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RESEARCH PAPER

Species of the genus *Reicheiodes* from Taiwan (Coleoptera: Carabidae: Scaritinae)

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Abstract. The species of the genus *Reicheiodes* Ganglbauer, 1891 from Taiwan are reviewed. The Taiwanese fauna consists of three species: *Reicheiodes* (*Reichonippodes*) *kuankong* sp. nov., *R.* (*Reichonippodes*) *ursinus* sp. nov., and *R.* (*Reichonippodes*) *taiwanensis* Bulirsch, 2018; the latter previously known in the female holotype only. All species are (re)described, diagnosed, their habitus and male genitalia are illustrated, and the body measurements are provided for the newly collected specimens of *R. taiwanensis*. Keys to all Taiwanese species, as well to all species of the subgenus *Reichonippodes* Dostal, 1993, are provided. DNA barcodes are provided for all three species and used to reconstruct the phylogenetic relationship of the species and to estimate their age. Both morphological and DNA data indicate that all three species are closely related and probably represent within-island radiation in the last 2.4 million years. All three species are allopatric, inhabiting the northern (*R. kuankong*), central (*R. taiwanensis*) and southern (*R. ursinus*) Taiwan. All specimens were sifted from the leaf litter of lowland to submontane (*R. kuankong*) or higher montane (*R. taiwanensis* and *R. ursinus*) broadleaf forests.

Key words. Coleoptera, Carabidae, Scaritinae, Dyschiriini, *Reicheiodes, Reichonippodes*, DNA barcodes, key, new species, taxonomy, Taiwan

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:1FF59FAD-43F6-4CB1-A73B-E3A8BFC4E0C0

Introduction

Taiwan Island has diverse and highly endemic beetle fauna, yet many beetle groups remain unexplored or unstudied. Leaf litter beetles are an illustrative example: one sample of leaf litter in Taiwan may contain more than 600 specimens belonging to more than 55 species (Fikáček et al. 2024), which hinders sorting and identifying. Our preliminary study (Hu et al. 2024) using DNA barcoding and the expertise of more than 25 experts revealed many new records at family to species level, most of which referred to common and widespread species overlooked before. Ground beetles (Carabidae) were surprisingly uncommon in the samples from lowlands and lower montane forests, and more species were sampled only recently at higher altitudes, many being rare and local. Among them, we collected species of the genus *Reicheiodes* Ganglbauer, 1891 from multiple localities in northern, central and southern Taiwan, and summarize these finding in this study.

The genus *Reicheiodes* (Carabidae: Scaritinae: Dyschiriini) comprises 31 species distributed exclusively in the Palaearctic Region (Bulirsch 2018) and is divided into five subgenera (Dostal 1993, Fedorenko 1996): *Reicheiodes* s. str. is relatively broadly distributed in the Alps, the Balkan mountains, western Caucasus and southern Turkey; *Iberiodes* Dostal, 1993 is endemic to the Iberian Peninsula; *Himalayodes* Dostal, 1993 occurs exclusively in the Himalaya Mountains; *Reichonippodes* Dostal, 1993

is known from the Japanese islands and Taiwan, and the monotypic *Sinodyschirius* Fedorenko, 1996 is only known from eastern China (surroundings of Shanghai). *Sinodyschirius*, with its only species *R. dewaillyi* (Kult, 1949), differs from *Reichonippodes* in having elytra with a distinct humeral tooth and shortened pronotal lateral border, reaching maximally half the distance between the lateral setiferous punctures. Both subgenera do not seem to be closely related, and Fedorenko (1996) assumed that *Sinodyschirius* may be an intermediate taxon between *Reicheiodes* and the subgenus *Eudyschirius* Fedorenko, 1996 of *Dyschiriodes* Jeannel, 1941.

The subgenus *Reichonippodes* has originally been defined by Dostal (1993) and confirmed by Fedorenko (1996) for two Japanese species, *R. igai* (Nakane & Ueno, 1953) and *R. yanoi* (Kult, 1949), based on the combination of not distinctly reduced eyes, indistinct genae, pronotum with lateral channel reaching posterior setiferous punctures, strongly convex elytra, each with seven recognisable striae and 2–3 dorsal, three posthumeral and two apical setiferous punctures. Another species, *R. nishii* Morita & Bulirsch, 2010, was discovered in the Iriomote Island (Ryukyus, Japan), and two more species, *R. matobai* Morita, 2015 and *R. yokozekii* Morita, 2015 were described from Honshu Island (Japan). Bulirsch (2018) reported *Reichonippodes* from Taiwan for the first time, based on a single female collected by V. Grebennikov in the upper montane forest in Daxueshan.

Here we report the first comprehensive material of *Reichonippodes* from Taiwan, including descriptions of two new species, as well as males of *R. taiwanensis* Bulirsch, 2018, and provide the first DNA data for Taiwanese species. We also provide the key to all species of *Reichonippodes* and discuss the distribution of the subgenus. This study is the fourth taxonomic contribution of the Taiwanese Leaf Litter Beetles projects, after Ho et al. (2022), Löbl (2023) and Hu et al. (2024).

Material and methods

Taxonomic study. The study of dry-mounted specimens, including measurements and examination of microsculpture, was done at a magnification up to 98×. Up to 30 specimens of each species were measured. Body length (including closed mandibles) is given with accuracy 0.05 mm, ratios and means are down to two decimal places. Label data of all specimens are quoted verbatim except standardized data. Aedeagi were fixed either in Euparal (the male holotypes) or with water soluble glue on a label and placed on the same pin below the beetle. Macrophotographs were taken by the second author using a Nikon D2X or D800 digital camera, applied to a Nikon Labophot II binocular optical microscope or a Nikon SMZ 1000 stereomicroscope, with diaphragmed lenses. Morphological terminology follows Fedorenko (1996) and Bulirsch (2018). The armature of the protibia is referred to as follows: on the outer edge it consists of the apical spine (Fig. 1F: spi) and two teeth (distal tooth and proximal tooth; Fig. 1F: dt, pt), on the inner edge it bears the movable apical spur (Fig. 1F: spu).

Examined specimens are deposited in the following collections:

ADWA	Alexander Dostal collection, Vienna, Austria;
BHHC	Bin-Hong Ho collection, Taipei, Taiwan;
BMNH	Natural History Museum, London, U.K. (M.V.L. Barclay, K. Matsumoto);
NMNS	National Museum of Natural Science, Taichung (J.-F. Tsai);
NMPC	National Museum of the Czech Republic, Prague, Czech Republic (J. Hájek, L. Sekerka);
PBPC	Petr Bulirsch collection, Prague, Czech Republic;
PMFI	Paolo Magrini collection, Firenze, Italy.

