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## RESEARCH ARTICLE

# First record of the litter-inhabiting weevil genus *Protacallobodes* (Coleoptera: Curculionidae: Molytinae) from outside of Japan, with description of a new species from Taiwan

CHRISTOPH GERMANN<sup>1</sup> & VASILY V. GREBENNIKOV<sup>2</sup>

## Abstract

We clarify the taxonomic and phylogenetic identity of two conspecific, litter-inhabiting female weevils from the Huisun forest in Taiwan. These beetles are most similar to those of the genera *Protacalles* Voss, 1957, *Protacallinus* Morimoto, 1962 and *Protacallobodes* Morimoto, 2011, which are all endemic to Japan. We performed a phylogenetic analysis of 37 terminals and 83 parsimony-informative adult morphological characters. The single most parsimonious tree recovered a clade of these three genera, with the Taiwan species sister to *Protacallobodes*. Statistical support for this tree was low and these clades collapsed after bootstrapping. We describe the Taiwan weevils as *Protacallobodes bhudevi* sp. n., the third species of the genus and a new generic record for Taiwan. We illustrate the newly-described species and its possible relatives, and update the identification key to *Protacallobodes* and related genera.

**Keywords:** East Asia, morphology, new genus record, phylogeny, taxonomy.

## Zusammenfassung

Wir klären die taxonomische Zugehörigkeit und die phylogenetische Stellung zweier konspezifischer weiblicher Rüsselkäfer aus der Streuschicht des Huisun-Waldes auf Taiwan. Diese Rüsselkäfer sind denjenigen der Gattungen *Protacalles* Voss, 1957, *Protacallinus* Morimoto, 1962 und *Protacallobodes* Morimoto, 2011 am ähnlichsten, welche alle endemisch für Japan sind. Wir führten eine phylogenetische Analyse mit 37 Taxa und 83 parsimony-informativen morphologischen Merkmalen durch. Der sparsamste Baum ergab eine Klade dieser drei Gattungen, mit der Art aus Taiwan als Schwesterart zu *Protacallobodes*. Der Baum wird statistisch nur schwach unterstützt und die Kladen kollabierten nach dem Bootstrapping-Verfahren. Wir beschreiben die taiwanesischen Rüsselkäfer als *Protacallobodes bhudevi* sp. n. Dies ist die dritte Art der Gattung und der Erstnachweis der Gattung für Taiwan. Die neue Art und ihre möglichen verwandten Arten werden illustriert und in einem angepassten Bestimmungsschlüssel vorgestellt.

## Introduction

In 2013, when sifting the leaf litter in the high-altitude Huisun forest of Taiwan, one of us collected two seemingly conspecific females of an unknown Molytine weevil (Fig. 1). A preliminary morphological comparison suggested affinities with the genera *Protacallobodes* (Fig. 2), *Protacalles* (Fig. 3) and *Protacallinus* (Fig. 4). These genera consist of four named species, all restricted to Japan. MORIMOTO (2011), however, indicated that *Protacallinus* was known to him in “a good number of species”, while *Protacallobodes* “has a wide range of distribution from Japan to southern China and Vietnam according to unnamed species in our collection”. One of these species, *Protacallobodes ryukyuensis* Morimoto, 2011, is known from the Ishigaki (MORIMOTO 2011) and Kumejima Islands (YOSHITAKE 2020), part of the Ryukyus, the former one at a mere 400 km from the Huisun forest. Both Taiwanese specimens resemble these Japanese weevils habitually

and agree with the morphological diagnosis of this group of genera (MORIMOTO 2011: 325). Additionally, all these beetles display the same habitat preference for the forest floor and leaf litter. Consequently, these three Japanese genera became the first candidates in our search to identify the closest relatives of our two unnamed Taiwanese specimens.

Uncertainties arose when we attempted to search the literature for other taxa potentially related to our find. As pointed out by MORIMOTO (2011: 325), the three aforementioned Japanese genera and at least three other potentially closely related genera are scattered between the two potentially non-monophyletic molytine tribes Ithyoporini and Sthereini (ALONSO-ZARAZAGA & LYAL 1999; LÖBL & SMETANA 2013; LYAL 2014; ALONSO-ZARAZAGA et al. 2017). These three potentially related genera are the monotypic *Darumazo* Morimoto & Miyakawa, 1985 from Japan (Fig. 5) and the two trans-Beringian oligotypic genera *Lobosoma* Zimmermann, 1964 and *Sthereus*

Motschulsky, 1845. No phylogenetic analysis has targeted any of these genera. The existing taxonomic ambiguity is, therefore, not surprising, because the majority of Molytinae tribes and the subfamily itself are likely non-monophyletic (SHIN et al. 2017).

We designed our study to face and resolve, as far as possible, the taxonomic and phylogenetic uncertainties pertaining to our Taiwanese weevils. The present paper, therefore, has two goals. First, we introduce the Taiwanese species to science by describing and naming it. This we do based on a phylogenetic analysis, the latter forming our second goal. As before (GERMANN & GREBENNICKOV 2020), our overall objective is to shed phylogenetic light on the obscure and diverse litter-inhabiting molytine weevils.

### Material and methods

Museum abbreviations, with the name of contact person(s) in parentheses:

CGC	CHRISTOPH GERMANN collection, Rubigen, Switzerland
KUZC	Kyushu University Museum, Fukuoka, Japan (MUNETOSHI MARUYAMA)
NHMB	Naturhistorisches Museum Basel, Switzerland (CHRISTOPH GERMANN)
NMNS	National Museum of Natural Science, Taichung, Taiwan (MING-LUEN JENG, JING-FU TSAI)

This study follows the methodology of our earlier work on the molytine subtribe Cotasteromimina (GERMANN & GREBENNICKOV 2020). We re-use the Cotasteromimina morphological matrix and adapt it to our current purposes. For the present analysis, we define the ingroup by restricting it to six terminals altogether, representing the Taiwanese species, all three Japanese genera, and two genera from the potentially closely related tribe Ithyoporini: *Darumazo* and *Sclerocardius* Schoenherr, 1847. The out-group consists of 23 representatives of other Molytinae. The root is formed, in addition to a representative of the subfamily Curculioninae, *Gymnetron veronicae* (Germar, 1821), by a representative of the more distantly related (SHIN et al. 2017) subfamily Entiminae: *Otiorhynchus singularis* (Linnaeus, 1787). Our matrix (Appendix 1) consists of 31 terminals and 87 adult morphological characters (Appendix 2). Label data of the seven newly scored terminals are given in Appendix 3. Five newly scored ingroup terminals are depicted in Figs. 1–5. We conducted a single parsimony analysis using the same analytical procedures as before (GERMANN & GREBENNICKOV 2020). In this analysis, we treated all characters as of equal weight, and all multistate characters are unordered. Four parsimoniously uninformative characters (36, 66, 70 and 77) were deactivated before the analysis. Throughout this paper we adhere for practical reasons to the current and unsatisfactory (see Introduction) tribe classification of Molytinae and, therefore, do not modify the existing tribal placement of any genus.

