subgen. of *Bagous*). Dieckmann 1983: 353, 357 (subgen. of *Bagous*). Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Dicranthus Motschulsky, 1845: 102 [type species: *Dicranthus vittatus* Motschulsky, 1845 (=*Lixus elegans* Fabricius, 1801)]. Schilsky 1907: D. Hustache 1930: 203. Klima 1934: 107. Hoffmann 1954: 712. Dieckmann 1983: 350, 352. Kodada *et al.* 1992: 196. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Ephimeropus Hochhuth, 1847: 543 (type species: *Ephimeropus geniculatus* Hochhuth, 1847). Tournier 1874: 103. Schilsky 1907: Solari 1930: 46. Klima 1934: 108. Hoffmann 1954: 716, 717 (subgen. of *Bagous*). Dieckmann 1983: 353, 354 (subgen. of *Bagous*). Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Elmidomorphus Cussac, 1851: 205 [type species: *Elmidomorphus aubei* Cussac, 1851 (= *Curculio petro* Herbst, 1795)]. Bedel 1884: 103 (*Helmintimorphus* err.). Schilsky 1907: N (subgen. of *Bagous*). Sharp 1917b: 107. Hustache 1930: 206 (subgen. of *Bagous*). Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Anactodes Brisout de Barneville, 1863: 497 (type species: *Lixus elegans* Fabricius, 1801). Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Bagoimorphus Desbrochers des Loges, 1906: 11 [type species: *Bagoimorphus laticollis* Desbrochers des Loges, 1906 (= *Rhynchaenus limosus* Gyllenhal, 1827]. Klima 1934: 129. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Parabagous Sharp, 1917a: 28 (not Schilsky, 1907) [type species: *Curculio frit* Herbst, 1795). Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Pnigodes LeConte, 1876: 188 (type species: *Pnigodes setosus* LeConte, 1876). Klima 1934: 127. Tanner 1943: 33. O'Brien & Wibmer 1982: 93. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172. Oberprieler *et al.* 2014: 456; **syn. n.**

Probagous Sharp, 1917b: 102 [type species: *Bagous measleri* Newberry, 1902 (= *B. czwalinai* Seidlitz, 1891)]. Caldara 2013: 172.

Bagous subgen. *Heterobagous* Solari, 1930: 44 [type species: *Bagous nupharis* Apfelbeck, 1906 (= *Bagous rotundicollis* Boheman, 1845)]. Caldara & O'Brien 1998: 137. Alonso-Zarazaga & Lyal 1999: 88. Caldara 2013: 172.

Diagnosis. Penis body long, more than four times longer than wide (char. 57.0), more or less parallel sided in basal 2/3. Laminar orificial lateral sclerites absent (char. 74.0). Penis apodemes short, at most one-third as long as penis body (char. 110.1).

Remarks. The name *Macropelmus* is used here for the first time as a valid name although it is downgraded to a lower rank (resurrected name). It was considered as an available name by Alonso-Zarazaga & Lyal (1999) and subsequently reported only by Caldara (2013) as synonymous with *Bagous*. Previously, but not recently, the name given to a small part of this group of species (the *B. tubulus* group) was *Lyprus* (Schilsky 1907; Sharp 1917b; Hustache 1930; Hoffmann 1954; Dieckmann 1983). This subgenus includes all the species characterized by short apodemes and a long parallel-sided penis body, although this latter character state is also found in a few species belonging to other subgenera.

In the all-species analysis (Fig. 9) this subgenus was only weakly supported in BI (62% pp). The species belonging to this subgenus clustered in a clade also in MP and ML, but with support lower than 50%. However, in the type-species analysis *Macropelmus* had a strong support in BI (97% pp) and was also supported in ML (84% bs) and MP (61% sr) (Fig. 10).

The species of this subgenus are here distributed in 30 morphological groups, some of which are also supported in the phylogenetic analysis. Ten of them are currently monospecific. Many groups are defined only by characters of male genitalia, which often have a very peculiar shape.

1. *Bagous affaber* group

Diagnosis. Ventral punctures distinctly large, excavate (char. 43.1). Orificial lateral sclerites with basal margin distinct. Sclerite complex within tube of penis body with pair of submedian, subapical well-separated sclerites (char. 84.1). Dorsal surface at base truncate (char. 64.1). Penis body subbasally notched in lateral view (char. 69.1).

Remarks. This group was strongly supported in all analyses. It has four synapomorphies (char. 43.1, 64.1, 69.1, 84.1), three of which are on the male genitalia. This group is represented by two Palaearctic species (both occurring also on the Indian subcontinent) and one Indian species.

Species included. **ORR:** *[2]*B. frontalis* O'Brien, 1995; **ORR & PAL:** *[1]*Bagous affaber* Faust, 1887, [1]*B. latepunctatus* Pic, 1904.

2. *Bagous pictus* group

Diagnosis. Sclerites complex within tube of penis body with a pair of submedian subapical and posteriorly joined sclerites (char. 84.2).

Remarks. This monospecific group is mainly characterized by the shape of the penis and the presence of a pair of submedian subapical and posteriorly joined sclerites that are unique within the tribe.

Species included. **NAR:** **Bagous pictus* Blatchley, 1920.

3. *Bagous humeridens* group

Diagnosis. Pronotal disc moderately to strongly transversely convex. Median impression of ventrite 5 with carinate margin (char. 44.2). Median orificial sclerites with U-shaped, hooked process (char. 82.1). Penis body ventrolaterally with oval lobe in apical third (char. 64.1). Arms of spiculum ventrale with inner margins strongly convergent, joined at ca. midlength (char. 112.1).

Remarks. This group, formed by one Indian and one Australian species, is characterized by one character of ventrite 5 and three unequivocal apomorphic characters in the genitalia. O'Brien & Askevold (1994) placed this group as the sister-group of the *B. apicalis* group on the basis of several external characters, but this relationship was not supported by our analysis.

Species included. **AUS:** [1]*Bagous utriculariae* O'Brien, 1992; **ORR:** *[1]*B. humeridens* Hustache, 1926.

4. *Bagous sellatus* group

Diagnosis. Median orificial sclerites with U-shaped, hemispherical sclerite (char. 82.2).

Remarks. This group, formed by two North-American species, is characterized by a unique apomorphy consisting of two orificial sclerites uncommon in their shape and doubtfully related to those observed in the species of the *B. humeridens* group.

Species included. **NAR:** [1]*B. blatchleyi* Tanner, 1943, *[1]*B. sellatus* LeConte, 1876.

5. *Bagous apicalis* group

Diagnosis. Penis body with unmovable, broad, horizontal plate over orifice (char. 79.2). Shape of venter of penis body ventrolaterally triangular in cross-section, in about middle region (char. 68.1). Apex of penis body very long, asymmetrically deflected to left.

Remarks. This group, composed of one Australian and one Indian species, is characterized by two apomorphies in the penis, unique in the Bagoini. In our matrix we used *B. tuberculatus* since the female of *B. apicalis* is unknown.

Species included. **AUS:** [1]*Bagous apicalis* O'Brien, 1992. **ORR:** *[1]*B. tuberculatus* O'Brien, 1995.