The following taxa of the subgenus *Reichonippodes* were studied for the differential diagnosis and the key:

R.* (*R.*) *yanoi (Kult, 1949). Holotype (ADWA): Japan, Kashiwagi.

R.* (*R.*) *igai (Nakane & Ueno, 1953). 1 spec. (PBPC): Japan, Shikoku, Ehime Pref., Keyakidara, 33.479°N 132.994°E.

R.* (*R.*) *nishii Morita & Bulirsch, 2010. Paratypes: 3 spec. (PBPC): Japan, N Iriomote Jima, Uraushi river, hiking trail to Kanbire Falls.

R.* (*R.*) *matobai Morita, 2015. paratypes: 2 spec. (PBPC): Japan, Honshu, Wakayama Pref., Kozagawa chô, Ikenoyama.

R.* (*R.*) *yokozekii Morita, 2015. paratypes: 2 spec. (PBPC): Japan, Honshu, Mie Pref., Oodai-chô, Mt. Mayoi-dake.

The abbreviations in the text are as follows:

ASP	apical setiferous puncture(s) of elytron;
BSP	basal (prescutellar) setiferous puncture(s) of elytron;
DSP	dorsal setiferous puncture(s) of elytron;
HT	holotype(s);
L.	length of body including closed mandibles;
Mya	millions of years ago;
PASP	preapical setiferous puncture(s) of elytron;
PHSP	posthumeral setiferous puncture(s) of elytron;
PT	paratype(s);
SP	setiferous puncture(s) of pronotum.

DNA analyses. We extracted the complete genomic DNA from one adult for each Taiwanese *Reicheiodes* species and from one specimen of *Trilophidius alternans* (Balkenohl, 1999) (Clivinini) as an outgroup; we used the FavorGen Tissue Genomic DNA Extraction Mini Kit following the manufacturer's protocol (lysis temperature = 60°C), but with adapted incubation periods (14 hours in proteinase K + FATG1 buffer). We amplified the 5′ fragment of the cytochrome oxidase I (CO1) mitochondrial gene using the standard LCO1490/HCO2198 primers (Folmer et al. 1994) with the following PCR protocol: 94°C for 3 min, 35× (94°C for 0:30 min, 48°C for 0:45 min, 72°C for 1:00 min), 72°C for 8 min. Sequencing was done by Macrogen Korea. One set of analyses was done using these four specimens only, the second set also included additional representatives of Dyschiriini downloaded from the BOLD database: *Akephorus obesus* (LeConte, 1866) (BBCCN430_10), *A. marinus* LeConte, 1852 (NEONU1895_13), *Reicheiodes lederi* (Reitter, 1888) (CII119_15), *Reicheiodes* sp. from Georgia (CII130_15), *Dyschiriodes aeneus* (Dejean, 1825) (GBMIN41238_14), *D. salinus* (Schaum, 1843) (EUCAR167_10), *D. dejeanii* (Putzeys, 1846) (CCON156_08), *D. globulosus* (Say, 1823) (BETN14677_22), *Dyschiriodes* sp. from Pakistan (MACOL1899_12), and *Dyschirius angustatus* (Ahrens, 1830) (FBCOA891_10). Alignment was done using the MUSCLE algorithm in Geneious ver. 6.1. Dated trees were constructed using BEAST2 (Bouckaert et al.

2019), using a uniform a priori substitution rate of 0.0113 nucleotide substitutions per site per million years per lineage estimated for COI-5' of Carabidae by Andújar et al. (2012). Genetic distances among species were calculated in MEGA11 (Tamura et al. 2021). Sequenced vouchers are part of the material examined (see below). The newly generated sequences have been submitted to the Barcoding of Life Database (BOLD).

Maps and ecological niche. The latitude-longitude and latitude-altitude distribution maps were created using the custom R script and adapted in InkScape. Since the northern species seems to live in lower altitudes than the other species, we also compared the climatic niche of all species, using mean annual temperature and mean annual rainfall as basic climatic data. We extracted the climatic data for Taiwan from the freely available WorldClim data depository (https://www.worldclim.org/; Fick & Hijmans 2017). We used the bio1 (mean temperature) and bio12 (mean precipitation) variable with resolution of 2.5 minutes and extracted the data for *Reicheiodes* localities and for 1000 random points across Taiwan by an R script; the graph was also constructed in R and adapted in InkScape. The occurrence data are also available in DarwinCore format in the online supplementary file.

Taxonomy

Reicheiodes (*Reichonippodes*) *kuankong* sp. nov.

(Figs 1A–E)

Type locality. Taiwan, New Taipei, 0.8 km SEE of Wulai City, 24.85652°N 121.5536°E, 320 m a.s.l.

Type material. Holotype: ♂ (NMNS): 'TAIWAN, New Taipei / 0.8 km SEE of Wulai City, Laka / Trail; 24.85652°N 121.5536°E / 5.v.2018; 320 m; Fikáček, Leong / & Chang lgt.; 2018-TW11, // sifting of small leaf litter / accumulations in the secondary / lowland moist forest on a steep / slope, with sparse understory'. Paratypes: **TAIWAN: New Taipei:** 1 ♂ (PBPC): 'TAIWAN, New Taipei / 2.5 km SWW of Wulai City / Meilushan Mt. above Baoquing / Temple; 24.85445°N 121.53°E / 760 m; 6.v.2018; Fikáček, Chang / & Zelený lgt.; 2018-TW12 // leaf litter accumulations in / primary moist forest with sparse / understory: sifting'; 1 ♂ (NMPC): 'TAIWAN: New Taipei, Fushan / Botanical Garden, ForestGEO / Vegetation Ecology plot / quadrat 1711, 665 m // 24.7514°N 121.555°E; 7.vii.2022 / M. Fikáček; TW2022_005B // FS1-029 / Fushan / (TW2022_005B) / OTU 687 (adult)'; 1 ♀ (PBPC): TAIWAN: New Taipei / Yanmingshan National Park / Erzhiping Trail, 830 m / 25.17932[°N] 121.51613[°E] / 13.viii.2021, sifting leaf / litter, HY Lin, WZ Tseng [leg.].

Description. *Habitus* as in Fig. 1A. Body length 2.40–2.50 mm (HT 2.50 mm, mean 2.45 mm; n = 4).