### Results

The phylogenetic analysis resulted in a single shortest tree of 529 steps (Fig. 6), with consistency index 23 and

retention index 44. The Taiwanese weevil was recovered as a member of the *Protacalles*, *Protacallinus* and *Protacallobodes* clade, sister to the latter genus. The former clade was supported by two unambiguously optimized synapomorphies (UOS): 24/1 (head, antenna, funicle, ratio of second antennomere length to that of first, dorsal view: 0.5 and more) and 57/0 (elytra, raised and bowed bristles, shape of tip: rounded). The next less inclusive clade of *Protacalles* sister to *Protacallobodes* is supported by five UOS: 3/0 (body, ratio of body length to maximum height, lateral view: < 2.5), 10/2 (head, rostrum, fronto-dorsal length compared to that of pronotum in dorsal view: > 1.1), 21/1 (antenna, funicle, number of distal-most antennomeres with vestiture similar to that of club: 1), 35/1 (prothorax, longitudinal channel on sternum anterior of procoxae, ventral view: present) and 55/1 (elytra, raised bristles, dorsal or lateral view: present). The monophyly of the genus *Protacallobodes* including the herein described new species was supported by five UOS: 4/2 (body, scales, including those on head and legs: appressed and erect), 17/1 (head, eyes, smallest distance between compared to width of base of rostrum, dorso-frontal view: smaller than 0.8), 33/0 (prothorax, anterior edge, ocular lobes, lateral view: absent), 50/2 (scutellum, if visible externally, dorsal view: not visible) and 67/1 (legs, all tibiae, premucro: present). Bootstrapping this tree resulted in an almost completely unresolved bush, with only three clades supported over the 50% threshold: *Darumazo* + *Himalanchnus* Zherikhin, 1987 (55%), *Orthorhinus* Schoenherr, 1825 + *Vanapa* Pouillaude, 1915 (52%) and all three included species of the genus *Seticotasteromimus* Germann, 2013 (99%). Unambiguous optimization of evolutionary events on branches demonstrated the preponderance of non-unique evolutionary events, i.e., of either parallelisms or reversals (open circles in Fig. 6).

Consistently with the obtained results, and considering the morphological similarity and geographical proximity between our Taiwanese specimens and those of the genus *Protacallobodes*, we introduce our Taiwanese specimens as belonging to a new species of this genus.

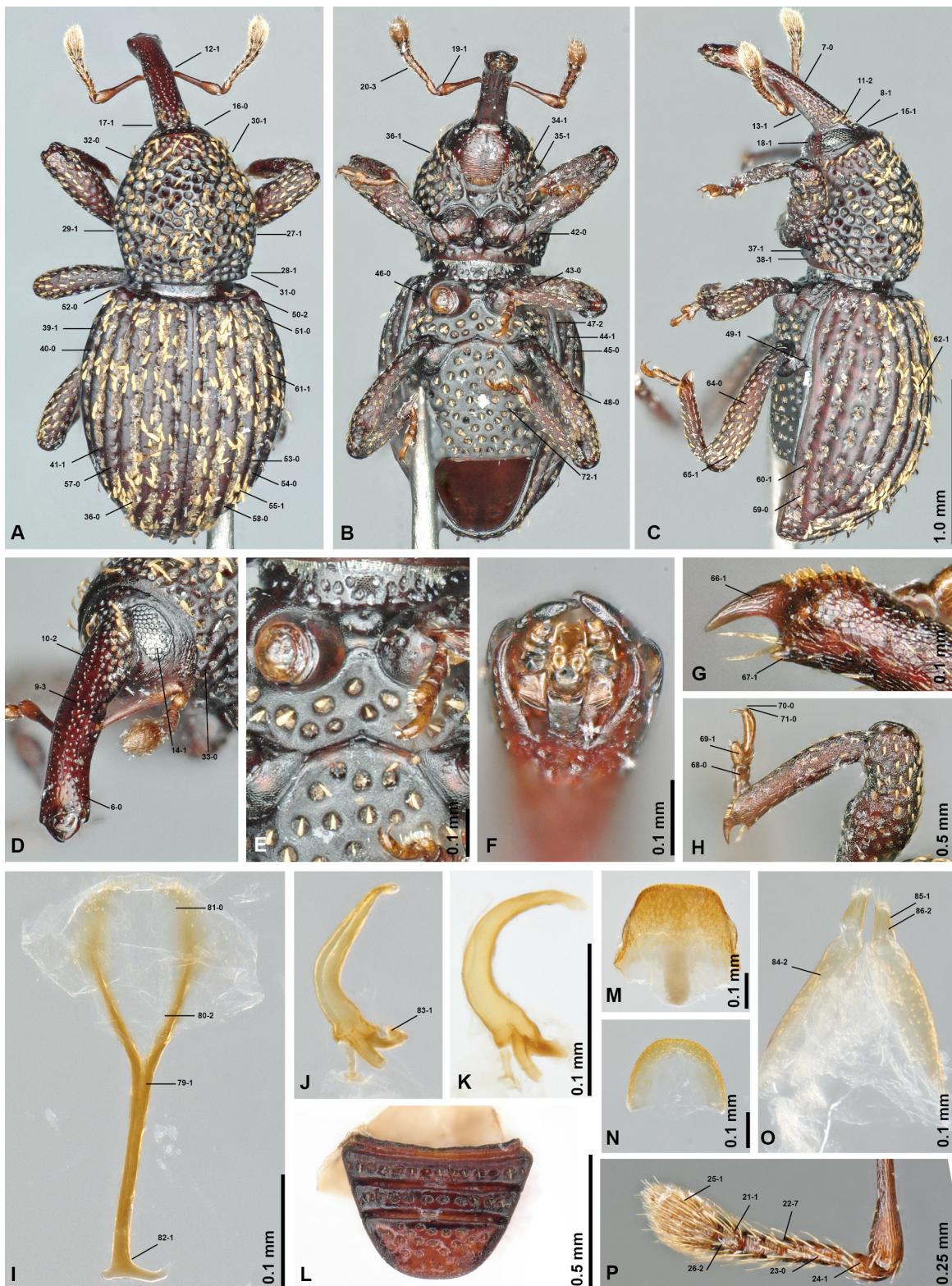
#### *Protacallobodes bhudevi* sp. n. (Fig. 1)

Type locality  
Taiwan, Taichung, Huisun forest, N24.0640° E121.0245°, 1647 m.