6. *Bagous exilis* group

Diagnosis. Body short and broad-oval, very small (length < 2 mm) (Char. 1.1). Forehead between eyes broad. Elytra short, subrectangular, with greatly shortened caudal prolongation (char. 37.1), and lacking declivital callosity (char. 36.0). Scales of elytral intervals arranged in regular pairs, side by side, each interval with two, individually distinct rows of round scales across each interval (char. 41.1). Tibiae with apices only moderately arcuate, lacking denticles; tarsi short, with tarsomere 3 subquadrate and as wide as tarsomere 2. Penis body compressed, dorsoventrally flattened. Median orificial sclerites with upturned Y-shaped process (char. 82.3).

Remarks. This group is formed by three very closely related small-sized Palaearctic species, which are characterized by the lack of declivital callosities and the pattern of the elytral vestiture, which they share with other unrelated groups, and which are differentiated by characters of the male genitalia.

Species included. **PAL:** §*[1]*Bagous exilis* Jacquelin du Val, 1854, [1]*B. fuentei* Pic, 1908, [1]*B. minutissimus* Faust, 1887.

7. *Bagous tempestivus* group

Diagnosis. Elytra elongate, distinctly wider than pronotum; elytral vestiture tessellate, with distinct stripe in front of declivity. Tarsi long, sublinear. Penis body with pair of movable (char. 80.1), elongate sclerotized plates covering orifice and attached to the orificial margin (char. 79.3), and with median short prominence only visible when plates are opened (char. 81.1).

Remarks. This group is well distinguished from the other species groups by the general habitus, which is characterized by the elongate elytra that are also distinctly wider than the pronotum and which are partly covered with white scales forming a distinct subapical stripe. However, the main difference is in the uncommon shape of the penis body, in which two submedian sclerites are attached to the basal margin of the orifice. Presently this group is composed of three very closely related Palaearctic species, which are reciprocally distinguished by the slightly different shape of tarsomere 3 and/or the shape of the penis. Based on the mtCOI analysis (Fig. 12), *B. tempestivus* resulted associated with *B. monanthifagus* and *B. exilis*, with 81% pp support.

Species included. **PAL:** [1]*Bagous czwalinai* Seidlitz, 1891, [1]*B. macedon* Caldara & O'Brien, 1998, §*[1]*B. tempestivus* (Herbst, 1795).

8. *Bagous lutosus* group

Diagnosis. Body elongate-oval. Tarsi short, tarsomere 3 subcordate and slightly wider than tarsomere 2. Penis body robust, with one pair of elongate sclerotized plates, up-turned at base and covering orifice (char. 79.4), movable (char. 80.1), and with ventral median vermiform sclerite (char. 81.1) only visible when plate is opened. Endophallus with W-shaped sclerite complex basally articulate (char. 84.4), entwined by membranous saccule with many very small spicules and open dorsally (char. 88.1).

Remarks. This monospecific group, presently composed only of *B. lutosus*, a species widespread in Europe and western and central Asia, is easily distinguishable from all other Bagoini by the unique characters of the sclerites of the penis.

Species included. **PAL:** **Bagous lutosus* (Gyllenhal, 1813).

9. *Bagous subruber* group

Diagnosis. Area over eye tuberculate. Tarsomeres short, nearly as long as wide and all of the same width. Sclerites complex within tube of penis body with two pairs of subapical sclerites, one submedian and the other sublateral and posteriorly joined (char. 84.3). Penis body laterally membranous and dorsally with two overlapping poorly sclerotized pairs of plates covering orifice (char. 67.1).

Remarks. Monophyly of this group is suggested by the uncommon shape of the body of the penis and the endophallic sclerites. Although the unique synapomorphies are in the features of the penis body, these species have a characteristic habitus (shape of pronotum, elytra and legs and elytral vestiture) which allows their easy recognition. The group is presently composed of five Palaearctic species.

Species included. **PAL:** [1]*Bagous aliciae* Cmoluch, 1983, [§1]*B. monanthiphagus* Stüben, 2010, [1]*B. septemcostatus* Chevrolat, 1860, *[1]*B. subruber* Reitter, 1890, [1]*B. turkmenicus* Egorov & Gratshev, 1990.

10. *Bagous dieckmanni* group

Diagnosis. Pronotum rugulose, strongly sulcated longitudinally in the middle. Elytral scales shining. Sclerites complex within tube of penis body with a pair of submedian subapical and posteriorly joined sclerites (char. 84.2). Median setal brush behind orifice situated at base of subapical sclerites (char. 92.1). Penis body with apex distinctly sagittate (char. 59.1).

Remarks. The single Palaearctic species presently included in this group is similar in habitus to those of the *B. argillaceus* group, from which it differs in the rugulose sculpture of the pronotum.

Species included. **PAL:** **Bagous dieckmanni* Egorov & Gratshev, 1990.

11. *Bagous biimpressus* group

Diagnosis. Segment 7 of antennal funicle elongate (char. 20.1), nearly as wide as segment 6 (char. 21.1). Antennal club structure indistinctly segmented, 1st segment elongate, glabrous and shining, 2nd and 3rd segments very short, distinctly pubescent (char. 23.1). Prosternal canal scarcely developed (char. 31.1), especially in its proximal half, which is higher than the distal half, forming a weak basal ridge (char. 32.1); postero-lateral margins of prosternal canal barely raised (char. 33.1). Female pygidium with apex broadly blunted (char. 54.1), forming a flat, thickened, arcuate margin (char. 55.1). Sclerites complex within tube of penis body with a pair of submedian subapical sclerites posteriorly joined (char. 84.2). Median setal brush behind orifice situated at base of subapical sclerites (excluding *B. petro*) (char. 92.1).

Remarks. This group was also strongly or moderately strongly supported in the phylogenetic analyses. It traditionally formed the subgenus *Ephimeropus* and is characterized by several genital as well as non-genital characters, in part shared with other groups. Caldara & O'Brien (1998) separated three species—*B. geniculatus*, *B. geniculatodes* and *B. mucronatus*—in the *B. geniculatus* group, on the basis of several synapomorphies from external morphology—postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin (char. 30.0); tibiae with long fine swimming hairs, many of which are much longer than diameter of tibia (char. 47.1); third tarsomere sub-glabrous beneath, with few long setae (char. 53.2)—and of the male genitalia—penis body with more or less sagittate apex (char. 5 9.1), with orificial lateral sclerites apically attached to the sides of the penis body (char. 77.1) and distinctly laterally movable (char. 78.1), appearing like a dorsal process ("false" dorsal process).

This group is currently composed of five Palaearctic and one Indian species.

Species included. **ORR:** [4]*Bagous geniculatodes* O'Brien, 1995; **PAL:** *[1]*B. biimpressus* Fåhraeus, 1845, *[4]*B. geniculatus* (Hochhuth, 1847), *[5]*B. mucronatus* Caldara & O'Brien, 1998, *[2]*B. perparvulus* Rosenhauer, 1856, §*[3]*B. petro* (Herbst, 1795).

12. *Bagous argillaceus* group

Diagnosis. Scales smooth and shiny, with at most a very fine pit (char. 3.1). Supraocular setae very slender, long, erect and curved. Pronotum with complete median longitudinal sulcus or impression. Prosternum with scarcely evident canal, lateral margin more or less parallel and weakly raised (char. 31.1). Sclerites complex within tube of penis body with two posteriorly joined pairs of subapical sclerites, one submedian and the other sublateral (char. 84.4). Penis body with pseudo-orifice large to very large, apparent orifice strongly extended proximally, ventrally sinuate in area beneath orifice, lateral surface ventral to flange concave. Apodemes of spiculum ventrale strongly divergent, contiguous only at extreme base.