Colour of dorsal surface in HT and one PT ferruginous without bronze luster, elytral base, apex and anterior part of head barely lighter, in two PT upper surface slightly darker; ventral surface and legs ferruginous, mouthparts and antennae dark yellowish.

Head. Clypeus bordered, with slightly and broadly protruded median part; lateral teeth bordered, moderately acute, distinctly projecting anteriorly, pointed at tip, divided from supraantennal plates by obtuse notch; clypeal field sub-quadrate, irregularly narrowed posteriorly, smooth, separated from frons by deep and broad transverse furrow; frons convex, smooth; supraantennal plates strongly convex, with blunt carina at top of convexity. Frontal furrows deep, broad, parallel to eyes mid-length then abruptly and strongly diverging posteriorly around eyes. Eyes moderately small, convex, facets distinct; genae very small, enclosing eyes in about posterior fifth. Antennae relatively long, antennomeres 5–10 submoniliform, about 1.2–1.3 times as long as wide. Neck with minute isodiametric reticulation laterally and with a few striae and punctures below eyes, constriction absent.

Pronotum subglobose, in lateral view moderately flattened posteriorly; outline between lateral SP slightly convex; indistinctly attenuated anteriorly 1.12–1.15 (HT 1.12, mean 1.13) times as wide as long, 1.48–1.54 (HT 1.53, mean 1.50) times as wide as head, broadest in about posterior third, with rounded anterior angles. Anterior transverse impression deep, broadened in middle, impunctate, sparse and rough cross-striate, cross-striae especially in middle third rather deep and subparallel; median line moderately deep, deeper basally, lateral channel deep and moderately broad, gently broadened anteriorly up to anterior SP, reflexed lateral margin just surpassing posterior SP. Surface shiny, with very few, almost indistinct transverse wrinkles and sparse micropunctures, lateral channel, without reticulation.

Elytra shortly ovate; disc moderately, apex more strongly convex in lateral view; 1.43–1.48 (HT 1.44, mean 1.46) times as long as wide, 1.18–1.23 (HT 1.18, mean 1.20) times as wide as pronotum. Elytra widest posterior to anterior third; base sloping to moderately rounded humeri without humeral tooth; lateral channel moderately broad from pedunculus to humeri, broadened apically; reflexed lateral margin distinct. Basal border distinct, basal tubercles and scutellar strioles absent; BSP large, isolated, situated just inside of projected extension of interval 2. Three PHSP, three PASP, two large ASP and three DSP (in interval 3, posterior one in about mid-length). Striae 1–(2) irregular, moderately deep, stria 1 indistinctly joining BSP and joining lateral channel at apex; striae (2)–3 irregularly, finely impressed, latero-apically mostly diminish; striae 1–6(7) coarsely punctured in basal half, punctuation finer latero-apically, almost diminish, stria 8 beginning as a few very fine punctures in middle third; intervals barely convex medio-basally, flattened latero-apically.

Metathoracic wings absent.

Protibiae. Apical spine distinctly curved ventro-laterally; apical movable spur shorter than spine, feebly curved; distal tooth moderately large, sharp, proximal one much finer, almost indistinct.

Male genitalia. Aedeagus as in Figs 1B, C, E, median lobe in lateral view short and very broad at mid-length; apex short, broadly rounded, distinctly bent ventrad. Parameres as in Fig. 1D, unisetose.

Differential diagnosis. *Reicheiodes kuankong* sp. nov. is most similar to *R.* (*Reichonippodes*) *nishii* from Iriomote-jima Island, Japan. The new species could be distinguished by longer antennae with the antennomeres 5–10 about 1.2–1.3 times as long as wide (1.0–1.1 times as long as wide in *R. nishii*); by the pronotum having the anterior impression more roughly cross-striate medially;

and especially by the elytra with its base distinctly less sloping to the more distinct humeri and with the striae latero-apically longer and more deeply punctured. The new species differs from *R. taiwanensis* in the body being smaller and lighter in colour (fuliginous in *R. taiwanensis*), in the narrower lateral channel of the pronotum (only slightly broader than reflexed lateral margin in latero-dorsal view, in contrast to twice broader in *R. taiwanensis*), and in the antennomeres 5–10 being 1.2–1.3 times as long as wide (1.0–1.1 times as long as wide in *R. taiwanensis*). For differences from *R. ursinus* sp. nov. see under that species.

Etymology. The new species is named after Kuan Kong, the deity worshiped in Chinese folk religion, Taoism and Buddhism, and usually depicted with a red face, resembling the reddish body coloration of this species. The name is a noun in nominative singular, standing in apposition.

Collection circumstances. All specimens were collected by sifting of moist leaf litter in primary lowland and lower montane forests at altitudes of 320–830 m a.s.l.

Distribution. Endemic to Taiwan. Only known from northern Taiwan, so far known from the northernmost part of the central mountain range (Fushan and Wulai) and from Yanmingshan National Park.

Reicheiodes (*Reichonippodes*) *ursinus* sp. nov.

(Figs 1K–O)

Type locality. Taiwan, Taitung, Haiduan, Jinping Logging Trail km 15, 23.163342°N 121.144153°E.

Type material. Holotype: ♂ (NMNS): 'TAIWAN, Taitung, Haiduan / Jinping Logging Trail, km 15 / 23.163342°N 121.144153°E, 1520 m / 3.iii.2024, BH Ho [leg.], TW2024-004'. Paratypes: **TAIWAN: Taitung:** 23 ♂♂ 17 ♀♀ (BMNH, BHHC, NMNS, NMPC, PMFI, PBPC): same label data as holotype.

Description. *Habitus* as in Fig. 1K. Body length 2.20–2.60 mm (HT 2.40 mm, mean 2.40 mm; n = 30).

Colour of dorsal surface ferruginous to dark ferruginous without bronze luster; ventral surface and legs ferruginous, mouthparts and antennae dark yellowish.

Head. Clypeus bordered, with very slightly and broadly to moderately protruded median part; lateral teeth bordered, moderately acute, distinctly projecting anteriorly, pointed at tip, divided from supraantennal plates by obtuse notch; clypeal field sub-quadrate, smooth, separated from frons by deep and broad transverse furrow; frons convex, smooth; supraantennal plates strongly convex, with blunt carina at top of convexity. Frontal furrows deep, moderately broad, parallel to eyes mid-length then abruptly and strongly diverging posteriorly around eyes. Eyes rather small, strongly convex, facets distinct; genae small, gently enclosing eyes posteriorly. Antennae relatively short, antennomeres 5–10 moniliform. Neck without isodiametric reticulation, with a few punctures below eyes, constriction absent.

