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RESEARCH ARTICLE

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

CHRISTOPH GERMANN¹ & VASILY V. GREBENNIKOV²

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 *Protacallodes* 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 *Protacallodes*. Statistical support for this tree was low and these clades collapsed after bootstrapping. We describe the Taiwan weevils as *Protacallodes 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 *Protacallodes* and related genera.

Key words: 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 *Protacallodes* Morimoto, 2011 am ähnlichsten, welche alle endemisch für Japan sind. Wir führten eine phylogenetische Analyse mit 37 Taxa und 83 parsimonie-informativen morphologischen Merkmalen durch. Der sparsamste Baum ergab eine Klade dieser drei Gattungen, mit der Art aus Taiwan als Schwesterart zu *Protacallodes*. Der Baum wird statistisch nur schwach unterstützt und die Kladen kollabierten nach dem Bootstrapping-Verfahren. Wir beschreiben die taiwanesischen Rüsselkäfer als *Protacallodes 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 *Protacallodes* (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 *Protacallodes* “has a wide range of distribution from Japan to southern China and Vietnam according to unnamed species in our collection”. One of these species, *Protacallodes ryukyensis* 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 Ithyporini 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 & GREBENNIKOV 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 & GREBENNIKOV 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 Ithyporini: *Darumazo* and *Sclerocardius* Schoenherr, 1847. The outgroup 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: *Otiorthynchus 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 & GREBENNIKOV 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 *Protacalloses* 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 *Protacalloses* 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 *Protacalloses* 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, premuro: 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 *Protacalloses*, we introduce our Taiwanese specimens as belonging to a new species of this genus.

Protacalloses 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.