Remarks. This group is characterized by one synapomorphy from external morphology, the vestiture composed of almost smooth and distinctly shiny scales, and two synapomorphies from the genitalia. It was supported in all of the phylogenetic analyses. Prevously, *B. affinis* was placed in a separate monotypic group by O'Brien & Askevold (1995) due to two autapomorphies (scales on pronotal disc sublunate and distinctly emarginate and penis apodemes extremely short; char. 28.1 and 110.2, respectively) and the lack of four synapomorphies of the genitalia possessed by the other species of the *B. argillaceus* group—laminar orificial lateral sclerites present although sometimes only distinguishable at the apical portion (char. 74.1); orificial lateral sclerites obliquely uniformly raised (char. 75.1) and with basal margin distinct; orifice with lateral, transverse vertical sclerite (char. 83.1); and presence of a bursa with sclerites more or less bilobed and convex (char. 116.1). It is represented by four Palaearctic species, three of which with an eastern distribution, and two Indian species.

Species included. **ORR:** *[3]*Bagous affinis* Hustache, 1926; [1]*Bagous laevigatus* O'Brien & Pajni, 1989; **PAL:** *§[1]*B. argillaceus* Gyllenhal, 1836, [1]*B. foersteri* Hartmann, 1899, *[2]*B. fremuthi* Dieckmann, 1975, [1]*B. sulcicollis* Hartmann, 1899.

13. *Bagous interruptus* group

Diagnosis. Pronotum with prominent to acute anterolateral tubercle (scarcely evident in *B. peregrinus* and *B. meregallii*) (char. 27.1). Sclerites complex within tube of penis body with two posteriorly joined pairs of subapical sclerites, one submedian and the other sublateral (char. 84.5). Pseudo-orifice large to very large, apparent orifice strongly extended proximally (excluding *B. meregallii*). Arms of spiculum ventrale in relation to apodemes sometimes in a lower level.

Remarks. Whereas the external habitus of some species that belong to this group, like *B. meregallii*, is markedly different from others, the shape of the very characteristic male genitalia is extraordinarily similar in all of them. Monophyly of this group was weakly supported in BI (66% pp) and ML (65% bs) but was not supported in MP. The two North American species *B. setosus* and *B. buchanani* belong to this group, and LeConte (1876) created for these species the new genus *Pnigodes*, on the basis of the shape of the pronotum.
This group presently includes species from all regions except Australia.

Species included. **AFR:** [2]*Bagous fragosus* Marshall, 1920, [2]*B. hybridus* Hustache, 1923; **NAR:** [2]*B. buchanani* (Tanner, 1943), *[2]*B. setosus* (LeConte, 1876); **ORR:** *[1]*B. interruptus* Faust, 1891, [2]*B. salebrosus* O'Brien & Pajni, 1995, [2]*B. sumatrensis* Faust, 1891, [2]*B. tonkinianus* Hustache, 1926; **PAL:** *[3]*B. bulgaricus* Angelov, 1989, [2]*B. foveifrons* Hustache, 1923, [2]*B. meregallii* Caldara & O'Brien, 1998, [2]*B. peregrinus* Gratshev, 1993, [2]*B. sardiniensis* Brisout de Barneville, 1863.

14. *Bagous cylindricus* group

Diagnosis. Body elongate-cylindrical. Rostrum distinctly short (char. 4.1), subrectangular, scarcely sexually dimorphic. Pronotum 0.90x or more as long as broad (char. 26.1). Sclerites complex within tube of penis body with two pairs of subapical sclerites, one submedian and well separated from each other and the other sublateral and posteriorly joined (char. 84.5). Tube of penis body ventrally with a V-shaped median sclerite fused to the ventral portion and not movable (char. 85.1). Tegmen lacking parameroid lobes (char. 111.2). Gonocoxite with stylus (char. 117.0) although this is very small.

Remarks. This group is characterized by the rostrum which is shorter than in all other bagoines and by a unique pattern of the endophallic sclerites. In ML and MP this group was very weakly associated to the *B. tubulus* group, but such a relationship was not supported in BI.

This group is composed by one Palaearctic species and one Afrotropical species

Species included. **AFR:** [1]*Bagous cylindricollis* Hustache, 1923; **PAL:** *[1]*B. cylindricus* Rosenhauer, 1856.

15. *Bagous tubulus* group

Diagnosis. Body elongate-cylindrical. Pronotum 0.90x or more as long as broad (char. 26.1). Rostrum cylindrical, narrow, elongate (especially in female). Elytra nearly as wide as pronotum, without calli (char. 36.0). Sclerites complex within tube of penis body with a pair of submedian subapical sclerites posteriorly joined (char. 84.2), with chela-like basal portion. Median setal brush behind orifice situated at base of subapical sclerites (char. 93.1). Penis body elongate, with sinuate and subparallel sides. Tegmen lacking parameroid lobes (char. 111.2). Arms of spiculum ventrale longer than apodemes, with long apical setae (char. 113.1). Gonocoxites elongate.

Remarks. This group is characterized by the rostrum being cylindrical, narrow, and elongate (especially in the female), and a series of non-genital characters, *e.g.*, the elongate body, and genital character states in part shared also by the species of the *B. cylindricus* group. Previously, *B. elegans* and *B. majzlani* (formerly *Dicranthus*) were separated in a distinct group by Caldara & O'Brien (1998) due to their very distinctive habitus, including the pattern of the dorsal vestiture (char. 39.1 and 39.2), and the shape of the elytra in which the confluence of intervals 3 and 9 is markedly raised and forms a long posteriorly-projecting process (char. 38.1). In both all-species (Fig. 9) and type-species (Fig. 10) analyses this group was strongly supported; the complex comprising *B. tubulus / B. friwaldszkyi* was sister to the complex *B. elegans / B. majzlani*. This group is composed of seven Palaearctic species.

Species included. **PAL:** §*[3]*Bagous elegans* (Fabricius, 1801); *[2]*Bagous friwaldszkyi* Tournier, 1874, [1]*B. henoni* Hustache, 1927, *[4]*B. majzlani* (Kodada, Holecova & Behne, 1992); [1]*B. mingrelicus* Tournier, 1874, [1]*B. minutus* Hochhuth, 1847, *[1]*B. tubulus* Caldara & O'Brien, 1994.

16. *B. nodulosus* group

Diagnosis. Penis body elongate with sides convergent from base to apex, with ventrobasal margin truncate; dorsal process very high and composed of a pair of very elongate sclerotized pieces, in dorsal view sinuate and joined at base with two small V-shaped vertical orificial sclerites (char. 83.1) and with membrane from dorsal process to proximal margin of orifice.

Remarks. This group is characterized by a very peculiar shape of the penis, especially due to the high dorsal process, and the sclerites. This group was also supported in the phylogenetic analysis (BI: 95% pp; ML: 75% bs; MP: 59% sr). Moreover, the two taxa included in this group, which are largely widespread in the western Palaearctic region, are apparently the only two species living on *Butomus umbellatus* L. (Butomaceae). However, they differ from each other in several external characters. Apart from the general habitus which is distinctly thinner, *B. nodulosus* has a very well-developed declivital callus of interval 5, long and distinctly apically curved tibiae, with distinct denticles, elongate and linear tarsi. In contrast, *B. validus* has a rostrum with numerous scale-like setae along the ventro-lateral margins (char. 12.1) and penis body with sclerotized subtriangular plate behind the dorsal process, (char. 95.1). Due to these differences these species were placed in two separated monotypic groups by Caldara & O'Brien (1998).