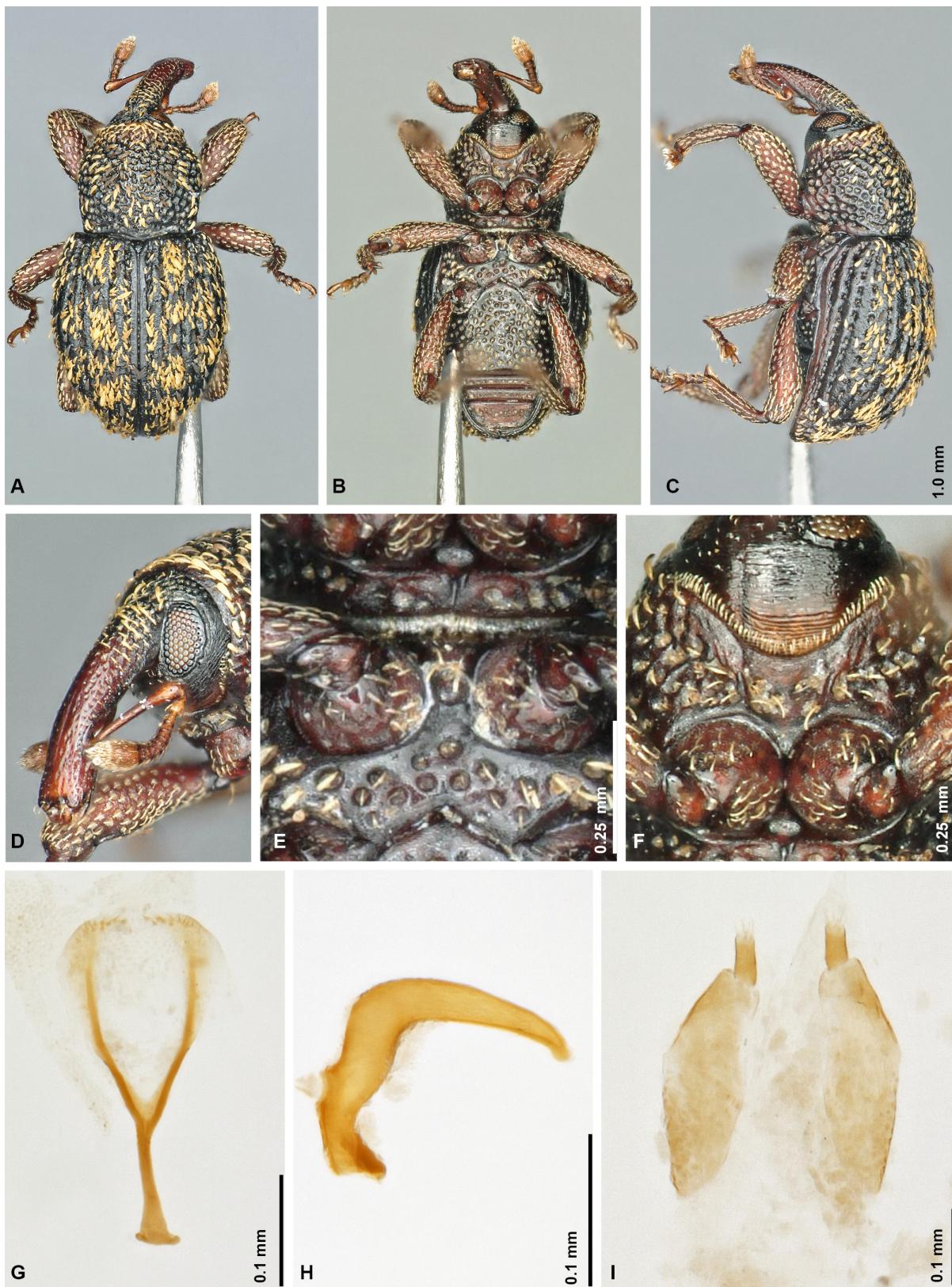
#### Type material

Holotype (NMNS): female, “TAIWAN, Taichung, Huisun forest, 24.0640 121.0245, 1647m, 3.ix.2013, sift TW16, V. Grebennikov”//CNCCOLVG00006978//CNCCOLVG00006979.

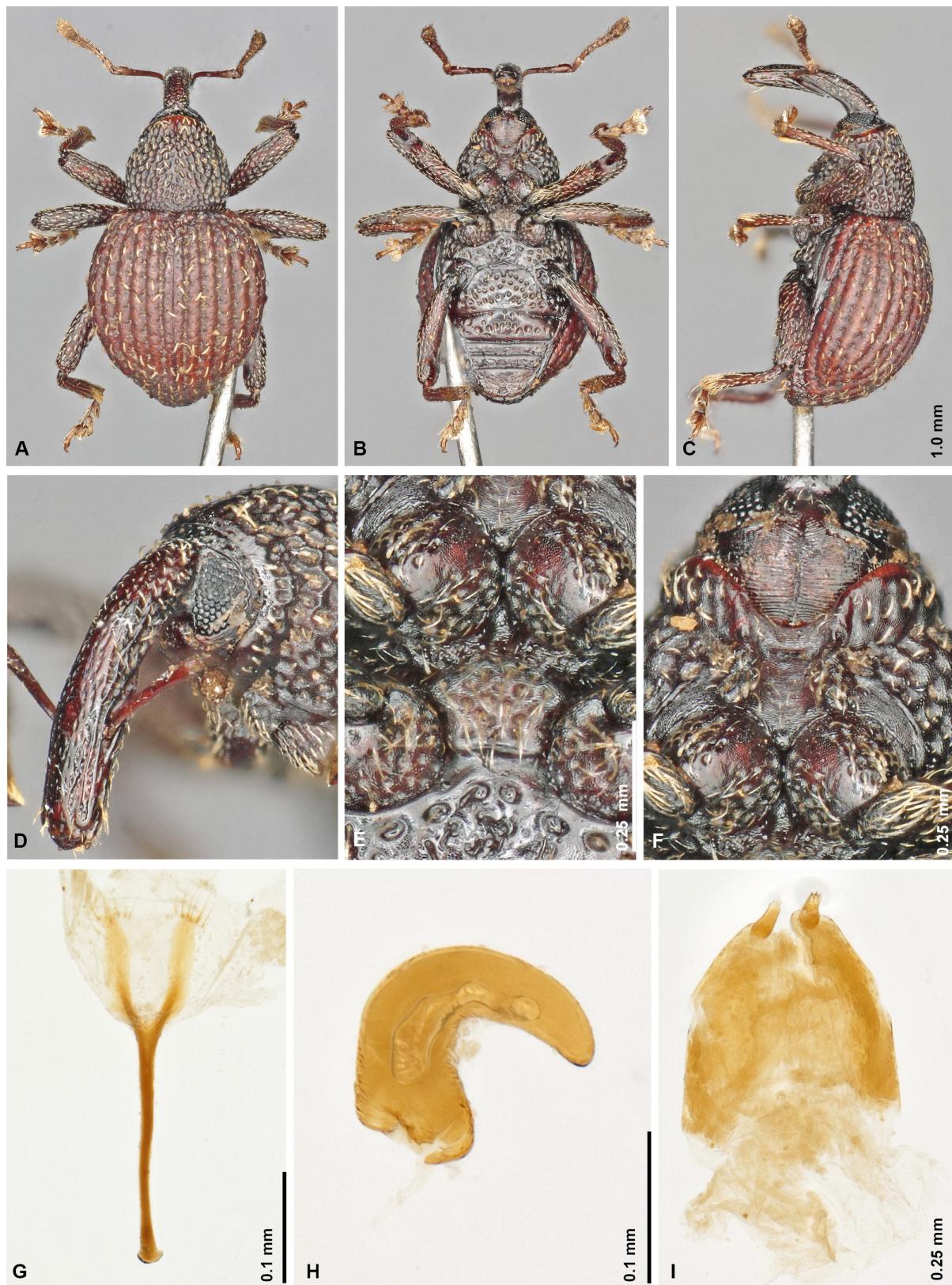
Paratype (NHMB): female, “TAIWAN, Taichung, Huisun forest, 24.0671 121.0291, 1682m, 13.viii.2013, sift TW06, V. Grebennikov”//CNCCOLVG00006778//CNCCOLVG00006779.