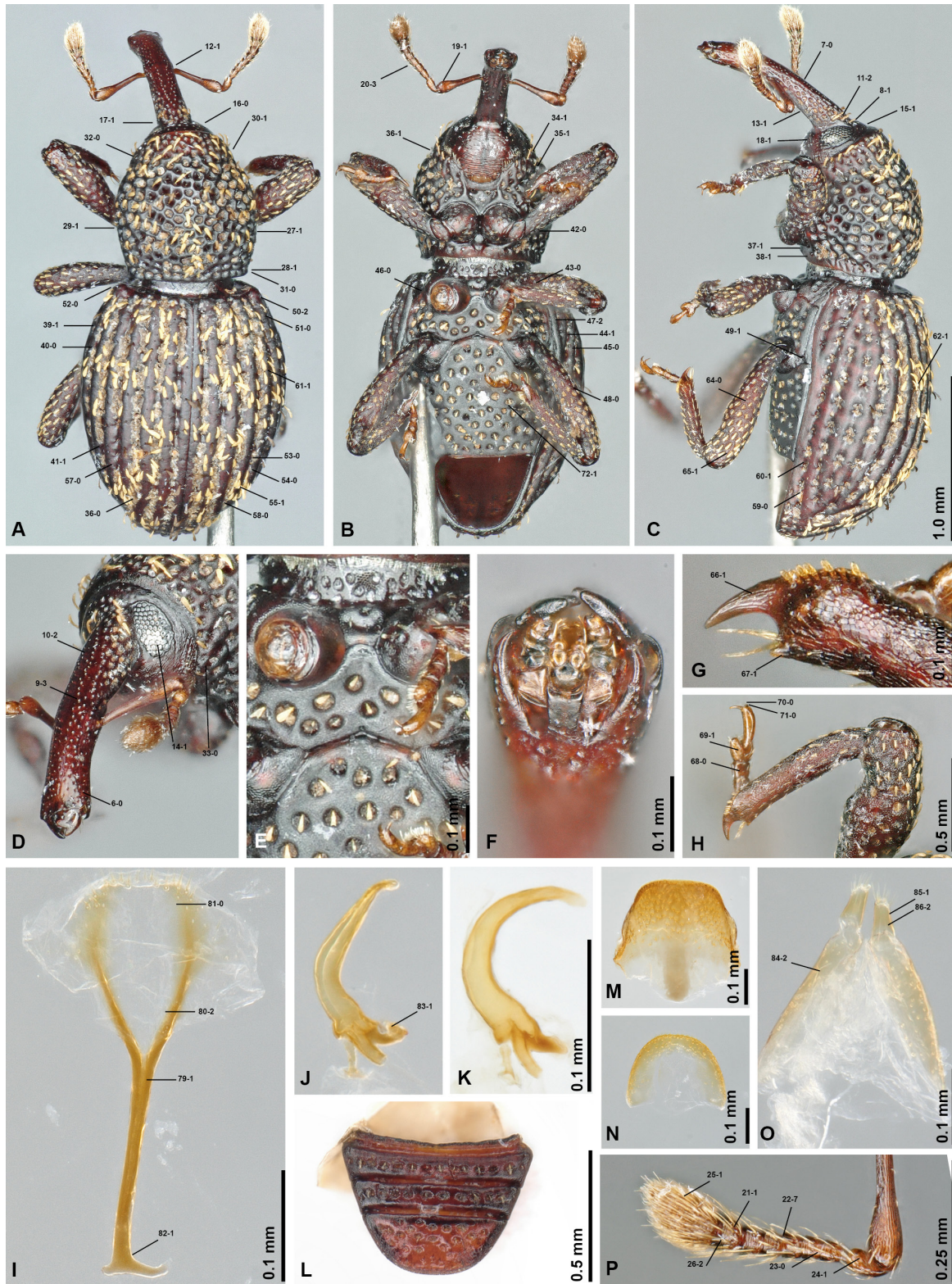


Fig. 1. *Protacalloses bhudevi* sp. n., females. A–J, L–P: holotype; K: paratype. A–C. Habitus dorsal, ventral and lateral. D. Head and rostrum. E. Mesoventral process. F. Mouthparts. G. Right protibia with uncus, premucro and stiff yellow spines on outer side. H. Right fore leg showing femur with small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