Pronotum subglobose, in lateral view moderately flattened posteriorly; outline between lateral SP slightly convex; indistinctly attenuated anteriorly 1.09–1.16 (HT 1.11, mean 1.13) times as wide as long, 1.45–1.54 (HT 1.52, mean 1.48) times as wide as head, broadest in about posterior third, with rounded anterior angles. Anterior transverse impression deep, broadened in middle, impunctate, very sparsely and shortly cross-striate, especially in middle third; median line rather fine on disc, deeper basally, lateral channel deep and moderately broad, not broadened anteriorly up to anterior SP, reflexed lateral margin just surpassing posterior SP. Surface shiny, with very few, almost indistinct transverse wrinkles and sparse micropunctures, lateral channel shiny, without reticulation.

Elytra shortly ovate; disc moderately, apex more strongly convex in lateral view; 1.47–1.53 (HT 1.48, mean 1.50) times as long as wide, 1.21–1.28 (HT 1.26, mean 1.24) times as wide as pronotum. Elytra widest after anterior third; base sloping to moderately rounded humeri without tooth; lateral channel moderately broad from pedunculus to humeri, broadened apically; reflexed lateral margin distinct. Basal border distinct, basal tubercles and scutellar strioles absent; BSP mostly missing, in nine PT present on one elytron. Three PHSP, three PASP, two large ASP and two DSP (in anterior part of interval 3, posterior DSP missing). Striae 1–(2) irregular, moderately deep, stria 1 joining lateral channel at apex; striae (2)3–5 irregularly, finely impressed, latero-apically mostly diminish; striae 1–4 punctures rough in basal half, latero-apically punctuation finer, stria 5–7 punctures fine latero-apically, diminish on apex, stria 8 indistinct; inner intervals barely convex medio-basally, flattened latero-apically.

Metathoracic wings absent.

Protibiae. Apical spine moderately curved ventrolaterally; apical movable spur shorter than spine, feebly curved; distal tooth moderately large, sharp, proximal one much finer, almost indistinct.

Male genitalia. Aedeagus as in Figs 1L, M, O. Median lobe in lateral view moderately broad, rather narrow at mid-length, ventral margin almost evenly regularly concave, apex short, broadly rounded, indistinctly bent ventrad, apex in ventral view broadly rounded at tip, distinctly turned right. Parameres as in Fig. 1N, unisetose.

Differential diagnosis. *Reicheiodes ursinus* sp. nov. is similar to *Reicheiodes* (*Reichonippodes*) *kuankong* sp. nov. The new species can be distinguished by shorter antennae with the antennomeres 5–10 about as long as broad, by the elytra with only two DSP and none or unilaterally one BSP, and by having finer striae punctuation latero-apically.

Etymology. *Ursinus* is a Latin adjective derived from *Ursus* (bear). We name the new species in this way as its type locality is also famous for the population of the Taiwanese bear (*Ursus thibetanus formosanus* Swinhoe, 1864).

Collection circumstances. All specimens were collected by sifting moist leaf litter in the primary montane forest.

Distribution. Endemic to Taiwan. Only known from the type locality on the eastern slope of the central mountain range above the Taitung Valley.