Species included. **PAL:** §*[1]*Bagous nodulosus* Gyllenhal, 1836; *[2]*Bagous validus* Rosenhauer, 1847.

17. *Bagous proprius* group

Diagnosis. Penis body with dorsal surface at base transverse (char. 64.1), with median setal brush behind orifice absent (char. 93.0). Dorsal surface sulcate behind dorsal process, producing distinctly costate lateral margin, apodemes very short. Penis body widest in front of dorsal process (char. 97.1). Post-orificial dorsal process of penis body almost horizontal, directed distally (char. 98.1).

Remarks. This group is distinctive in the structure of the penis body, especially in the shape of the dorsal process.

Species included. **ORR:** [1]*Bagous indistinctus* O'Brien, 1995; **PAL:** *[1]*B. proprius* O'Brien & Morimoto, 1994.

18. *Bagous rotundatus* group

Diagnosis. Body short, broad-oval. Inner surface of dorsal process covered with a dense area of denticles (char. 100.1). Relatively short dorsal process projecting a little proximally, with broad depression behind. Sides behind dorsal process swollen (char. 104.1).

Remarks. This monospecific group is distinctive exclusively in two very peculiar male genital characters (char. 100.1 and char. 104.1).

Species included. **PAL:** **Bagous rotundatus* O'Brien & Morimoto, 1994.

19. *Bagous transversus* group

Diagnosis. Inner surface of dorsal process covered with a dense area of denticles (char. 100.1). Lateral margin of penis body at base of dorsal process with subapical lateral incision (char. 102.1), with areas laterad and distad of orifice denticulate (char. 66.1). Penis body widest in front of dorsal process (char. 97.1) and markedly constricted immediately proximad of this (char. 107.1); dorsal process semicircular laterally with anterior concavity, very slightly asymmetrical distad of orifice (char. 96.1).

Remarks. This largely widespread group, which includes species from all regions except the Australian and Afrotropical regions, is separated from other species only by male genital characters (three synapomorphies). In the mtCOI analysis *B. limosus* formed a strongly supported clade (96% pp) together with *B. frit, B. longitarsis* and *B. collignensis. Bagous limosus* differs from the other species of the group by the elytra with strial punctures large, one-third to more than one-half of intervals width, a character state shared with other unrelated species.

Species included. **NAR:** [1]*Bagous cavifrons* LeConte, 1876, [1]*B. maculatus* Blatchley, 1916, [1]*B. texanus* Tanner, 1943, *[1]*B. transversus* LeConte, 1876; **ORR:** [1]*B. loisae* O'Brien, 1995, [1]*B. similis* O'Brien, 1995, [1]*B. youngi* O'Brien, 1995; **PAL:** §*[2]*B. limosus* (Gyllenhal, 1827).

20. *Bagous frit* group

Diagnosis. Apical margin of pygidium deeply emarginate (char. 55.2). Inner surface of dorsal process covered with a dense area of denticles (char. 100.1). Sublateral margin of penis body behind dorsal process with dorsal, sublateral, carinate, V-shaped, denticulate ridge bordering median depression behind dorsal process (char. 106.2). Lateral margin laterad and distad of orifice denticulate (char. 66.1). Penis body in cross-section T-shaped, the sides deeply compressed behind dorsal process and almost joined at midline (char. 58.1). Sublateral margin of penis body behind dorsal process denticulate (char. 105.1). Apical third of penis body asymmetrically deflected to left and asymmetrically flattened (char. 61.1).

Remarks. This group, composed of the European species *B. frit* and the Japanese species *B. fritodes*, is characterized by several synapomorphies, especially in the male genitalia. Concerning character state 57.1, this must not be confused with a slight left deflection of the strict apex present in several unrelated species. *B. frit* and the species belonging to the previous group formed a monophyletic clade, supported in BI and ML (respectively, 69% pp and 57% bs) and not supported in MP; relationships between these groups were also suggested by the molecular analysis, where the reciprocal position of *B. frit* and *B. limosus* was, however, reversed.

Species included. **PAL:** [§*1]*Bagous frit* (Herbst, 1795), [1]*B. fritodes* O'Brien & Morimoto, 1994.

21. *Bagous buckinghami* group

Diagnosis. Body elongate-cylindrical. Apex of penis body slightly asymmetrical. Gonocoxite sinuate (char. 118.1), lacking stylus (char. 117.1).

Remarks. This monospecific group is only distinguishable by some character states of the genitalia, especially in the female. The male genitalia are morphologically similar to those of the species of the *B. fractus* and *B. collignensis* groups.

Species included. **PAL:** **Bagous buckinghami* O'Brien & Morimoto, 1994.

22. *Bagous fractus* group

Diagnosis. Penis body widest in front of dorsal process (char. 83.1), with ventral surface distinctly bicarinate (char. 71.2). Arms of spiculum ventrale apically broadly fused, leaving a small to large membranous central fenestra.

Remarks. O'Brien *et al.* (1995) included *B. fractus* and *B. fractodes*, reciprocally similar in habitus, in the same group, expressing however reservations concerning important differences they share in the shape of the penis. A close relationship between these two species was not supported by our analysis. In *B. fractus* the apex of the penis body is curved on the left only at its strict apex (as in *B. simulans* and *B. apicalis*) but not as in *B. frit* where the penis body is curved on the left from the apical third.

Species included. **PAL:** **Bagous fractus* O'Brien & Morimoto, 1994.

23. *Bagous fractodes* group

Diagnosis. Penis body widest in front of dorsal process (char. 97.1). Lateral margin behind dorsal process acute (char. 103.1).

Remarks. Due to the results of our analyses, this species is here referred to a distinct group and not classified together with *B. fractus* as previously proposed by O'Brien *et al.* (1995).

Species included. **PAL:** **Bagous fractodes* O'Brien & Morimoto, 1995.

24. *Bagous collignensis* group

Diagnosis. Apex of penis body angulately explanate, more or less sagittate (char. 59.1), with lateral margin behind dorsal process acute (char. 103.1). Dorsal process with apex directed backward (char. 94.1), with setal brush situated anteromedially (char. 92.2). Penis body widest in front of dorsal process (char. 97.1), broad area behind dorsal process depressed.

Remarks. This group was present as a monophyletic clade also in BI (94% pp), ML (70% bs) and MP (not supported, 49% sr). The molecular analysis (Fig. 12) included this group in the *B. frit* clade, with a strong support (98% pp). All the species included in this group share an almost identical penis, differing only in length and in the shape of the more or less sagittate apex, or by the lateral margin laterad and distad of the orifice being denticulate (as in *B. confusus*, char. 65.1). Some species, like *B. collignensis*, *B. claudicans*, *B. rufimanus*, *B. longitarsis* and *B. vivesi*, are also very similar externally, differing only by small features (length of tarsi and punctures of the pronotum). Other species, like *B. rotundicollis*, *B. riedeli* and *B. lyali*, are characterized mainly by a slender body, flattened elytral dorsum and long legs. However, *B. lyali* is distinguishable from the other two species by the dense pubescence of the sixth funicular segment (char. 22.1). On the contrary, *B. diglyptus* is easily distinguished by its robust broad-oval body.

This group is composed of Palaearctic, North American and Indian species.