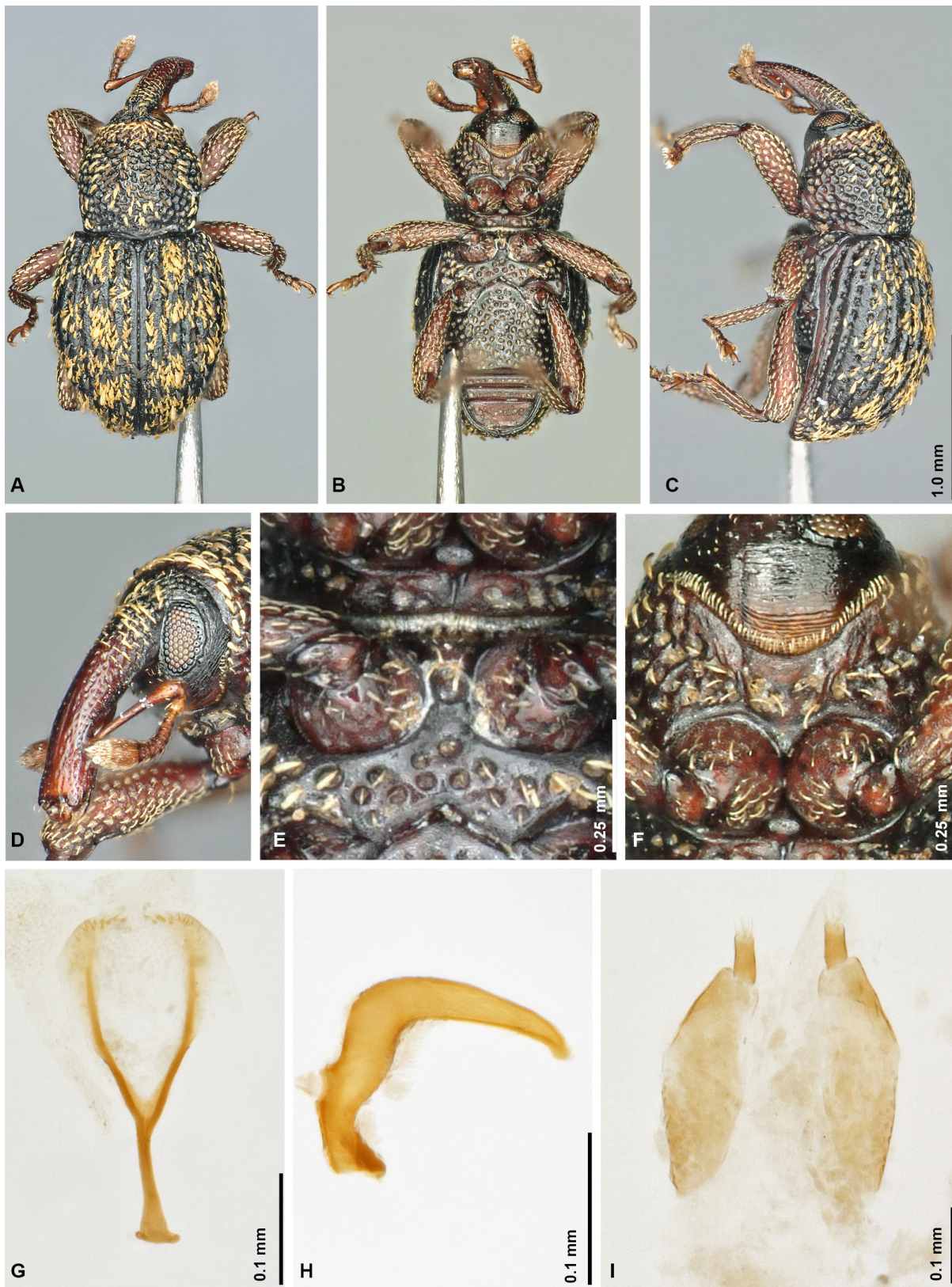


Fig. 2. *Protacallodes masumotoi* Morimoto, 2011, female. A–C. Habitus dorsal, ventral and lateral. D. Head and rostrum. E. Mesoventral process. F. Prosternum. G. Ventrite 7. H. Spermatheca. I. Gonocoxites. (© CHRISTOPH GERMANN)