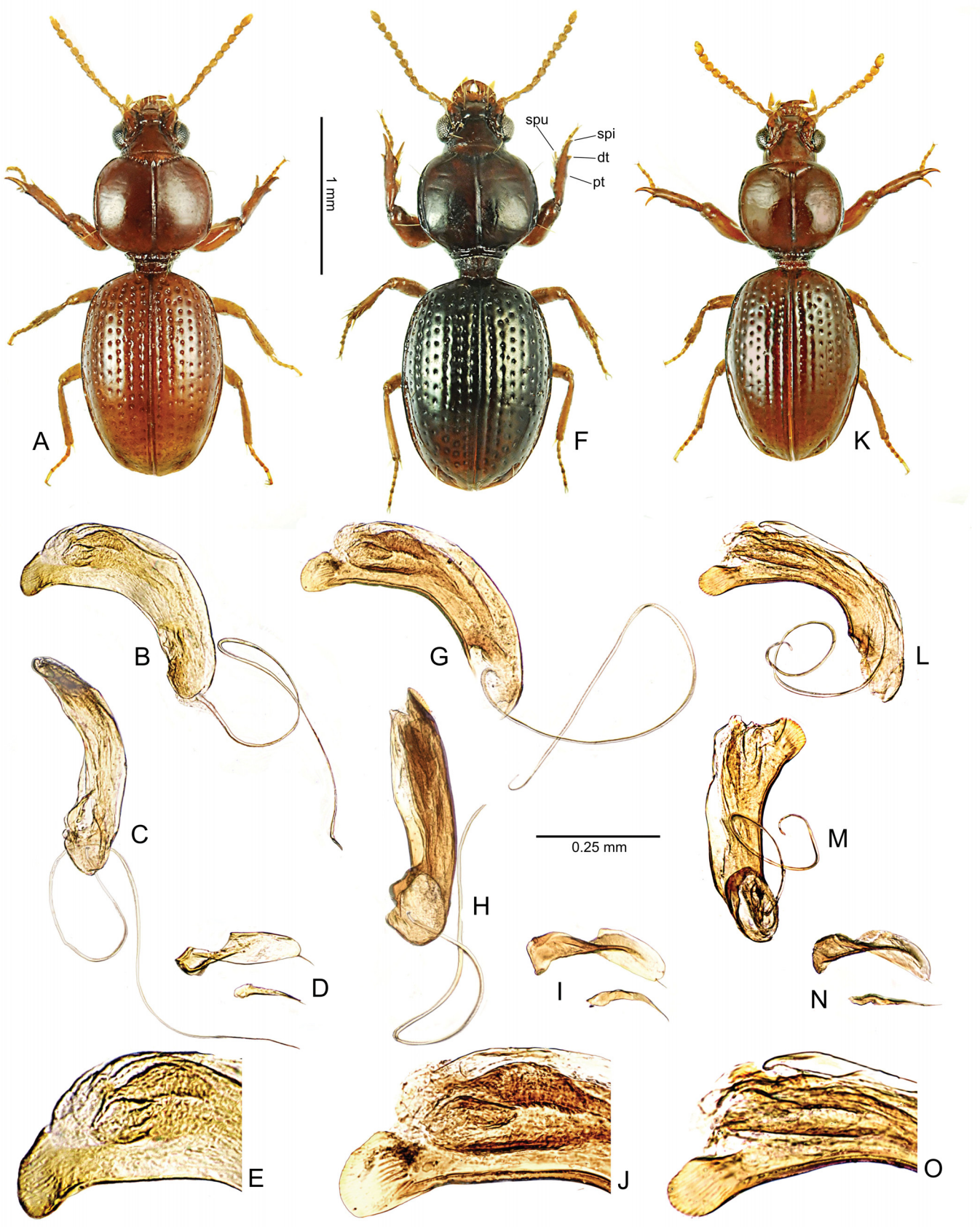


Fig. 1. Habitus and male genitalia of Taiwanese *Reicheiodes* Ganglbauer, 1891. A–E – *R. kuankong* sp. nov., holotype. F–J – *R. taiwanensis* Bulirsch, 2018, non-type. K–O – *R. ursinus* sp. nov., holotype. A, F, K – dorsal habitus; B, G, L – aedeagus in left lateral view; C, H, M – aedeagus in ventral view; D, I, N – parameres; E, J, O – detail of apex of the aedeagus in left lateral view. All figures (except E, J, O) to scale. Abbreviations: dt – distal tooth of protibia; pt – proximal tooth of protibia; spi – apical spine of protibia; spu – apical movable spur of protibia.

Reicheiodes (*Reichonippodes*) *taiwanensis* Bulirsch, 2018

(Figs 1F–J)

Type material examined. HOLOTYPE: ♀ (NMPC): 'Taiwan, Taichung / Dasyueshan forest / 24.2334[°N] 120.9664 [°E] / 2140 m; 10.viii.2013, sift. / TW01, V. Grebennikov'.

Additional material examined. TAIWAN: TAICHUNG: 4 ♂♂ 6 ♀♀ (ADWA, PBPC): 'Taiwan, Taichung; 178 / Xueshan rd. (to Daxueshan / Nat. Forest Recr. Area) / Prim. Forest, 24°13'36.4"N / 120°58'34.7"E, 1700 m [sic!, the altitude at the GPS position given is 1990 m!], 30.v.2019 / leg. Berger-Dostal'; 2 ♂♂ (NMNS, NMPC): Taiwan, Taichung / Daxueshan Nat. Forest Area / at Rd. 1 S of Shaolaishan Mt. / 24.22601[°N] 120.975772[°E] / 28.vi.2023 / Fikáček, Růžička, Ho, Hu, Král [leg.] / TW2023-031 // sifting of small accumulations / of leaf litter in a montane forest / with huge trees.

Supplementary description. Male as in Fig. 1F. Measurements (n = 13, including holotype). Body length 2.60–2.95 mm (mean 2.75 mm, HT 2.75 mm); pronotum 1.10–1.18 (mean 1.13, HT 1.18) times as wide as long, 1.50–1.59 (mean 1.55, HT 1.59) times as wide as head; Elytra 1.40–1.48 (mean 1.45, HT 1.40) times as long as wide, 1.21–1.28 (mean 1.24, HT 1.22) times as wide as pronotum.

Male genitalia. Aedeagus as in Figs 1G, H, J; median lobe in lateral view moderately long, moderately broad at mid-lenght, apex short, very broadly rounded, barely bent ventrad. Parameres as in Fig. 1I, unisetose.

Collection circumstances. All specimens were collected by sifting leaf litter in a primary montane forest.

Distribution. Endemic to Taiwan. The species is only known from the Daxueshan area in the central mountain range, from two close localities along the Daxueshan Rd. at altitudes 1990–2140 m a.s.l.

DNA analyses

We got a good quality *cox1* sequence for all three Taiwanese species. The comparison of the sequences revealed 3.25–3.90 % genetic distances among the species (uncorrected p-distance, Table 1). The phylogenetic analyses confirmed that all three species are closely related (bootstrap b = 100, posterior probability pp = 1), with the northern *R. kuankong* sp. nov. being resolved as the earliest-branching species in all ML and Bayesian analyses, yet without support in the analysis of all specimens (b = 50, pp = 0.49) and moderately supported in the analysis of Taiwanese species only (b = 84, pp = 0.81). The estimates of branching times were not affected much by the inclusion of non-Taiwanese outgroups. The divergence of *R. kuankong* sp. nov. was estimated to happen 2.45 Mya (95% CI 1.29–4.13 Mya) in the analysis of Taiwanese species only, and 2.3 Mya (CI 1.48–3.20 Mya) when all outgroups were included. The divergence of *R. taiwanensis* and *R. ursinus* sp. nov. was estimated to happen 1.71 Mya (CI 0.82–2.91 Mya) when only Taiwanese specimens were included, and 1.79 Mya (CI 1.08–2.58 Mya) when all outgroups were included.

Table 1. Uncorrected p-distances between the Taiwanese *Reicheiodes* Ganglbauer, 1891 species based on *cox1* gene.

Species pair	Distance (%)
R. kuankong – R. taiwanus	3.25
R. kuankong – R. ursinus	3.90
R. taiwanus – R. ursinus	3.58

Key to the species of the subgenus *Reichonippodes*

1 (2) Humeri with small, moderately sharp humeral tooth; elytral striae roughly punctured medio-basally. Honshu. ..... ***R. matobai*** Morita, 2015

2 (1) Humeri without humeral tooth; elytral striae finely to roughly punctured medio-basally.

3 (6) Elytron with 2 DSP.

4 (5) Elytral striae very finely punctured, almost diminish basally; intervals flat. BSP present, fine. Honshu. ..... ***R. yanoi*** (Kult, 1949)

5 (4) Elytral striae roughly punctured medio-basally; intervals convex medio-basally. BSP missing, rarely present on one elytron. Taiwan. .... ***R. ursinus* sp. nov.**

6 (3) Elytron with 3 DSP.

7 (12) Pronotal channel superficial, narrower or as broad as lateral reflexed margin in latero-dorsal view. Species from Japan.

8 (9) Elytral striae very finely and very sparsely punctured, almost diminish basally; intervals flat. Honshu ..... ***R. yokozekii*** Morita, 2015

9 (8) Elytral striae moderately roughly and more densely punctured, intervals at least slightly convex medio-basally.

10 (11) Pronotal channel superficial, narrower than lateral margin in latero-dorsal view; elytral base slightly slopping, humeri moderately rounded. Kyushu and Shikoku. .... ***R. igai*** (Nakane & Ueno, 1953)

11 (10) Pronotal channel deep, as broad as lateral margin in latero-dorsal view; elytral base strongly slopping, humeri broadly rounded. Iriomote-jima. ..... ***R. nishii*** Morita & Bulirsch, 2010

12 (7) Pronotal channel broader than reflexed lateral margin in latero-dorsal view. Species from Taiwan.