Species included. **NAR:** [1]*Bagous bituberosus* LeConte, 1876, [1]*B. nebulosus* LeConte, 1876, [1]*B. pauxillus* Blatchley, 1916, [1]*B. pusillus* LeConte, 1876; **ORR:** *[4]*B. confusus* O'Brien, 1995, [1]*B. myriophylli* O'Brien, 1995: **PAL:** [1]*B. claudicans* Boheman, 1845, *[§1]*B. collignensis* (Herbst, 1797), [1]*B. diglyptus* Boheman, 1845, [§1]*B. longitarsis* Thomson C.G., 1868, *[3]*B. lyali* Caldara & O'Brien, 1998, [2]*B. riedeli* Caldara & O'Brien, 1998, *[2]*B. rotundicollis* Boheman, 1845, [1]*B. rufimanus* Pericart, 1989, [1]*B. tersus* Egorov & Gratshev, 1990, [1]*B. vivesi* González, 1967.

25. *Bagous brevis* group

Diagnosis. Tarsi sublinear, short; tarsomere 3 as wide as tarsomere 2. Penis body widest at level of dorsal process and constricted behind dorsal process (excluding *B. lutulosus*), with apex subtruncate, very bluntly rounded; dorsal process low, flattened, laterally with pair of short wings obliquely arranged (char. 101.1), with setal brush situated anteromedially (excluding *B. lutulosus*); with costate lateral margin behind dorsal process; ventrally bicarinate from base to below orifice.

Remarks. This Palaearctic group is characterized by the shape of the dorsal process, which is flattened and with pair of lateral wings (char. 101.1). In our analyses it was supported in BI (75% pp) and ML (60% bs). It was recovered as a group, but not supported in MP (44% sr).

Species included. **PAL:** *[1]*Bagous brevis* Gyllenhal, 1836, [1]*B. lothari* Caldara & O'Brien, 1998, *[2]*B. lutulosus* (Gyllenhal, 1827), [1]*B. revelieri* Tournier, 1874, [1]*B. rufipennis* Egorov & Gratshev, 1990, [1]*B. uralensis* Egorov & Gratshev, 1990.

26. *Bagous descarpentriesi* group

Diagnosis. Apex of penis body bluntly rounded. Dorsal process with setal brush. Presence of two long orificial sclerites distinctly angulated in apical third (char. 74.1).

Remarks. In this monospecific group, the shape of the dorsal process is similar to that of the *B. collignensis* and *B. brevis* groups, from which it is clearly distinguishable by the presence of two orificial sclerites with peculiar shape (char. 74.1).

Species included. **AFR:** **Bagous descarpentriesi* Hustache, 1933.

27. *Bagous humeralis* group

Diagnosis. Apex of penis body acute but not expanded. Orifice with long setal brush (char. 73.1).

Remarks. This monospecific group was weakly associated in BI to the *B. adelaidae, B. fractus* and *B. trapae* groups (52% pp), from which it is, however, distinguishable by the presence of an uncommonly long orificial setal brush, autapomorphic for this species.

Species included. **AFR:** **Bagous humeralis* Marshall, 1906.

28. *Bagous adelaidae* group

Diagnosis. Side margins of prosternum in lateral view strongly acute and projecting posterad over procoxae (char. 33.2). Declivital callus of interval 5 small but distinct. Tarsi moderately short and sublinear. Penis body with vertical dorsal process and with setal brush. Basoventral area medially depressed and indistinctly sclerotized, ventrolaterally distinctly bicarinate from apodeme to about one-third length of penis body (char. 71.2). Sublateral margin of penis body behind dorsal process with dorsal, sublateral, carinate (char. 105.1), and denticulate (char. 106.1) ridge bordering median depression.

Remarks. This group is distinguishable by four apomorphic characters, one nongenital and three from the male genitalia, one of which homoplastic (char. 71.2). *B. dostinei* differs from the other two species of the group by the apex of the dorsal process not directed backward. It is supported in all analyses (BI: 100% pp; ML: 84% bs; MP: 80% sr).

Species included. **AUS:** *[1]*Bagous adelaidae* Blackburn, 1894, *[2]*B. dostinei* O'Brien, 1992, [1]*B. simulans* O'Brien, 1992.

29. *Bagous americanus* group

Diagnosis. Tarsi elongate; all tarsomeres with similar width. Penis body with ventrobasal area medially depressed, ventrolaterally slightly costate at base (char. 71.1). Postorificial dorsal process of penis body almost horizontal, directed distally (char. 98.1). Lateral margin of penis body behind dorsal process markedly carinate, the surface ventral to the carina markedly excavate, the dorsal surface mesad of the carina markedly depressed (char. 108.1). Dorsal surface of penis body, medially, behind dorsal process more or less markedly raised, forming acute, longitudinal, median carina (char. 109.1).

Remarks. This North American group is distinguished by two unique character states of the male genitalia (char. 108.1 and 109.1).

Species included. **NAR:** *[1]*Bagous americanus* LeConte, 1876, [1]*B. blanchardi* Blatchley, 1916, [1]*B. longirostrus* Tanner, 1943, [1]*B. magister* LeConte, 1876.

30. *Bagous trapae* group

Diagnosis. Tibiae with long fine swimming hairs, many much longer than diameter of tibia (char. 47.1). Tibiae broad, with outer and inner margin more or less perpendicular to apex, the apex not slightly narrowed (char. 49.1). Tarsi elongate and linear, tarsomere 3 subglabrous beneath, with few long setae (char. 53.2). Orificial lateral sclerites with basal margin distinct, raised and basally recurved upwards (char. 75.2), distinctly laterally movable (char. 78.1). Median setal brush behind orifice situated on ventral surface of dorsal process (char. 92.3). Dorsal surface of penis body, behind dorsal process with broad depression (char. 99.1). Post-orificial dorsal process of penis body almost horizontal, directed distally (char. 98.1). Arms of spiculum ventrale apically broadly fused, leaving small to large membranous central fenestra. Insertion of spermathecal gland attached on body, anteapically (char. 115.1).

Remarks. This group is well-distinguished by a series of synapomorphies of the legs and especially of the penis, which bears an extremely curious dorsal process that is rich in apomorphies. In *B. colossus* the elytral strial punctures are large, one-third to more than one-half intervals width, similar to other unrelated species.

Species included. **AFR:** [1]*Bagous punctipennis* Marshall, 1906, [1]*B. remaudierei* Hoffmann, 1954; **AUS:** [1]*B. natator* O'Brien, 1992; **ORR:** *[2]*B. colossus* O'Brien, 1995, *[1]*B. trapae* Parshad, 1961.