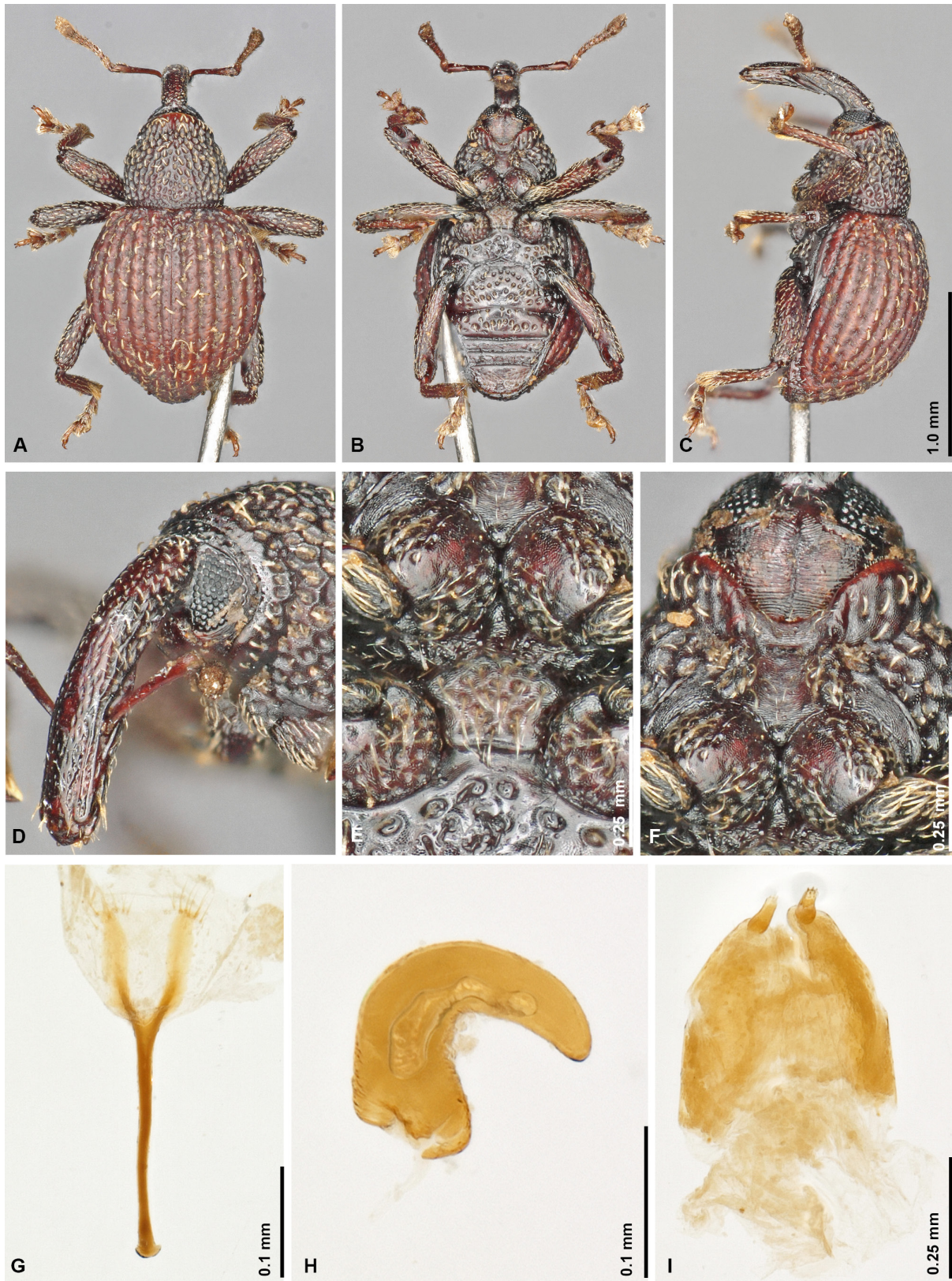


Fig. 3. *Protacalles monticola* Voss, 1957, female. **A–C.** Habitus dorsal, ventral and lateral. **D.** Head and rostrum. **E.** Mesoventral process. **F.** Prosternum. **G.** Ventrite 7. **H.** Spermatheca. **I.** Gonocoxites. (© CHRISTOPH GERMANN)



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)

