

The identities of two species in the *Pterostichus macrogenys* species group of subterranean carabid beetles (Coleoptera, Carabidae) revealed by external morphometric analysis and comparative genital morphology

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Abstract

The *Pterostichus macrogenys* species group is an endemic subterranean Japanese carabid lineage that shows marked regional differentiation, but unresolved taxonomic issues remain, even at the species level. Based on morphological examinations of the genital structures of newly collected specimens and an external morphometric analysis of all the species concerned, *P. falcispinus* Sasakawa, 2005 **syn. nov.** is synonymized with *P. asahinus* Habu & Baba, 1960, and *P. awashimaensis* **sp. nov.** is described from Awashima Island, a small island off the coast of Honshu. Based on external morphometrics, *P. awashimaensis* was determined to be most similar to *P. yahikosanus* Sasakawa, 2009, but its external and genital features differ distinctly from the latter species and it is thought to be more ancestral.

Keywords

Discriminant analysis, ground beetle, Japan, new species, new synonym, *Nialoe*

Introduction

The *macrogenys* species group of *Pterostichus* subgenus *Nialoe* Tanaka, 1958 (s. lat., i.e., *Nialoe* sensu Sasakawa 2021) is a Japanese endemic subterranean lineage in the beetle family Carabidae. This group shows marked differentiation in mountainous areas of Honshu, and ca. 30 species are currently recognized (Sasakawa et al. 2020). Members of the species group are flightless due to their atrophied hind wings, and are characterized by a large head with long mandibles and flattened body, which is thought to be associated with a subterranean lifestyle. Sasakawa et al. (2020) were the last to revise the group and revealed that coexisting different-sized species and disjunct distributions are more common than previously recognized (Fig. 1). However, some issues remained unresolved.

This study sought to resolve two taxonomic issues in the *macrogenys* species group: the relationship between *P. asahinus* Habu & Baba, 1960 and *P. falcispinus* Sasakawa, 2005, and the identity of the population on Awashima Island, a small island off the coast of Honshu. The fact that the holotype of *P. asahinus* and the available specimen from the Awashima population are both females, which provide less taxonomic information than males, has hampered resolution of these taxonomic issues. To overcome this, we performed external morphometric analysis, a useful taxonomic method that can also be applied to females (e.g., Sasakawa and Kubota 2007; Ober, and Connolly 2015; Ortuño et al. 2021), in addition to the usual genital morphology examinations.

Materials and methods

Specimens newly examined here were collected using subterranean baited traps, which were also used in our previous studies (Sasakawa and Itô 2017). This study applied discriminant analysis using external morphometrics of female specimens, morphological examinations of the endophallus of male genitalia of a male specimen newly collected near the type locality of *P. asahinus*, and morphological examinations of genital membranous parts of the female specimen from Awashima Island.

The discriminant analysis was used to investigate morphometrically whether the identity of the *P. asahinus* holotype and our newly defined *P. asahinus* is supported and to which species the Awashima specimen is most similar. The following specimens were examined together with the Awashima specimen and *P. asahinus* holotype: *P. adatarasanus* 3♀, *P. asahinus* (redefined here to include *P. falcispinus*) 17♀, *P. chokaisanus* 2♀, *P. eboshiyamanus* 3♀, *P. iwakiensis* 7♀, *P. monolineatus* 1♀, *P. ohsawacavus* 1♀, *P. takadateyamanus* 25♀, and *P. yabikosanus* 6♀. These samples include all species to which the Awashima specimen and *P. asahinus* holotype may belong and for which female specimens are available. Scaled photos obtained previously (Sasakawa et al. 2020), from the specimens newly examined here, and of the *P. asahinus* holotype in the type-specimen database of the National Agriculture and Food Research Organization (Division of Informatics and Inventory, Insect Systematics Unit, Institute for Agro-