13 (14) Larger species, body length 2.60–2.95 mm. Body fuliginous. Pronotal channel deep, twice as broad as reflexed lateral margin in latero-dorsal view. Antennomeres 5–10 about 1.0–1.1 times as long as wide. ..... ***R. taiwanensis*** Bulirsch, 2018

14 (13) Smaller species, body length 2.20–2.60 mm. Body ferruginous. Pronotal channel only slightly broader than reflexed lateral margin in latero-dorsal view. Antennomeres 5–10 about 1.2–1.3 times as long as wide. ..... ***R. kuankong* sp. nov.**

Key to the Taiwanese species of *Reicheiodes*

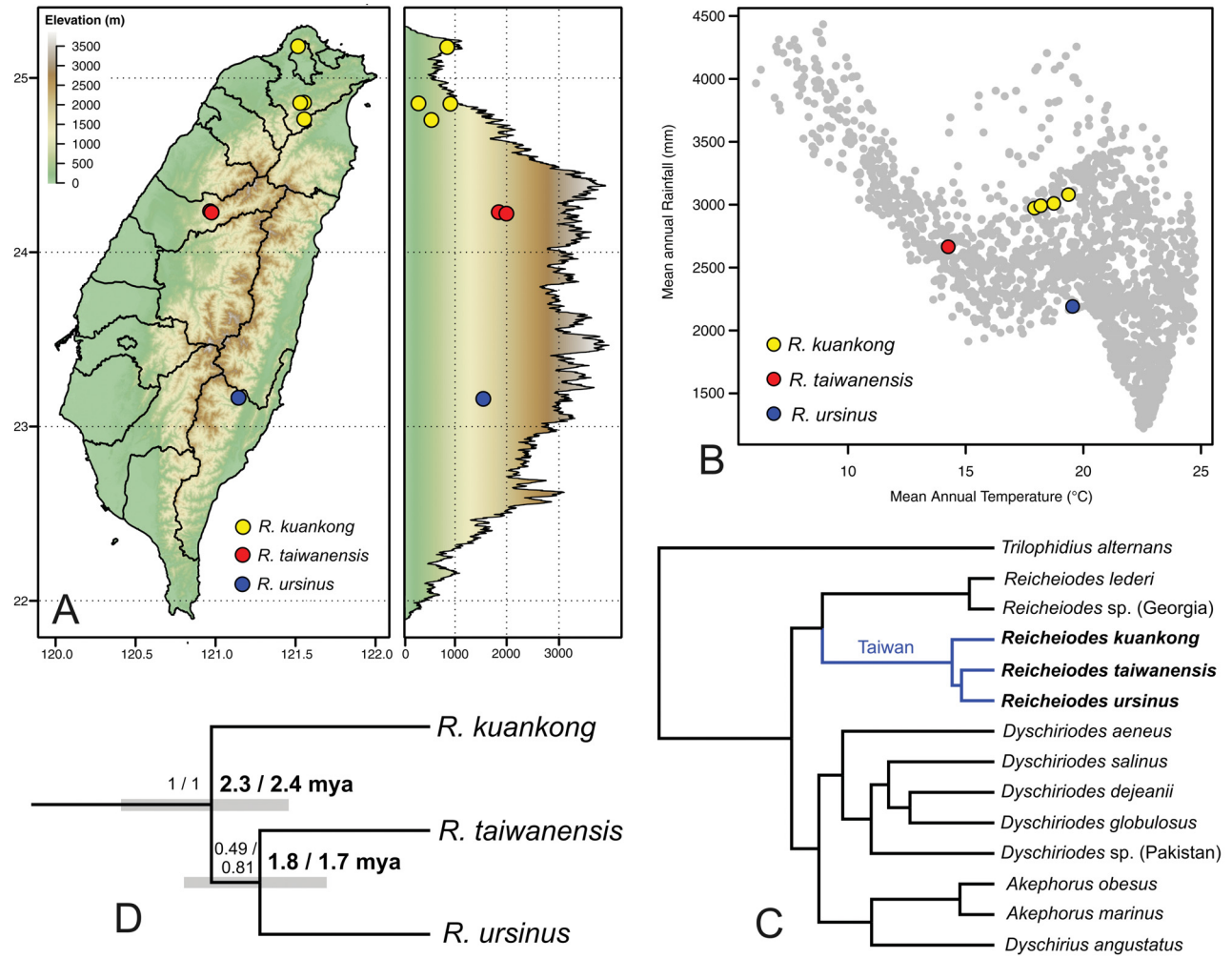
1 (2) Larger species, body length 2.60–2.95 mm. Body coloration fuliginous. Pronotal channel deep and wide, twice as broad as reflexed lateral margin in latero-dorsal view. Antennomeres 5–10 about 1.0–1.1 times as long as wide. .... ***R. taiwanensis*** Bulirsch, 2018

2 (1) Smaller species, body length 2.20–2.60 mm. Body coloration ferruginous. Pronotal channel narrower, only slightly broader than reflexed lateral margin in latero-dorsal view. Antennomeres 5–10 about 1.0–1.3 times as long as wide.
3 (4) Antennomeres 5–10 about 1.2–1.3 times as long as wide; BSP distinct, 3 DSP. .... ***R. kuankong* sp. nov.**
4 (3) Antennomeres 5–10 about 1.0 times as long as wide; BSP missing (rarely vestigial BSP on one elytron only), 2 DSP (posterior DSP missing). .... ***R. ursinus* sp. nov.**