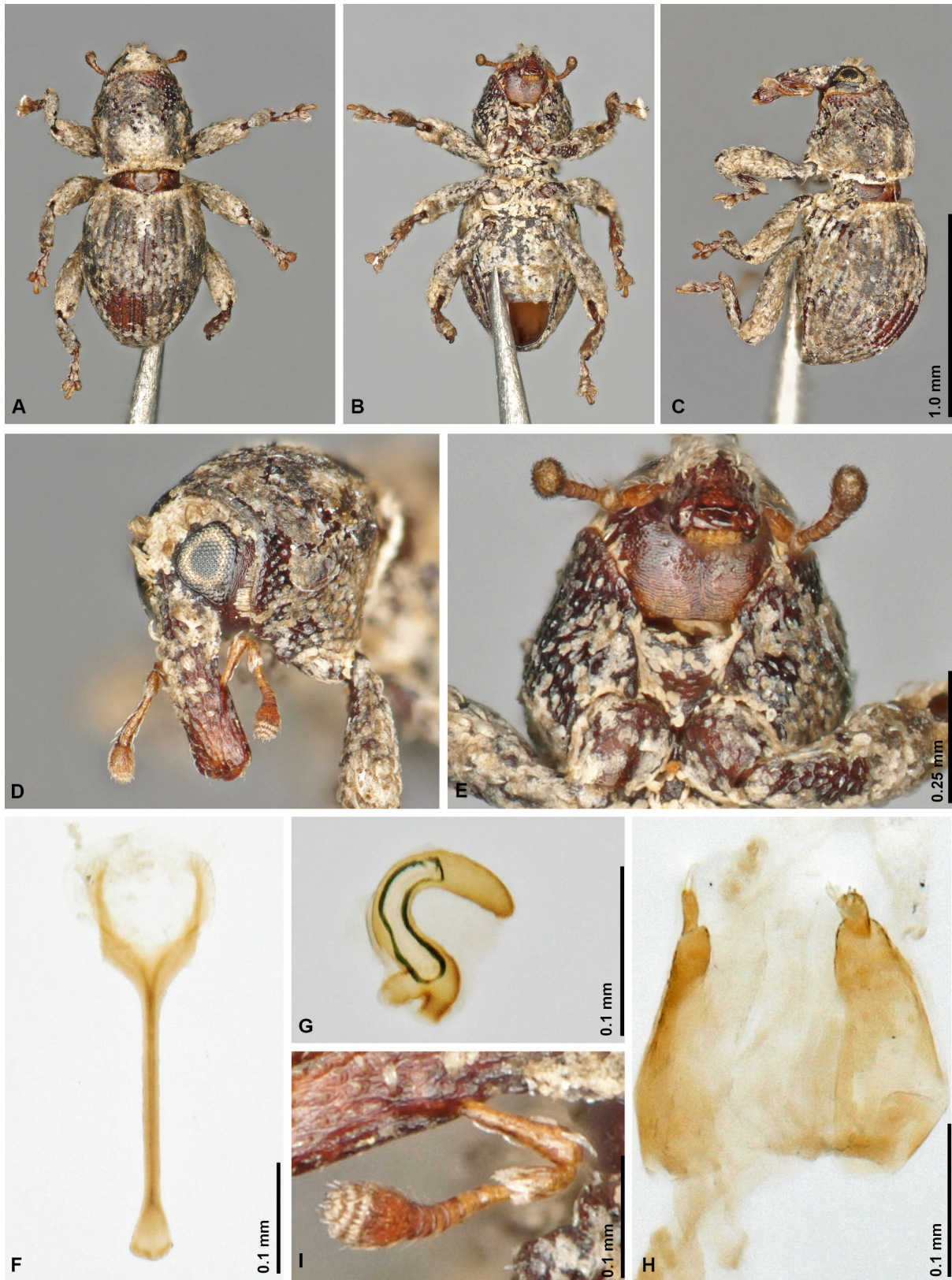


Fig. 5. *Darumazo distinctus* Morimoto & Miyakawa, 1985, female. A–C. Habitus, dorsal, ventral lateral. D. Head and rostrum. E. Prosternum. F. Ventrite 7. G. Spermatheca. H. Gonocoxites. I. Antenna. (© CHRISTOPH GERMANN)