**Fig. 1.** *Protacallodes bhudevi* sp. n., females. A–J, L–P: holotype; K: paratype. A–C. Habitus dorsal, ventral and lateral. D. Head and rostrum. E. Mesoventral process. F. Mouthparts. G. Right protibia with uncus, premucro and stiff yellow spines on outer side. H. Right fore leg showing femur with small tooth. I. Sternite 8. J–K. Spermatheca. L. Ventrites 3–5. M. Tergite 8. N. Tergite 7. O. Gonocoxites. P. Antenna. (© CHRISTOPH GERMANN)



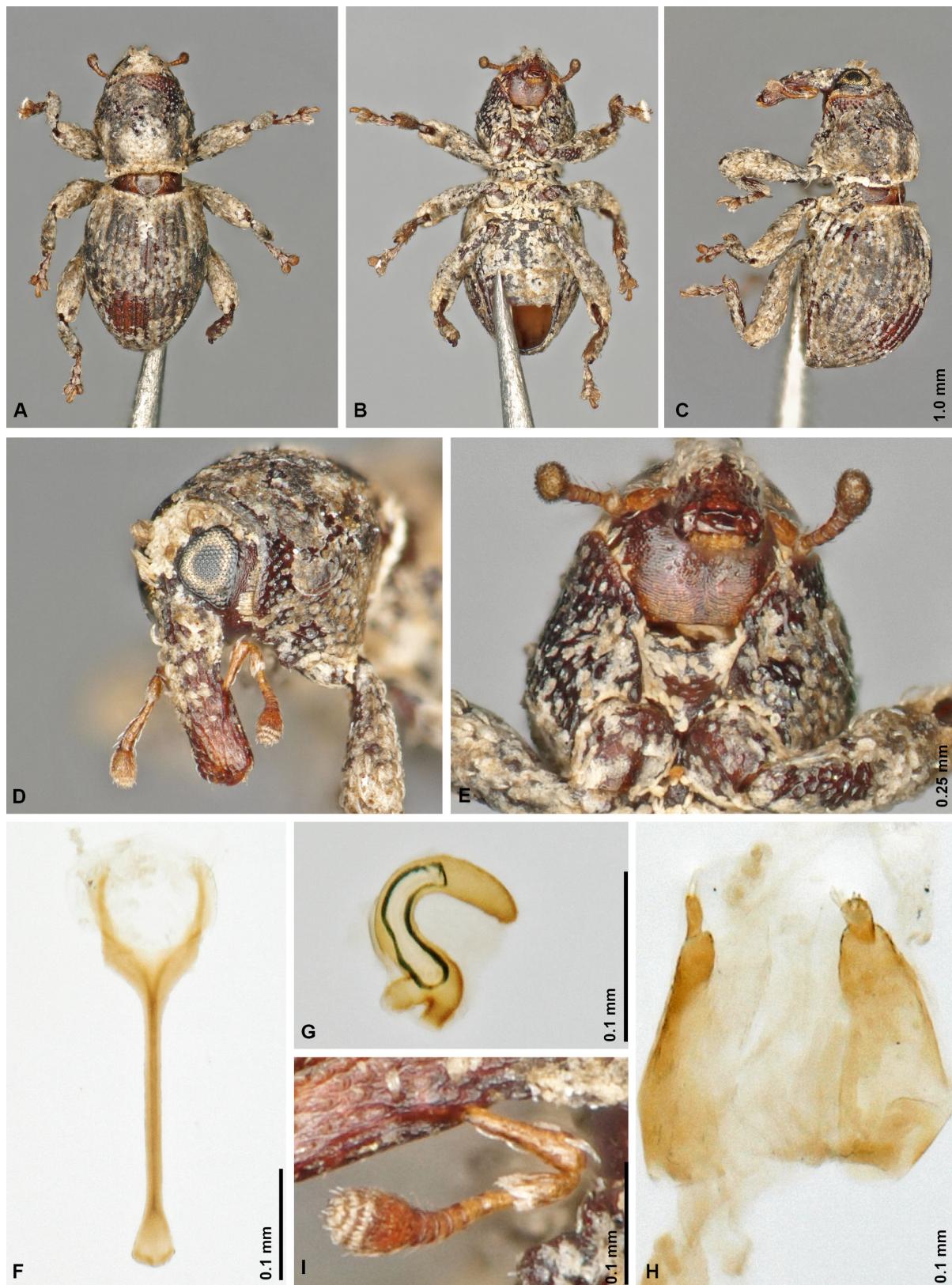
**Fig. 2.** *Protacalles masumotoi* Morimoto, 2011, female. A–C. Habitus dorsal, ventral and lateral. D. Head and rostrum. E. Mesoventral process. F. Prosternum. G. Ventrite 7. H. Spermatheca. I. Gonocoxites. (© CHRISTOPH GERMANN)



**Fig. 3.** *Protacalles monticola* Voss, 1957, female. A–C. Habitus dorsal, ventral and lateral. D. Head and rostrum. E. Mesoventral process. F. Prosternum. G. Ventrite 7. H. Spermatheca. I. Gonocoxites. (© CHRISTOPH GERMANN)



**Fig. 4.** *Protacallinus uenoi* Morimoto, 1962, female. **A–C.** Habitus dorsal, ventral and lateral. **D.** Head and rostrum. **E.** Prosternum. **F.** Ventrite 7. **G.** Spermatheca. **H.** Gonocoxites. (© CHRISTOPH GERMANN)



**Fig. 5.** *Darumazo distinctus* Morimoto & Miyakawa, 1985, female. **A–C.** Habitus, dorsal, ventral lateral. **D.** Head and rostrum. **E.** Prosternum. **F.** Ventrite 7. **G.** Spermatheca. **H.** Gonocoxites. **I.** Antenna. (© CHRISTOPH GERMANN)



**Fig. 6.** The single most parsimonious tree obtained after a phylogenetic analysis of *Protacalodes bhudevi* sp. n. and its potential relatives. The clade of the genera *Protacalles*, *Protacallinus* and *Protacalodes* is highlighted. Unambiguously optimized evolutionary events are plotted on internodes. Character numbers are above the circles, newly acquired character states are below the circles. Black circles indicate unique evolutionary events; white circles indicate parallelisms or reversals.

### Description

Body length in dorsal view excluding rostrum: 2.56–2.94 mm. Body dark auburn (Fig. 1A–D), prothorax and elytra with bowed and club-shaped, appressed, yellowish scales.