Key to the genera and subgenera of Bagoini

1. Scrobe not reaching eye and squamose (Fig. 1A). Prosternum without rostral canal and without transverse ridge at its base (Fig. 3A) . . . . *Hydronomus* Schoenherr

\- Scrobe reaching eye and glabrous (Figs 1B–D). Prosternum with weak (Fig. 3B) to deep rostral canal (Fig. 3C); if rostral canal lacking then prosternum with transverse ridge at base (Fig. 3D) 2

2. Rostrum in lateral view strongly curved (Fig. 1B); apex of rostrum with a lateral plica (Fig. 1F); basal 2/3 of lateral margin of rostrum (close to ventral margin) with a row of sparse, regularly distributed setae (Fig. 1F). Apodemes of spiculum ventrale fully bifurcate, arising laterally on plate of sternite, apparently forming two straight rods with arms (Fig. 8F) . . . . *Memptorrhynchus* Iablokoff-Khnzorian

\- Rostrum in lateral view moderately curved to almost straight; apex of rostrum without a lateral plica; basal 2/3 of lateral margin of rostrum with sparse and irregularly distributed setae. Apodemes of spiculum ventrale not bifurcate (Figs 8E and 8G) . 3

3. Body short and broad-oval; very small in size, 2.0 mm or less in length (rostrum excluded). Pronotal disc moderately to strongly transversely convex. Postocular lobe ventrally indistinct, not raised, not forming discontinuity with anterior prosternal margin. Prosternal canal weak. Lateral margins of prosternal canal barely raised. Elytra subquadrate (Fig. 4A), with posterior

declivity in lateral view strong at 75 degrees (Fig. 4B); declivital callus absent on interval 5 (Fig. 4A); scales of elytral intervals arranged in almost regular pairs, side by side, each interval with two, individually distinct rows of round scales; vestiture with a semicircular white stripe at posterior third (Fig. 4A). . . . . *Azollaebagous* n. gen.

\- Species without all these characters taken together. Postocular lobes well-developed; prosternum with deep rostral canal and with lateral margins well-developed (Fig. 3C), except for *B. geniculatus* group of *Bagous* subgen. *Macropelmus* (Fig. 3D) . . 4

4. Vestiture of odd-numbered elytral intervals generally tessellate, with alternate rectangles of dark and pale scales, or completely whitish. Elytra lacking declivital callosities. Tibiae stout, with inner margin weakly bisinuate. Outer margin of tibiae, especially on hind tibiae, straight or nearly so toward apex (in lateral view). Tarsi short, with tarsomere 3 broadly cordate to subcordate (Fig. 2F). Basal sclerite complex of endophallus with two pairs of subclavate sclerites variously articulated (Fig. 5C–D). In female apodemes of spiculum ventrale very broadly and arcuately divergent from base (U-shaped) (Fig. 8G), and bursa with digitate sclerotized structure (Fig. 8I) . . . . *Bagous* subgen. *Parabagous* Schilsky

\- Vestiture of odd-numbered elytral intervals with different pattern. Elytra usually at least with a weak to strong callus at the declivity of interval 5 (Figs 3F–G). Tibiae usually longer and with inner margin distinctly bisinuate. Outer margin of tibiae, especially on hind tibiae, more or less curved toward apex (in lateral view). Tarsi longer, rarely with tarsomere 3 subcordate. Basal sclerite complex of endophallus, if present, differently shaped. In female apodemes of spiculum ventrale not broadly and arcuately divergent from base (Fig. 8E), and bursa rarely with sclerotized structure and when present not digitate 5

5. Rostrum flattened at apex and with dorsal surface at point of antennal insertion distinctly angulate (Fig. 1D). Scrobe in dorsal view visible for its entire length (Fig. 1G). Forehead with tuberculate elevation along margin of eye. Pronotum long, 0.90x or more as long as broad. Elytra always elongate . . . . *Bagous* subgen. *Hydronoplus* Fairmaire

\- Rostrum regularly convex from base to apex and with dorsal surface at point of antennal insertion not angulate. Scrobe in dorsal view visible at last in its basal portion (Fig. 1E). Forehead without tuberculate elevation along margin of eye. Pronotum shorter. Elytra from short to long 6

6. Penis with apodemes long, at least half as long as body (Figs 5A–H) 7

\- Penis with apodemes short, at most one-third as long as body (Figs 6B–G, 7A–I and 8A–D) . . . .*Bagous* subgen. *Macropelmus* Dejean

7. Orificial lateral sclerites of penis body not reaching anterior margin of orifice (Figs 4A–B, D–E). Endophallus without subbasal pair of dense concentrations of fine elongate spicules. Base of endophallus without sacule containing elongate, curved spicules. Penis body at apex at most with short narrow lip, widest at base, thence slightly tapered at least in basal 2/3 (Figs 5E–F, 5G). Tegmen with long parameroid lobes . . . .*Bagous* Germar *s. str.*

\- Orificial lateral sclerites of penis body reaching anterior margin of orifice. Endophallus with sub-basal pair of dense concentrations of fine elongate spicules (excluding *B. pauxillulus*). Base of endophallus with sacule containing elongate, curved spicules forming dark, somewhat paired masses (except *B. blyxae* and *B. matthewsi*) (Fig. 6A). Penis body at apex with distinct broad lip, more or less parallel-sided in basal 2/3 (Fig. 6A). Tegmen with very short parameroid lobes . . . . *Bagous* subgen. *Hydrillaebagous* n.subgen.

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TABLE 1. Matrix of the morphological characters used for the phylogenetic analysis.

Species \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
A_frumentarium	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
C_nucum	0	0	–	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
I_crassirostris	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
O_setiger	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
N_scirpi	0	0	–	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
P_sinuatocollis	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	–	0	0	1	1	0	1	0	0	0
L_oryzophylus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	–	0	1	–	–	0	1	0	0	0
T_lemnae	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	–	–	0	0	0	0	0
H_abietis	0	0	–	0	0	0	0	0	0	0	1	0	0	0	0	0	–	1	0	0	0	0	0	0	0	0
alismatis	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0
brevipennis	0	2	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0
crispus	0	2	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0
pygmaeodes	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
clarencensis	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
franzi	0	2	0	0	1	0	0	0	0	1	1	2	0	0	0	1	0	1	0	0	1	0	0	1	0	0
longirostris	0	2	0	0	1	0	0	0	0	1	1	2	0	0	0	1	0	1	0	0	1	0	0	1	0	0
belloi	0	2	0	0	1	0	0	0	0	1	1	2	0	0	0	1	0	1	1	–	–	0	0	1	0	0
costulatus	0	2	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0
cyperorum	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0
hydrillae	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
blyxae	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
pauxillulus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
fornoae	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
meridionalis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
joyi	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
minor	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
parvus	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
deceptus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
josephi	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
signatifrons	0	2	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1
nymphaeae	0	2	0	0	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1
compertus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1
pyrrhocnemus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1
quadrimaculatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
yamazakii	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
bipunctatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
bagdatensis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
kagiashi	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
robustus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
glabrirostris	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
occultus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
difficilis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
vicinus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
mamillatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
picturatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
fastosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
binodulus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0
affaber	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
frontalis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
pictus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
tempestivus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
humeridens	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
sellatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
tuberculatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0

Species \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
exilis	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
subruber	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
dieckmanni	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
biimpressus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0
perparvulus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0
petro	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0
geniculatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0
mucronatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0
argillaceus	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
fremuthi	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
affinis	0	2	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
lutosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
bulgaricus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
interruptus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
setosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
cylindricus	0	2	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1
friwaldszkyi	0	2	0	0	0	0	2	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
tubulus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
elegans	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
majzlani	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
nodulosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
validus	0	2	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0
proprius	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
fractodes	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
fractus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
buckinghami	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
rotundatus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
limosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
transversus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
frit	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
collignensis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
confusus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
rotundicollis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
lyali	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
brevis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
lutulosus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
descarpentriesi	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
humeralis	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
adelaidae	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
dostinei	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
americanus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
colossus	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
trapae	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0