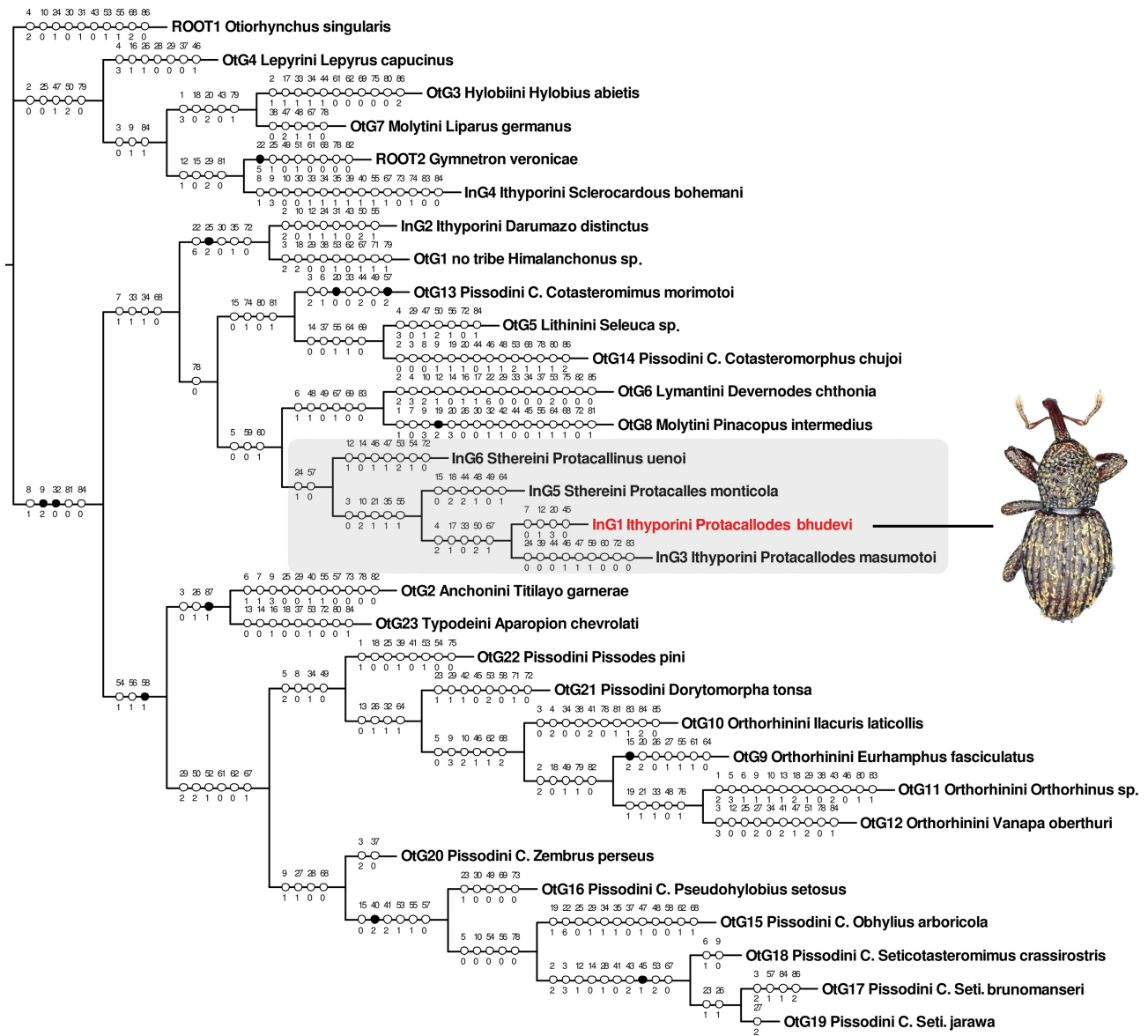


Fig. 6. The single most parsimonious tree obtained after a phylogenetic analysis of *Protacallodes bhudevi* sp. n. and its potential relatives. The clade of the genera *Protacalles*, *Protacallinus* and *Protacallodes* is highlighted. Unambiguously optimized evolutionary events are plotted on internodes. 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 anteriorly. 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 punctate, 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, polyhedric 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 uncinatae; 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*” (GREBENNIKOV & 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 Ryukyus 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 Ryukyus’ 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 Ryukyus 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 *Protacalodes 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 *Protacalodes*—*P. masumotoi* Morimoto, 2011 and *P. bhudevi* sp. n.—differ by 13 morphological characters (Fig. 6). The other described Japanese species, *P. ryukyensis* 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 *Protacalodes bhudevi* sp. n. and similar or related weevils

[Modified from MORIMOTO (2011).]

- 1(4) Antero-lateral corner of first ventrite and metepisternum narrowly separated (metaxocae and elytra contiguous); longitudinal groove on prosternum present, with lateral carinae part of *Ithyporini* [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) *Protacalloses* 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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ZooBank registration: <https://zoobank.org/References/035C7E00-4E09-48B6-A53F-23EEA9C622DA>