Head globular, deeply retracted in pronotum (Fig. 1B–D). Rostrum as long as pronotum, its dorsal surface evenly curved in lateral view (Fig. 1D); scrobes lateral, oblique. Rostrum in dorsal view weakly narrowed at antennal

insertion, widening anteriad. Eyes oval, in lateral view comparable in their greatest dimension to the width of the rostrum at its base, in dorsal view eye contours not protruding outside head contour (Fig. 1D). Epistome glabrous and finely punctuate, vaulted laterally above mandibular base (Fig. 1D). Mandibles visible in frontal view, with three teeth. Labium rounded; maxillae with broad and stout palpomeres (Fig. 1F). Antennal funicle with seven antennomeres (Fig. 1P). First and sixth antennomeres of

funicle subequal in width (Fig. 1P). Pedicel 1.5 times as long as wide; funicle antennomeres 2–4 as long as wide; 5–7 gradually widening, wider than long. Antennal club oval (Fig. 1P).

Pronotum oval, about 1.1x as long as wide (Fig. 1A); pronotal surface with coarse, polyhedral punctures separated by narrow ridges (Figs 1A, C). Anterior margin of prothorax in ventral view rounded and emarginate (Fig. 1B). Procoxae subcontiguous; metacoxae separated by less than half their diameter; metacoxae separated by twice their length (Fig. 1B). Elytra short, oval, without shoulders, hind wings absent. Elytral base about 1.25x as wide as hind margin of pronotum (Fig. 1A). Elytra with ten punctuate striae; elytral intervals vaulted, twice wider than width of striae. Inner surfaces of elytra at apex with stridulatory ridges. Vaulted intervals on elytra with small and irregularly placed punctures; each puncture with a clubbed, bowed and yellowish scale. Elytral stria 10 as short as basal quarter of elytra; striae 6–8 merging before reaching elytral base, striae 4, 5, 7 and 8 merging before reaching elytral apex. Externally visible part of scutellum small and triangular. Meso-, metaventrites and abdominal ventrites coarsely punctuate; each puncture with a narrow, clubbed and bowed, yellowish scale (Fig. 1B). Legs slender, femora clubbed, profemora with obtuse ventral tooth (Fig. 1H). Tibiae uncinate; premucro present (Fig. 1G). Tarsi with entire (not bilobed) third tarsomere; claws free. Apex of tibiae on inner and outer side with a row of stiff, yellowish spines (Fig. 1G).

Abdomen with first and second ventrites fused; suture between them obliterated at middle and visible at sides (Fig. 1B). Ventrites three to five free (Fig. 1L). Female sternite 8 paddle-shaped (Fig. 1I), with manubrium longer than plate; plate bifurcate, not sclerotized in middle; base of sternite 8 handle-like and broadened (Fig. 1I). Spermatheca with short and bowed nodulus, with long and slender cornu attenuated towards its tip (Fig. 1J, K), with ramus and duct (Fig. 1J, K). Tergite 8 with posterior margin angular (Fig. 1M); posterior margin of tergite 7 rounded (Fig. 1N). Gonocoxites elongate, weakly sclerotized; styli cone-shaped, twice as long as wide at middle, with straight setae posteriorly (Fig. 1O). Male unknown.

#### Comment

Three DNA fragments of the holotype were previously released under the name “*Himalanchonus*” (GREBENNICKOV & ANDERSON 2021): the DNA barcode part of the mitochondrial cytochrome c oxidase I (GenBank accession number MT889118), the nuclear internal transcribed spacer 2 (MT889140) and the nuclear 28S ribosomal DNA (MT889164).

#### Etymology

The species is named after Bhudevi, the Hindu goddess of Mother Earth, as a noun in apposition.

#### Biogeographical interpretation

The weak statistical support of our morphological phylogenetic tree leaves doubts about the identity of the more inclusive clade to which the new species belongs. Moreover, much of the leaf litter biodiversity, including weevils related to our new species, remains undocumented, particularly in mainland China. Assuming, however, that the new species is a member of the previously Japan-only clade, its herein reported discovery in Taiwan is not surprising. The continental islands of Taiwan and Ryukyu emerged some nine million years ago (Mya) and “attained their modern features and their current flora and fauna from the adjacent mainland and tropical Asia only 5–6 Mya” (CHIANG & SCHAAL 2006). These lands were isolated as three larger islands since the Late Miocene period (KAITO & TODA 2016). The subsequent Quaternary glaciation and the drop of the sea level resulted in the formation of the Early Pleistocene land bridge connecting the Taiwan-Ryukyu Archipelago to the mainland and facilitating biotic interchange (CHIANG & SCHAAL 2006). Among better-documented plants, some 53% of Ryukyu’s 1,220+ species also occur in Taiwan, while both floras share a close affinity with that of mainland China rather than with that of the rest of Japan (CHIANG & SCHAAL 2006). A few well-documented animal examples also demonstrate a closer relatedness of the Taiwan and Ryukyu faunas to mainland China rather than to Japan’s main islands [e.g., the wood-feeding cockroaches, see MAEKAWA et al. (1999)]. We therefore interpreted the herein hypothesized placement of the Taiwanese *Protacallobodes bhudevi* sp. n. among the Japan-only relatives as (1) a bias resulting from a markedly uneven taxonomic knowledge of the weevil faunas of mainland China and Japan and (2) an indicator that closely related species will soon be discovered and documented in mainland China.

#### Diagnosis

Both herein analysed species of the genus *Protacallobodes*—*P. masumotoi* Morimoto, 2011 and *P. bhudevi* sp. n.—differ by 13 morphological characters (Fig. 6). The other described Japanese species, *P. ryukyuensis* Morimoto, 2011 (not included in the analysis), is very similar to *P. masumotoi* according to the description and differs in its larger size, subcordate elytral outline, rudimentary femoral tooth and penis shape (MORIMOTO 2011).

#### Identification key to *Protacallobodes bhudevi* sp. n. and similar or related weevils

[Modified from MORIMOTO (2011).]

- 1(4) Antero-lateral corner of first ventrite and metepisternum narrowly separated (metacoxae and elytra contiguous); longitudinal groove on prosternum present, with lateral carinae ..... part of Ithyphorini [sensu MORIMOTO (2011), LÖBL & SMETANA (2013), but not ALONSO-ZARAZAGA et al. (2017)—see below]

- 2(3)** Scutellum not visible externally (Fig. 3A); ultimate striae of elytra notably shallower posterior to the level of hind coxae; mesoventral process between mesocoxae as wide as base of mesofemur (Fig. 3E), not bulged; elytra circular (Fig. 3A), with scattered scales (Figs 3A–C) ..... *Protacalles* Voss
- 3(2)** Scutellum visible externally (Fig. 2A); ultimate striae of elytra of similar depth along their entire length. Ultimate stria entire (Japanese species) or obliterated at middle, only visible at anterior edge and towards apex of each elytron (Fig. 1C; *P. bhudevi* sp. n.); mesoventral process between mesocoxae narrower than base of mesofemur, either bulged (Fig. 2E; Japanese species) or not (Fig. 1E; *P. bhudevi* sp. n.); elytra oval (Fig. 2A), with denser scales (Fig. 2A, C). ..... *Protacallobdes* Morimoto
- 4(1)** Antero-lateral corner of first ventrite and metepisternum contiguous (separating metacoxae from elytra); longitudinal groove on prosternum absent or present ..... *Sthereini*
- 5(10)** Funicle with seven antennomeres; eyes smaller, forehead between eyes scarcely narrower than base of rostrum, without erect scales along inner margin of eyes; prosternum flat or shallowly depressed, with or without lateral carinae
- 6(9)** Prosternum at anterior margin deeply emarginate
- 7(8)** Third tarsomere shallowly emarginate at anterior margin to not more than a quarter its length; socket of fourth tarsomere located in distal half of third tarsomere; prosternum anterior to procoxae shallowly to deeply depressed (Fig. 4E), with or without lateral carinae ..... *Protacallinus* Morimoto
- 8(7)** Third tarsomere deeply emarginate at anterior margin to almost half its length; socket of fourth tarsomere located at middle or in proximal half of third tarsomere; prosternum anterior to procoxae shallowly depressed, without lateral carinae, sides of depression obtusely raised. .... *Lobosoma* Buchanan and *Philostratus* Zimmermann
- 9(6)** Prosternum at anterior margin weakly emarginate ..... *Sthereus* Motschulsky
- 10(5)** Funicle with six antennomeres (Fig. 5I); eyes larger, forehead between eyes much narrower than base of rostrum, with erect scales along inner margin of eyes (Fig. 5D); prosternum deeply depressed, with lateral carinae (Fig. 5E) ..... *Darumazo* Morimoto