Species \ Character	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
A_frumentarium	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0
C_nucum	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	1	0
I_crassirostris	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0
O_setiger	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	1	0
N_scirpi	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	1	0	0	0	0	1	0
P_sinuatocollis	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	0	1
L_oryzophylus	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	0	1
T_lemnae	0	0	0	0	0	0	-	1	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	1	0
H_abietis	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	1	0
alismatis	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
brevipennis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	0	1
crispus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	0	1
pygmaeodes	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	–	1	0	1	0	0	0	1
clarencensis	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	–	1	0	1	0	0	0	1
franzi	1	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	1	1
longirostris	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	1	1
belloi	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	1	1
costulatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	0	0	0	1	1
cyperorum	0	0	0	1	2	0	1	0	0	0	0	0	0	0	1	0	0	1	–	1	0	0	0	0	0	1
hydrillae	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
blyxae	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
pauxillulus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
fornoae	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
meridionalis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
joyi	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
minor	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
parvus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
deceptus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
josephi	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
signatifrons	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
nymphaeae	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
compertus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
pyrrhocnemus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
quadrimaculatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
yamazakii	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
bipunctatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
bagdatensis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
kagiashi	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
robustus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
glabrirostris	0	0	0	1	2	0	1	0	0	1	1	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
occultus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
difficilis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
vicinus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
mamillatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
picturatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
fastosus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
binodulus	0	0	1	1	2	0	1	0	1	1	0	0	0	0	0	0	0	2	1	1	0	1	0	0	0	1
affaber	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	1	1	1	–	1	0	1	0	0	0	1
frontalis	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	1	1	–	1	0	1	0	0	0	1
pictus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
tempestivus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
humeridens	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	2	0	1	0	1	0	0	0	1
sellatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
tuberculatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1

Character / Species	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
exilis	0	0	0	1	2	0	1	0	0	0	1	0	0	0	1	0	0	1	–	1	0	1	0	0	0	1
subruber	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
dieckmanni	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
biimpressus	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	1	–	1	0	1	0	0	0	1
perparvulus	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
petro	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
geniculatus	1	0	0	0	0	2	-	0	0	1	0	0	0	0	0	0	0	1	–	1	1	1	0	0	0	1
mucronatus	1	0	0	0	0	2	-	0	0	1	0	1	0	0	0	0	0	1	–	1	1	1	0	0	0	1
argillaceus	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
fremuthi	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
affinis	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
lutosus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
bulgaricus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
interruptus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	1	0	1
setosus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
cylindricus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
friwaldszkyi	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
tubulus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
elegans	0	0	0	1	2	0	1	0	0	1	0	2	1	0	0	0	0	1	–	1	0	1	0	0	0	1
majzlani	0	0	0	1	2	0	1	0	0	1	0	2	2	0	0	0	0	1	–	1	0	1	0	0	0	1
nodulosus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
validus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
proprius	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
fractodes	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
fractus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
buckinghami	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
rotundatus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
limosus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	1	0	1	–	1	0	1	0	0	0	1
transversus	1	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
frit	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
collignensis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
confusus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
rotundicollis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
lyali	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
brevis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
lutulosus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
descarpentriesi	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
humeralis	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
adelaidae	0	0	0	1	2	0	2	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
dostinei	0	0	0	1	2	0	2	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
americanus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	0	1	0	0	0	1
colossus	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	1	0	1	–	1	1	1	1	0	0	1
trapae	0	0	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1	–	1	1	1	1	0	0	1

Character / Species	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
A_frumentarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
C_nucum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
I_crassirostris	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
O_setiger	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
N_scirpi	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
P_sinuatocollis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
L_oryzophylus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
T_lemnae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
H_abietis	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
alismatis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
brevipennis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
crispus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
pygmaeodes	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
clarencensis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
franzi	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
longirostris	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
belloi	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
costulatus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
cyperorum	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
hydrillae	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0
blyxae	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0
pauxillulus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
fornoae	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0
meridionalis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
joyi	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
minor	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
parvus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
deceptus	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
josephi	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
signatifrons	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
nymphaeae	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
compertus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
pyrrhocnemus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0
quadrimaculatus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
yamazakii	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
bipunctatus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
bagdatensis	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
kagiashi	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
robustus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
glabrirostris	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
occultus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
difficilis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
vicinus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
mamillatus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
picturatus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
fastosus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
binodulus	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0
affaber	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
frontalis	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
pictus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
tempestivus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
humeridens	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	–	–	–	–
sellatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
tuberculatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	–	–	–	–

Character / Species	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
exilis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
subruber	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	–	–	–	–
dieckmanni	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
biimpressus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
perparvulus	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
petro	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
geniculatus	2	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
mucronatus	2	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
argillaceus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
fremuthi	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
affinis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
lutosus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
bulgaricus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
interruptus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
setosus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
cylindricus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
friwaldszkyi	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
tubulus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
elegans	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
majzlani	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
nodulosus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
validus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
proprius	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	–	–	–	–
fractodes	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
fractus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	–	–	–	–
buckinghami	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
rotundatus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–
limosus	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	–	–	–	–
transversus	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	–	–	–	–
frit	1	0	2	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	–	–	–	–
collignensis	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
confusus	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	–	–	–	–
rotundicollis	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
lyali	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
brevis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
lutulosus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
descarpentriesi	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0
humeralis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	–	–	–	–
adelaidae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	–	–	–	–
dostinei	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	–	–	–	–
americanus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	–	–	–	–
colossus	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	2	0	0	1
trapae	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	2	0	0	1

Character / Species	79	80	81	82	83	84	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103
A_frumentarium	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
C_nucum	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
I_crassirostris	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
O_setiger	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
N_scirpi	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
P_sinuatocollis	0	–	–	0	0	0	–	0	0	0	5	0	0	0	–	–	–	–	–	–	–	–	–	–
L_oryzophylus	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
T_lemnae	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
H_abietis	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
alismatis	0	–	–	0	0	0	–	0	0	0	3	0	0	0	–	–	–	–	–	–	–	–	–	–
brevipennis	0	–	–	0	0	0	–	0	0	0	2	0	0	0	–	–	–	–	–	–	–	–	–	–
crispus	0	–	–	0	0	1	0	0	0	0	2	0	0	0	–	–	–	–	–	–	–	–	–	–
pygmaeodes	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
clarencensis	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
franzi	0	–	–	0	0	0	–	0	0	0	1	0	0	0	–	–	–	–	–	–	–	–	–	–
longirostris	0	–	–	0	0	0	–	0	0	0	1	0	0	0	–	–	–	–	–	–	–	–	–	–
belloi	0	–	–	0	0	0	–	0	0	0	1	0	0	0	–	–	–	–	–	–	–	–	–	–
costulatus	1	0	0	0	0	0	–	0	0	2	1	0	0	0	–	–	–	–	–	–	–	–	–	–
cyperorum	0	–	–	0	0	0	–	0	0	0	1	0	0	0	–	–	–	–	–	–	–	–	–	–
hydrillae	0	–	–	0	0	0	–	0	0	1	0	1	0	0	–	–	–	–	–	–	–	–	–	–
blyxae	0	–	–	0	0	0	–	0	0	1	0	0	0	0	–	–	–	–	–	–	–	–	–	–
pauxillulus	0	–	–	0	0	0	–	0	0	0	0	1	0	0	–	–	–	–	–	–	–	–	–	–
fornoae	0	–	–	0	0	0	–	0	0	1	0	1	0	0	–	–	–	–	–	–	–	–	–	–
meridionalis	0	–	–	0	0	0	–	0	0	1	0	1	0	0	–	–	–	–	–	–	–	–	–	–
joyi	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
minor	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
parvus	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
deceptus	0	–	–	0	0	1	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
josephi	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
signatifrons	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
nymphaeae	0	–	–	0	0	0	–	0	0	0	6	0	0	0	–	–	–	–	–	–	–	–	–	–
compertus	0	–	–	0	0	3	1	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
pyrrhocnemus	0	–	–	0	0	3	1	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
quadrimaculatus	0	–	–	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
yamazakii	0	–	–	0	0	0	–	1	0	0	0	2	0	0	–	–	–	–	–	–	–	–	–	–
bipunctatus	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
bagdatensis	0	–	–	0	0	1	0	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
kagiashi	0	–	–	0	0	1	0	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
robustus	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
glabrirostris	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
occultus	0	–	–	0	0	0	–	2	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
difficilis	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
vicinus	0	–	–	0	0	0	–	2	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
mamillatus	0	–	–	0	0	0	–	1	0	0	4	0	0	0	–	–	–	–	–	–	–	–	–	–
picturatus	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
fastosus	0	–	–	0	0	0	–	1	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
binodulus	0	–	–	0	0	1	1	0	0	0	4	0	0	0	–	–	–	–	–	–	–	–	–	–
affaber	0	–	–	0	0	1	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
frontalis	0	–	–	0	0	1	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
pictus	0	–	–	0	0	2	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
tempestivus	3	1	1	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
humeridens	0	–	–	1	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
sellatus	0	–	–	2	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
tuberculatus	2	0	0	0	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–