Discussion

In this study, we document the occurrence of three species of the genus *Reicheiodes* in Taiwan. *Reicheiodes kuankong* sp. nov. is more widely distributed in the northern Taiwan, currently known from the nearby localities of Wulai and Fushan in the northern part of the central mountain range, but also from the Yanmingshan National Park that is separated from the central mountain range by ca. 25 km wide lowland gap. The species occurs at altitudes as low as 320 m a.s.l., indicating that the lowland forests do not prevent its dispersal. Nowadays, the Yanmingshan population may be isolated due to the replacement of lowland forests by the quickly growing Taipei City, but in the recent past a continuous distribution was likely. Despite being more widespread, the species is rare and local, and we have got four samples with a single specimen, and no specimens in other samples taken in Fushan and Wulai. The other two species, *R. taiwanensis* from the Daxueshan area, and *R. ursinus* sp. nov. from the eastern slopes above Taitung Valley, occur at higher altitudes (1.520–2.140 m a.s.l.) in montane primary forests and seem to be very local. All known specimens of *R. taiwanensis* were collected at sites ca. 1.5 km from each other, and *R. ursinus* sp. nov. is known from a single site only. We collected more leaf litter samples in similar types of forests at similar altitudes in both areas but failed to find more specimens. However, the fact that we got 41 specimens of *R. ursinus* sp. nov. in a single sifting sample indicates that the species can be locally common, when a correct season or microhabitat is sampled. The occurrence of *R. kuankong* sp. nov. at lower altitudes in northern Taiwan may correspond to the pattern seen in plants (e.g. *Gentiana* L.: Chen & Wang 1999; *Trochodendron aralioides* Siebold et Zucc.: Lin & Chiu 2019) where montane species also often occur at lower altitudes in the north, corresponding to lower mean and minimum temperatures and higher rainfall in northern Taiwan. Our mapping of climatic niches of all species indicates that the mean annual temperatures at the sites with *R. kuankong* sp. nov. correspond to those at sites with *R. ursinus* sp. nov. situated ca. 1000 m higher. Only *R. taiwanensis* lives in colder areas close to the upper edge of montane cloud forests. The distribution of different but likely closely related flightless species at different altitudes is also a pattern found in flightless genera, such as the Madagascan *Brachypelus* Putzeys, 1867 (Clivinina) and South African *Antireicheia* Basilewsky, 1951 (Reicheiina): some species occur in lowlands or even near sea shores, while others are found at a high altitude up to ca. 2.000 m a.s.l., often in isolated forest patches (Bulirsch et al. 2005, Bulirsch & Moravec 2009, Bulirsch & Magrini 2016). Despite different ecological requirements of individual species, the flightless leaf litter Scaritinae, including the Taiwanese *Reicheiodes*, seem to be restricted to patches of well-preserved primary forests.

All Taiwanese species of *Reicheiodes*, and all species of the subgenus *Reichonippodes*, are flightless, with strongly reduced metathoracic wings, and may hence be suitable models for biogeographic studies. *Reichonippodes* is distributed in Taiwan, the Ryukyu Islands, and mainland Japan, but it is absent from the Asian continent. This distribution pattern resembles that of other invertebrate groups (e.g., *Acrenitis* Matsui & Nakane, 1985 water scavenger beetles: Hebauer 1994, *Geothelphusa* Stimpson, 1858 freshwater crabs: Shih et al. 2011), and may be the result of the evolution of these lineages on the margin of the Asian continent that started to separate from the mainland in the Late Miocene (ca. 10–6 million years ago (mya): Wang et al. 2014). Taiwan was formed in the south of this region ca. at the same time (10–5 mya: Huang et al. 2006). The whole Taiwan-Ryukyus-Japan region underwent a complex geological history with short-term connections between island and between the continent and Taiwan or Japan. The timing and extent of land bridges connecting Taiwan, the Ryukyus and Japan are not yet fully understood, with results contrasting between individual geological studies (e.g., Osozawa et al. 2012, Furukawa & Fujitani 2014), as well as between biological evidence and geology (e.g., Su et al. 2016, Kinoshita et al. 2025, Watanabe et al. 2023). The Taiwan-Ryukyus land bridges, whatever their extent was, were mainly present during the Pleistocene (i.e., 2.5 mya and after) and connected Taiwan with the southern and maybe central Ryukyus, allowing the colonization of the Ryukyus from Taiwan (Pleistocene Stepping Stone scenario, Su et al. 2016). Yet, more ancient colonizations from Japan through the Ryukyus to Taiwan are also known in some groups (pre-Pleistocene isolation scenario, e.g., in *Macrothele* Ausserer, 1871 spiders: Su et al. 2016). *Reichonippodes* is present in Taiwan and Iriomote Is. in the southern Ryukyus, which may correspond to the Pleistocene Stepping Stone scenario, i.e. the Pleistocene colonization from Taiwan; the age of the Taiwanese species inferred here (2.4–2.3 mya) would not contradict it, but DNA data for *R. nishii* would be necessary to confirm it. Surprisingly, *Reichonippodes* is absent from the Central Ryukyus that were likely more isolated from south and north due to the deep Kerama Gap and Tokara Straight. Yet, they host taxa related to those in Taiwan and Japan that are unable of overwater dispersal (e.g., blind cave-living beetles: Sugaya et al. 2023, endemic mammals: Kinoshita et al. 2025, spiders: Su et al. 2016), hence the absence of *Reicheiodes* is surprising. It would also be interesting to get DNA data for the species from Honshu and Shikoku to test monophyly of *Reichonippodes* and estimate the timing of the divergence between these species and the Taiwan+Iriomote ones. The distribution pattern of