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**Appendix 1.** A data matrix of adult morphological characters used in determining phylogenetic affinities of *Protacal洛des bhudevi* sp. n. Abbreviations before taxa are: “InG”: ingroup, “OtG”: outgroup. The letter “C.” after “Pissodini” indicates the subtribe Cotasteromimina. The first two lines, read vertically, provide the character number. The bottom line indicates four deactivated characters.

00000000011111111112	222222222333333334	444444444555555556	666666666777777778	88888888
12345678901234567890	12345678901234567890	12345678901234567890	12345678901234567890	1234567
ROOT1 <i>Oriorhynchus singularis</i>				
ROOT2 <i>Gymnetron veronicae</i>				
InG1 Ithyporini <i>Protacal洛des budhevi</i> sp. nov.	0701120110103	07011201101000-1130	1001202110-01010	11011002100110100122 11121120
00000200112111000103	050012012101000-1130	101020100211000-1010	1130110011011010002	00111110
01020001322111101103	170111211110001111110	1001020120000100001	110011101010122?2?212	01121210
02102011202111101102	0601220110101111120	1001020201210001010	11001100100011010122	01101110
00020011222011101102	17000201101001111100	1000211012000100010	110011101001101002 01101120	
InG4 Ithyporini <i>Sclerocardius bohemani</i>	20002101302111000103	07000201200111111111	00102010120100101010	11311111110010100102 01001110
0000001322011000202	1701102011001111110	1012202100-000100001	110111001001?2?2?222	01111110
01100011212111010102	0701121111100110-1120	100112111010-0210-0001	11001100100011010002	01121210
012020112121011101202	0600022110000111110-0	1011202010-0100-010	10001110101010100112 01101110	
01023111312011100102	07000101010000-1101	101?2?20-00111010	1100110110011010022 00001111	
OtG3 Hylobiini <i>Hylobius abietis</i>	310003000112011101002	17000201110110-1130	0001201012010000-010	00311101000110000110 11111120
OtG4 Lepyrini <i>Lepyrus capucinus</i>	20133000012001110103	170001000101000-0130	1010211011200000-010	110011010110110102 11121110
OtG5 Lithiniini <i>Seleuca</i> sp.	01133011212010000202	07001121101000-0120	10112010120000111010	1100110000001100020 11111110
OtG6 Lymantrini <i>Devernodes chthonia</i>	0213011122211011102	06001211010000-0110	1011202100-0200-1001	11001100001100022 00020-0
OtG7 Molytini <i>Liparus germanus</i>	30000000112011100002	170002011101000-10-0	000020211200000-010	110111111001101012 11111110
OtG8 Molytini <i>Pinacopus intermedius</i>	111000101312011100123	070010111001110-1110	1100020120100-0001001	1100111201000110022 11001110
OtG9 Orthorhinini <i>Burhamphus fasiculatus</i>	4210000320101211002	07001012110101-1130	1010211211011110	11300112100110112 00001110
OtG10 Orthorhinini <i>Tlacuris laticollis</i>	31020000322101010101	070011012101010-110	201221210211010-1110	0130111210011010022 11120-0
OtG11 Orthorhinini <i>Orthorhinus</i> sp.	2210310011111101211	1700101110110-10-0	10212020121010-110	01311121001101011 00101120
OtG12 Orthorhinini <i>Vanhala oberthuri</i>	42300000321001110111	17000121210110-1120	20121101221010-1110	013111121200110110112 00011120
OtG13 Pissodini C. <i>Cotasteromimus morimotoi</i>	012021112120101000200	07011211111010-1120	1012202000-0000-2010	1100110011001100020 11101110
OtG14 Pissodini C. <i>Cotasteromorphus chujoi</i>	00003010112010000111	07011211111110-0120	1010212110-020101010	110111010001111101021 11101120
OtG15 Pissodini C. <i>Obphylius arboricola</i>	01130001101201000113	06010210100001110132	211021101122110100001	01311111100110002? ?2?2?2?
OtG16 Pissodini C. <i>Pseudohylobius setosus</i>	01103001112011000201	071111210200000-1132	2011212102211110110	0031110000001100122 01101110
OtG17 Pissodini C. <i>Seticotasteromimus brunomanseri</i>	02210001102110000201	07101111210000-1132	01221021122121201101	00301100100022?2?2?2?20 11111120
OtG18 Pissodini C. <i>Seticotasteromimus crassirostris</i>	02310101002110000202	070101211210000-1132	0122102112212100101	0030110010001000?2? ?2?2?2?2?
OtG19 Pissodini C. <i>Seticotasteromimus jarawa</i>	02310001102110000201	071011211210000-1132	012210211221212010101	003011001000?2?2?2?21 11001110
OtG20 Pissodini C. <i>Zemnus perseus</i>	01203001112011100103	070011210210000-0130	111220211221010-1101	000011101001111101?2? ?2?2?2?
OtG21 Pissodini C. <i>Dorytomorpha tonsa</i>	01102000212001100101	071010111101010-1130	111200201211210-1010	00311111101010?2?2?2?21 01001110
OtG22 Pissodini C. <i>Pisodes pini</i>	11102000212111101002	070002012100010-1110	0112020021110-1110	0030111110011000121 01001100
OtG23 Typodeini <i>Aparopion chevrolati</i>	010330011212000111003	070011011100000-0120	1010012110-0110-1110	110011010100011111120 01011111
Deactivated		D D D		

**Appendix 2.** List of 87 adult morphological characters scored to analyze the phylogenetic position of *Protacallodes bhudevi* sp. n. [modified from GERMANN & GREBENNIKOV (2020)]; characters and their states are illustrated in Fig. 1.