Character / Species	79	80	81	82	83	84	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103
exilis	0	–	–	3	0	0	–	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
subruber	0	–	–	0	0	4	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
dieckmanni	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
biimpressus	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
perparvulus	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
petro	0	–	–	0	0	2	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
geniculatus	0	–	–	0	0	0	–	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
mucronatus	0	–	–	0	0	0	–	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
argillaceus	0	–	–	0	1	4	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
fremuthi	0	–	–	0	1	4	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
affinis	0	–	–	0	0	4	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
lutosus	4	1	1	0	0	4	0	0	1	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
bulgaricus	0	–	–	0	0	5	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
interruptus	0	–	–	0	0	5	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
setosus	0	–	–	0	0	5	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
cylindricus	0	–	–	0	0	5	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	–	–
friwaldszkyi	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
tubulus	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
elegans	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
majzlani	0	–	–	0	0	2	0	0	0	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–
nodulosus	0	–	–	0	1	0	–	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
validus	0	–	–	0	1	0	–	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
proprius	0	–	–	0	0	0	–	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0
fractodes	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1
fractus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	0
buckinghami	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	0	0	0	0	0	0	0
rotundatus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	1	0	0	0	1	0	0	0
limosus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	0	1	0	0	1	0	1	0
transversus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	0	1	0	0	1	0	1	0
frit	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	1	0	0	0	1	0	0	0
collignensis	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1
confusus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1
rotundicollis	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1
lyali	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	1
brevis	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	1	0	0
lutulosus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	0	0	0	0	1	0	0
descarpentriesi	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	0
humeralis	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	1	0	0	0	0	0	0	0
adelaidae	0	–	–	0	0	0	–	0	0	0	0	0	2	1	1	0	1	1	0	0	0	0	0	0
dostinei	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	1	1	0	0	0	0	0	0
americanus	0	–	–	0	0	0	–	0	0	0	0	0	2	1	0	0	1	1	1	0	0	0	0	0
colossus	0	–	–	0	0	0	–	0	0	0	0	0	3	1	0	0	1	1	1	1	0	0	0	0
trapae	0	–	–	0	0	0	–	0	0	0	0	0	3	1	0	0	1	1	1	1	0	0	0	0

Character / Species	104	105	106	108	109	110	111	112	113	114	115	116	117	118	119
A_frumentarium	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
C_nucum	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
I_crassirostris	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
O_setiger	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
N_scirpi	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
P_sinuatocollis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
L_oryzophylus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
T_lemnae	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
H_abietis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
alismatis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
brevipennis	–	–	–	–	–	0	0	0	0	2	0	0	0	0	0
crispus	–	–	–	–	–	0	0	0	0	2	0	0	0	0	0
pygmaeodes	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
clarencensis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
franzi	–	–	–	–	–	0	0	0	0	1	0	1	0	0	0
longirostris	–	–	–	–	–	0	0	0	0	1	0	1	0	0	0
belloi	–	–	–	–	–	0	0	0	0	1	0	1	0	0	0
costulatus	–	–	–	–	–	0	0	0	0	1	0	1	0	0	0
cyperorum	–	–	–	–	–	0	0	0	0	1	0	1	0	0	0
hydrillae	–	–	–	–	–	0	1	0	0	0	0	0	0	0	0
blyxae	–	–	–	–	–	0	1	0	0	0	0	0	0	0	0
pauxillulus	–	–	–	–	–	0	1	0	0	0	0	0	0	0	0
fornoae	–	–	–	–	–	0	1	0	0	0	0	0	0	0	0
meridionalis	–	–	–	–	–	0	1	0	0	0	0	0	0	0	0
joyi	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
minor	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
parvus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
deceptus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
josephi	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
signatifrons	–	–	–	–	–	0	0	0	0	0	0	0	1	0	1
nymphaeae	–	–	–	–	–	0	0	0	0	0	0	0	1	0	1
compertus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
pyrrhocnemus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
quadrimaculatus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
yamazakii	–	–	–	–	–	0	0	?	?	?	?	?	?	?	?
bipunctatus	–	–	–	–	–	0	0	0	0	0	0	1	0	0	0
bagdatensis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
kagiashi	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
robustus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
glabrirostris	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
occultus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
difficilis	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
vicinus	–	–	–	–	–	0	0	0	0	0	0	1	0	0	0
mamillatus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
picturatus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
fastosus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
binodulus	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0
affaber	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
frontalis	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
pictus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
tempestivus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
humeridens	–	–	–	–	–	1	0	1	0	0	0	0	0	0	0
sellatus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
tuberculatus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0

Character / Species	104	105	106	108	109	110	111	112	113	114	115	116	117	118	119
exilis	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
subruber	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
dieckmanni	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
biimpressus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
perparvulus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
petro	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
geniculatus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
mucronatus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
argillaceus	–	–	–	–	–	1	0	0	0	0	0	1	0	0	0
fremuthi	–	–	–	–	–	1	0	0	0	0	0	1	0	0	0
affinis	–	–	–	–	–	2	0	0	0	0	0	0	0	0	0
lutosus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
bulgaricus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
interruptus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
setosus	–	–	–	–	–	1	0	0	0	0	0	0	0	0	0
cylindricus	–	–	–	–	–	1	2	0	0	0	0	0	0	0	0
friwaldszkyi	–	–	–	–	–	1	2	0	1	0	0	0	0	0	0
tubulus	–	–	–	–	–	1	2	0	1	0	0	0	0	0	0
elegans	–	–	–	–	–	1	2	0	1	0	0	0	0	0	0
majzlani	–	–	–	–	–	1	2	0	1	0	0	0	0	0	0
nodulosus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
validus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
proprius	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
fractodes	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?
fractus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
buckinghami	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
rotundatus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
limosus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
transversus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
frit	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0
collignensis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
confusus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
rotundicollis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
lyali	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
brevis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
lutulosus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
descarpentriesi	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
humeralis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
adelaidae	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
dostinei	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
americanus	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
colossus	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
trapae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0

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