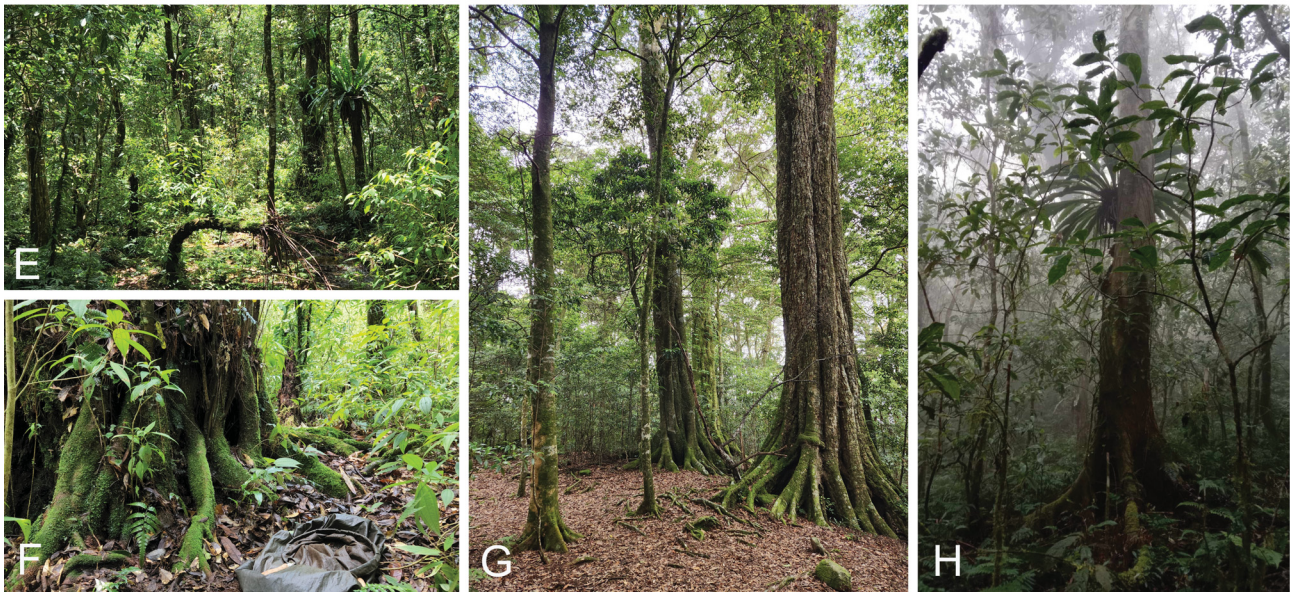


Fig. 2. Distribution and origin of *Reicheiodes* Ganglbauer, 1891 in Taiwan. A – geographic distribution: GPS and altitude + GPS position of collecting sites. B – distribution in the ecological space (grey dots indicate ecological conditions available in Taiwan). C – Bayesian inference of the *cox1* sequences of the Taiwanese and non-Taiwanese Dyschiriini; Taiwanese species highlighted in blue. D – dated phylogeny of the Taiwanese species of *Reicheiodes* (values above branch = posterior probability, values at nodes = mean age; the first value is based on the analysis with non-Taiwanese species, the second value is based on analysis of Taiwanese species only). E–H – localities of Taiwanese *Reicheiodes*: E–F – Fushan ForestGEO plot, locality of *R. kuankong* sp. nov.; G – Daxueshan Rd., 1.997 m a.s.l., locality of *R. taiwanensis* Bulirsch, 2018; H – Jinping Logging Trail, type locality of *R. ursinus* sp. nov.

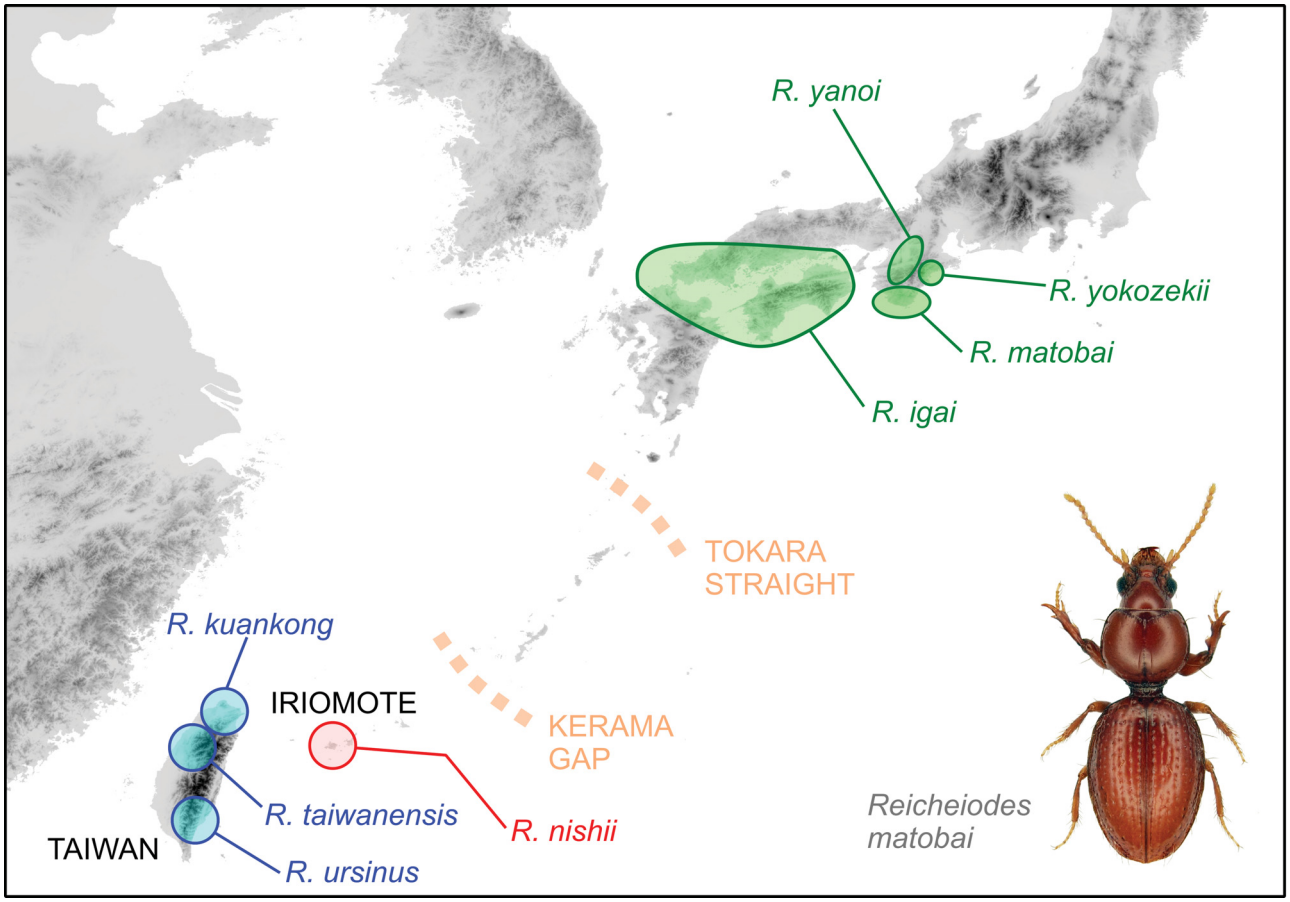


Fig. 3. Distribution of the species of the subgenus *Reichonippodes* Dostal, 1993. The photo of *R. matobai* Morita, 2015 adopted from Morita (2015).

these four species is similar to those in Taiwan in having non-overlapping, often very small, ranges. The Taiwanese species originated in the early Pleistocene (2.5–1.7 Mya), i.e. at the time when Taiwan was already emergent and likely connected to at least the southern Ryukyus. Without data about the non-Taiwanese *Reichonippodes*, this would correspond either with a within-Taiwan radiation, or with a repeated vicariance (range splitting) of the larger ranges when Taiwan-Iriomote land bridges disappeared. A more complete DNA sampling of *Reichonippodes* and a more careful dating strategy would also be desirable; see Su et al. (2016) and Seidel et al. (2021) for 9review of problems with *cox1* dating.

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