1. Body, length between anterior margin of pronotum and elytral apex, dorsal view: < 6 mm = 0; 6 to < 9 mm = 1; 9 to < 12 mm = 2; 12 to < 15 mm = 3; 15 mm and more = 4.
2. Body, ratio of body length to elytral width at midlength, dorsal view: < 2.0 = 0; 2.0 to < 2.5 = 1; 2.5 to < 3.0 = 2.
3. Body, ratio of body length to maximum height, lateral view: < 2.5 = 0; 2.5 to < 3.0 = 1; 3.0 to < 3.5 = 2; 3.5 and more = 3.
4. Body, scales (including those on head and legs): appressed, < 45° = 0; erect, > 45° = 1; both, appressed and erect = 2; no scales = 3.
5. Head, rostrum, shape in cross-section at midlength: circular = 0; vertical oval = 1; horizontal oval = 2; rectangular/quadrata = 3.
6. Head, rostrum, shape, fronto-dorsal view: widening anteriad = 0; parallel-sided = 1; narrowing anteriad = 2.
7. Head, rostrum, shape, lateral view: straight or weakly curved = 0; strongly curved = 1.
8. Head, transverse dorsal depression separating rostrum and frons, lateral view: absent = 0; present = 1.
9. Head, rostrum, length to width at middle ratio, fronto-dorsal view: < 3.0 = 0; 3.0 to < 4.0 = 1; 4.0 to < 5.0 = 2; 5.0 and more = 3.
10. Head, rostrum, fronto-dorsal length compared to that of pronotum in dorsal view: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2.
11. Head, rostrum, position of frons relative to position of upper margin of eyes, lateral view: below = 0; at level = 1; above = 2.
12. Head, rostrum, antennal attachment in relation to rostral length: in apical third = 0; in central third = 1.
13. Head, rostrum, scrobes, orientation relative to rostrum, lateral view: parallel, posterior ends not approximate each other = 0; oblique, posterior ends approximate each other = 1.
14. Head, eyes, number of ommatidia: 40 and less = 0; > 40 = 1.
15. Head, eyes, position in relation to imaginary posterior extension of rostrum: below = 0; at level = 1; above = 2.
16. Head, eyes, contour in relation to that of head capsule, dorsal view: not or weakly protruding = 0; markedly protruding = 1.
17. Head, eyes, smallest distance between compared to width of base of rostrum, dorso-frontal view: greater than 0.8 = 0; smaller than 0.8 = 1.
18. Head, retraction into pronotum, lateral view: not retreated, temples exposed by eye diameter or more = 0; weakly retracted, temples exposed for less than eye diameter = 1; moderately retracted, eyes not concealed, temples fully concealed = 2.
19. Head, antenna, antennal scape, ratio of its length to that of funicle and club together: < 0.9 = 0; 0.9 to < 1.1 = 1; 1.1 to < 1.3 = 2.
20. Antenna, funicle with club, ratio of their combined length to that of 3 basal funicular antennomeres: 1.0 to 1.5 = 0; 1.5 to 2.0 = 1; 2.0 to 2.5 = 2; > 2.5 = 3.
21. Antenna, funicle, number of distal-most antennomeres with vestiture similar to that of club: 0 = 0; 1 = 1.
22. Head, antenna, funicle, number of antennomeres: 5 = 5; 6 = 6; 7 = 7.
23. Head, antenna, first funicular antennomere, ratio of its maximal width to that of second antennomere: < 1.7 = 0; 1.7 and more = 1.
24. Head, antenna, funicle, ratio of second antennomere length to that of first, dorsal view: < 0.5 = 0; 0.5 and more = 1.
25. Head, antenna, club, the greatest width: in proximal half = 0; at middle = 1; in distal half = 2.
26. Head, antenna, proximal antennomere of club, length to width ratio: more than 1, elongate = 0; 1 = 1; less than 1, transverse = 2.
27. Prothorax, notum, ratio of maximal length to maximal width, dorsal view: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2.
28. Prothorax, notum, its sides, dorsal view: parallel = 0; rounded = 1.
29. Prothorax, notum, the greatest width, dorsal view: anterior of middle = 0; at middle = 1; posterior of middle = 2.
30. Prothorax, notum, constriction at fore margin, dorsal view: absent = 0; present = 1.
31. Prothorax, notum, constriction at hind margin, dorsal view: absent = 0; present = 1.
32. Prothorax, notum, punctures, dorsal view: as deep as wide, radii greater than width of walls, angular = 0; shallow, radii not greater than width of walls, rounded = 1.
33. Prothorax, anterior edge, ocular lobes, lateral view: absent = 0; present = 1.
34. Prothorax, anterior edge, ventral view: straight = 0; emarginate = 1.
35. Prothorax, longitudinal channel on sternum anterior of procoxae, ventral view: absent = 0; present = 1.
36. Prothorax, longitudinal ridges on each side of longitudinal channel on prosternum anterior of procoxae, ventral view: absent = 0; present = 1. [parsimoniously uninformative and deactivated].
37. Prothorax, dorsal and lateral surface, scales: absent = 0; present = 1.
38. Prothorax, dorsal and lateral surface, bristles: absent = 0; present = 1.
39. Pronotum and elytra, shape of bristles, ratio of their length to their width in middle: < 3 = 0; 3 to < 4 = 1; 4 to < 5 = 2; 5 and more = 3.
40. Prothorax, dorsal and lateral surface, vestiture, orientation: appressed, nearly parallel to surface = 0; semierect, at about 45° to surface = 1; erect, nearly 90° to surface = 2.
41. Prothorax, dorsal and lateral surface, vestiture, shape: straight = 0; curved = 1; both, straight and curved = 2.
42. Prothorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: < 0.3 (subcontiguous) = 0; 0.3 to 0.9 (moderately separated) = 1.
43. Mesothorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: < 0.3 (subcontiguous) = 0; 0.3 to 0.9 (moderately separated) = 1; > 0.9 (widely separated) = 2.
44. Mesothorax, process between mesocoxae, maximal width compared to width of mesofemur at base, ventral view: subequal = 0; narrower = 1; broader = 2.
45. Mesothorax, process between mesocoxae, shape, ventral view: parallel-sided = 0; widening posteriorly = 1; narrowing posteriorly = 2.
46. Mesothorax, process between mesocoxae, bulge, ventral view: absent (process flat) = 0; present = 1.
47. Metathorax, distance between inner edges of coxae in relation to coxal diameter, ventral view: 0.9 to 1.1 = 1; > 1.1 = 2.
48. Metathorax, abdominal process between metacoxae, width relative to that of coxa: 1.5 and less = 0; > 1.5 = 1.