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

0000000001111111112	2222222223333333333	4444444445555555556	6666666667777777778	8888888
12345678901234567890	12345678901234567890	12345678901234567890	12345678901234567890	1234567890
11123000002001101103	070112011011000-1130	1001202110-010101010	11011002100110100122	1112100
00000200112110000103	0500120120101000-1130	1010201002110000-1130	01300110011011010002	0011110
0102000132211101103	1701121111000111110	1001020120000100001	110011101001?????12	0112120
0210201120211101102	0601220110101111120	1001202012100001010	11001100100001010122	0110110
0002001122201101102	1700020110001111100	10002110120000100010	11001110100010110002	0101120
2000210130211000103	0700020120011111111	001020110201001010	11311111100101100102	0100110
00000011322011000202	1701202110011111110	1012202100-000100001	11011001001?????22	0111110
01100011212110100102	070112111100110-1120	1001211010-0210-0001	11001100100010110002	0112120
0120201121201101202	060022110000111110-0	1011202010-0100-010	1000111010101000112	0110110
0102311131201100102	070001010100000-1101	101????2010-001110110	11001101100101100022	0000111
3100300011201101002	17000201101110-1130	000120101201000--010	0031101000110000110	1111120
2013300001200110103	170001000101000-0130	101021101200000-1010	110011011001101010102	1112110
0113301121010000202	070012110100110-0120	10112010120000111010	1101100000011100020	1111110
0213011122211011102	060012110100000-0110	1011202100-0200-1001	11001110000110000022	00020-0
300000011201100002	17000201101000-10-0	000020211200000--010	1101111110011010012	1111110
1110010131201100123	0700101100110-1110	11100021100-000101001	11011110000101100022	1100110
42100000320101211002	07001012101010-1130	1010212112110111110	11300112100110100112	0000110
3102000032210110101	070011012101000-10-0	201221210211010--110	01310112100110100022	11120-0
221031001111101211	1700110110110-10-0	102120201211010--110	013111121001101011	0010120
4230000032100111011	170001212101100-1120	201121101221010-1110	0131111210011010012	0001120
01202111212011000200	07101211111010-1120	1012202000-0000-2010	11001100100111100020	1110110
00003010112010000111	07101211111110-0120	1010212110-020101010	110110100011110121	1110120
01130001102011000113	06010210110001110132	21102110122110100001	013111111001110000? ???????	???????
0110300112011000201	071112102000000-1132	2011212102211110110	0031111000000100122	0110110
0221000110211000201	07101112100000-1132	0122102112212010101	0030110010000?????20	1111120
02310101002110000202	070012112100000-1132	01221021122120100101	00301100100001010000? ???????	???????
0231000110211000201	071011212100000-1132	01221021122120100101	0030110010000?????21	1100110
0120300111201100103	070012102100000-0130	111220211221010-1101	00001110100111101? ???????	???????
01102000212001100101	07101101101010-1130	111200210211210-1010	003111111010?????21	0100120
1110200021211101002	070002012100010-1110	001120200211100-1110	0030111110011000121	0100100
0103300121200011003	070011011100000-0120	1010012110-0110-1110	11001101100011111120	0101111
			D	D
			D	D
			D	D
			D	D
ROOT1 <i>Otiorynchus singularis</i>				
ROOT2 <i>Gymnetron veronicae</i>				
InG1 <i>Ithyporini Protacallodes budhevi</i> sp. nov.				
InG2 <i>Ithyporini Darumazo distinctus</i>				
InG3 <i>Ithyporini Protacallodes masumotoi</i>				
InG4 <i>Ithyporini Sclerocardius bohemani</i>				
InG5 <i>Sthereini Protacalles monticola</i>				
InG6 <i>Sthereini Protacallinus uenoi</i>				
OtG1 no tribe <i>Himalanconus</i> sp.				
OtG2 <i>Anchonini Titilayo garnetae</i>				
OtG3 <i>Hylobini Hylobius abietis</i>				
OtG4 <i>Lepyriini Lepyris capucinu</i>				
OtG5 <i>Lithinini Seleuca</i> sp.				
OtG6 <i>Lymanitini Devernodes chthonia</i>				
OtG7 <i>Molytini Liparus germanus</i>				
OtG8 <i>Molytini Pinacopus intermedius</i>				
OtG9 <i>Orthorhinini Eurhamphus fasciculatus</i>				
OtG10 <i>Orthorhinini Iliacuris laticollis</i>				
OtG11 <i>Orthorhinini Orthorhinus</i> sp.				
OtG12 <i>Orthorhinini Vanapa oberthuri</i>				
OtG13 <i>Pissodini C. Cotasteromimus morimotoi</i>				
OtG14 <i>Pissodini C. Cotasteromorphus chufai</i>				
OtG15 <i>Pissodini C. Obhylius arboricola</i>				
OtG16 <i>Pissodini C. Pseudohyllobius setosus</i>				
OtG17 <i>Pissodini C. Seticotasteromimus brunomanseri</i>				
OtG18 <i>Pissodini C. Seticotasteromimus crassirostris</i>				
OtG19 <i>Pissodini C. Seticotasteromimus jarawa</i>				
OtG20 <i>Pissodini C. Zembrus perseus</i>				
OtG21 <i>Pissodini Porytomorpha tonsa</i>				
OtG22 <i>Pissodini Pissodes pini</i>				
OtG23 <i>Typodeini Aparopion chevrolati</i>				
Deactivated				

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/quadrangle = 3.
6. Head, rostrum, shape, fronto-dorsal view: widening anteriorly = 0; parallel-sided = 1; narrowing anteriorly = 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, unicus: 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 $20^\circ = 0$; 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 *Protacallodes 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, Pyrenées 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:** *Protacallodes 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:** *Protacallodes 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. **spOtG18:** *Seticotasteromimus crassirostris* Germann, 2022; see GERMANN (2022).