49. Metathorax, ventrum, separation between metacoxae and elytra (i.e., whether metepisternum and first ventrite are contiguous or not): absent = 0; present = 1.
50. Scutellum, if visible externally, dorsal view: not visible = 0; barely visible, shape indistinct = 1; clearly visible, shape distinct = 2.
51. Scutellum, its external part, shape, if distinct, dorsal view: triangular = 0; clearly rounded = 1; pentagonal = 2.
52. Elytra, shoulders, dorsal view: absent = 0; present = 1.
53. Elytra, striae, ratio of their width to that of elytral intervals, dorsal view: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2.
54. Elytra, elytral intervals, tubercles or bulges on at least some intervals, dorsal view (excepting elytral bulge at declivity): absent = 0; present = 1.
55. Elytra, raised bristles, dorsal or lateral view: absent = 0; present = 1.
56. Elytra, raised bristles, arrangement: in rows = 0; in tufts = 1.
57. Elytra, raised and bowed bristles, shape of tip: rounded = 0; pointed = 1; bifid = 2.
58. Elytra, elevation of odd versus even intervals, oblique dorsal view: similar = 0; odd intervals more elevated = 1.
59. Elytra, ultimate stria, length compared to elytral length, dorso-lateral view: short, not more than 50%; long, at least 60% = 1.
60. Elytra, ultimate stria, dorso-lateral view: entire = 0; interrupted at middle = 1.
61. Elytra, contour at middle, dorsal view: parallel-sided = 0; rounded = 1.
62. Elytra, dorsal contour at middle third, lateral view: straight = 0; curved = 1.
63. Hind wings (dissection required): absent = 0; present, vestigial, about half elytral length = 1; present, short, subequal to elytral length = 2; present, long, about 2x elytral length = 3.
64. Legs, all femora, posteriorly oriented spines: absent = 0; present = 1.
65. Legs, hind femora, length, ventral view: reaching apex of elytra = 0; not reaching apex of elytra = 1.
66. Legs, all tibiae, uncus: absent = 0; present = 1. [parsimoniously uninformative and deactivated].
67. Legs, all tibiae, premucro: absent = 0; present = 1.
68. Legs, all tarsi, tarsomere 2, shape in cross-section: round = 0; vertical oval = 1; horizontal oval = 2.
69. Legs, all tarsi, tarsomere 3, shape, dorsal view: entire = 0; bilobed = 1.
70. Legs, all claws, fusion in basal third: absent (claws free) = 0; present (claws fused) = 1. [parsimoniously uninformative and deactivated].
71. Legs, all claws, angle between them, dorsal view: less than 20° = 0; 45° and more = 1.
72. Abdomen, trace of fusion between visible ventrites 1 and 2 in their mid-third, ventral view: absent = 0; present = 1.
73. Male genitalia, aedeagus, cross-section at middle, shape: circular = 0; oval = 1.
74. Male genitalia, aedeagus, median lobe, dorsal surface appearance, sclerotization compared to that of lateral surface: membranous = 0; sclerotized = 1.
75. Male genitalia, aedeagus, median lobe, ventral surface, sclerotization compared to that of lateral surface: membranous = 0; sclerotized = 1.
76. Male genitalia, aedeagus, shape of apex: rounded = 0; pointed = 1.
77. Male genitalia, aedeagus, apex, dorsal or ventral view: symmetrical = 0; asymmetrical = 1. [parsimoniously uninformative and deactivated].
78. Male genitalia, aedeagus, one or more internal sclerites in endophallus: absent = 0; present = 1.
79. Female genitalia, sternite 8, ratio of length of apodeme to that of plate: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2.
80. Female genitalia, sternite 8, plate, length to width ratio: < 0.9 = 0; 0.9 to 1.1 = 1; > 1.1 = 2.
81. Female genitalia, sternite 8, plate, extend of its sclerotization (but not pigmentation): small, middle part not sclerotized, sternite 8 fork-like = 0; great, middle part sclerotized, sternite 8 paddle-like = 1.
82. Female genitalia, sternite 8, apodeme, abrupt widening in its part opposite to plate ("handle of a spade"): absent = 0; present = 1.
83. Female genitalia, spermatheca, nodulus and ramus: indistinct = 0; distinct = 1.
84. Female genitalia, each of two hemisternites 9 (= each gonocoxite, excluding styli), ratio of length to width: < 2.5 = 0; 2.5 to 3.5 = 1; > 3.5 = 2.
85. Female genitalia, styli: absent = 0; present = 1.
86. Female genitalia, styli, ratio of length to width in middle: < 1.5 = 0; 1.5 to 2.5 = 1; > 2.5 = 2.
87. Female genitalia, sclerotized bursa copulatrix: absent = 0; present = 1.

**Appendix 3.** Label data of specimens scored for the 31-terminal matrix to analyze the phylogenetic position of *Protacallobodes bhudevi* sp. n. Of them, 24 terminals have their label data given in GERMANN & GREBENNIKOV (2020); two of those 24 terminals (“InG05 nr *Pseudohylobius*” and “InG7 *Seticotasteromimus* sp.”) were subsequently named *Obhylius arboricola* Germann, 2021 and *Seticotasteromimus brunomanseri* Germann, 2021, respectively (see GERMANN 2021).

**ROOT1:** *Otiorhynchus singularis* (Linnaeus, 1787): male (CGC), France, Pyrénées Orientales, NE of Mont Louis, Fôret de Clavera, vii.2001, C. GERMANN leg.; female (CGC), Italy, Piemonte, Gran Paradiso, Ceresole Reale, 8.vii.2003, C. GERMANN leg. (CGC). **InG1:** *Protacallobodes bhudevi* sp. n.: see Description. **InG2:** *Darumazo distinctus* Morimoto & Miyakawa, 1985: unsexed paratype (KUZC) Japan, Nanto rindo, Miyake Jima Is., Izu-Shyoto Isls. May 16, 1979, S. MIYAKAWA leg.; unsexed paratype (KUZC) Japan, Yasundo go, Ochi yo, Aogashima Is., Izu-Shyoto Isls. May 20, 1979, J. OKUMA leg.; male (KUZC), Japan, Nagasaki, Danjo Islands, Meshima Island, 3.v.1982, J. ONAGAMITSU leg.; female (KUZC), Japan, Fukui, Ubejima Island, Mikata-Cho, 24.vii.1986, T. UENO leg. (KUZC). **InG3:** *Protacallobodes masumotoi* Morimoto, 2011, male (KUZC), Japan, Nagano, Kitamatazawa, 740 m, Kami-mura, Shimo-Ina-gun, Honshu, 23.viii.1997, H. SAKAYORI et al. leg.; unsexed paratype (KUZC), Japan, Nagano, Kitamatazawa, 740m, Kami-mura, Shimoina-gun, Honshu, 23.viii.1997, H. SAKAYORI et al. leg.; 1 male, 1 female (KUZC), same label data; unsexed specimen (KUZC) Japan, Saga, Mt. Kyogatake, 1050 m., 13.iii.2000, S. NOMURA leg., unsexed paratype (KUZC), Japan, Osaka, Mt. Kongosan, 22.xi.1989, T. NONAKA leg. **InG5:** *Protacalles monticola* Voss, 1957: three females (CGC), Japan, Tokyo, Hinohara Vil., Mt. Tsukiyomiya, 18.v.1997, T. SHIMADA leg.; female (KUZC), Japan, illegible Japanese characters, 2.vii.2000; female (KUZC), Japan, Shikoku, Mt. Tsurugi, 7.vi.1970, M. SAKAI leg. **InG6:** *Protacallinus uenoi* Morimoto, 1962: female (KUZC), Japan, Nara, Mt. Ohdaigahara, 30.v.1985, S. NOMURA leg.; female (KUZC), Japan, Nara, Mt. Kyogamine, Odaighara, Kamikitayama V., 13.x.2017, R. Ito leg. **sp****OtG18:** *Seticotasteromimus crassirostris* Germann, 2022; see GERMANN (2022).



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