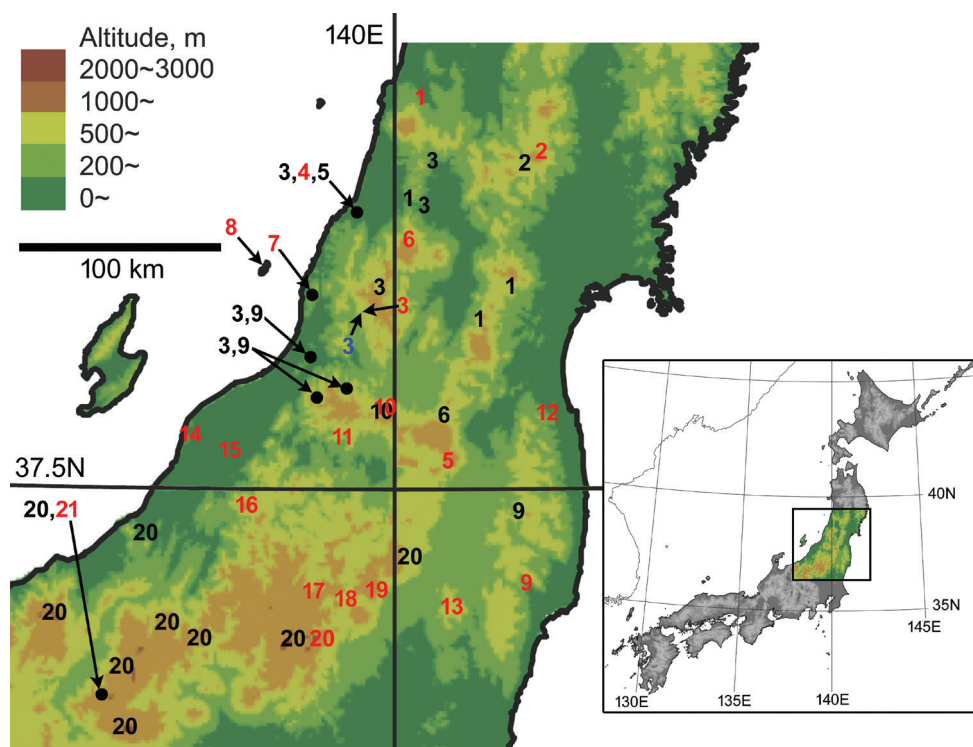


Figure 1. Distribution of the *Pterostichus macrogenys* species group in northern Chubu, northern Kanto, and southern Tohoku Districts, Honshu, based on specimens with unambiguous identities, modified from Sasakawa et al. (2020) and Satô (2021) **1** *P. chokaisanus* Sasakawa, 2009 **2** *P. kurikomasanus* Sasakawa, 2005 **3** *P. asahinus* Habu and Baba, 1960 **4** *P. takadateyamanus* Sasakawa, 2009 **5** *P. adatarasanus* Sasakawa, 2005 **6** *P. gassanus* Sasakawa, 2009 **7** *P. shinbodakensis* Sasakawa & Itô, 2017 **8** *P. awashimaensis* sp. nov. **9** *P. iwakiensis* Sasakawa, 2009 **10** *P. eboshiyamanus* Sasakawa, 2009 **11** *P. tateishiyamanus* Sasakawa & Itô, 2017 **12** *P. monolineatus* Sasakawa, Mitsuduka, & Itô, 2020 **13** *P. yamizosanus* Sasakawa, 2005 **14** *P. yabikosanus* Sasakawa, 2009 **15** *P. ohsawacavus* Sasakawa, 2005 **16** *P. sumondakensis* Sasakawa, 2005 **17** *P. isolatus* Sasakawa, 2005 **18** *P. nakamiyorinus* Morita, Ohkawa & Kurihara, 2013 **19** *P. momuranus* Morita, Ohkawa & Kurihara, 2013 **20** *P. macrogenys* Bates, 1883 **21** *P. nagasawai* Ito & Ogai, 2015. Red letters denote the type localities of each species. The blue letter indicates where the male specimen of *P. asahinus* newly examined here was collected.

Environmental Sciences, National Agriculture and Food Research Organization 2011) that were size-calibrated using information on the body length in the original description (15.2 mm; Habu and Baba 1960) were analyzed. Using these photos, four parts of the pronotum were measured with ImageJ v.1.50i (Rasband 2016) to the nearest 0.01 mm: pronotum length along the median line (PL), pronotal anterior margin width (PAW), pronotum width at the widest part (PW), and pronotal posterior margin width (PPW). Next, linear discriminant analysis was performed for a dataset excluding the Awashima

specimen and *P. asahinus* holotype, with “species” as the response variable and the four measurements as explanatory variables. Then, the species identities of the Awashima specimen and *P. asahinus* holotype were determined using the obtained function. To capture the results visually, scatterplots based on the first two canonical variates were created. All statistical analyses were performed in R v.3.4.3 (R Development Core Team 2017). Information on specimens and the raw data are in Appendix 1.

The male endophallus was everted and fully inflated by injecting toothpaste from the base of the aedeagus (Berlov 1992). For the female genitalia, muscles around the genitalia were dissolved using 5% potassium hydroxide, and the organs were cleaned and observed in pure water. The terminology of the male genitalia followed Sasakawa et al. (2020) and Sasakawa and Itô (2015). Both male and female genitalia were compared with photos of the organs of related species, which were taken during previous studies (Sasakawa and Itô 2015, 2017; Sasakawa et al. 2020).

Taxonomy

Pterostichus (Nialoe) asahinus Habu & Baba, 1960

Fig. 2

Pterostichus (Paralianoe) macrogenys asahinus: Habu and Baba (1960): 62 (original description), holotype ♀: “Mt. Dorokujin, Mts. Asahi, Niigata Pref.” [Miomote, Mt. Dôrokujinpô, Murakami-shi, Niigata Prefecture, Japan]; Habu and Baba (1972): 19.

Pterostichus (Paralianoe) asahinus: Habu (1977): 14 (part?).

Pterostichus macrogenys: Tanaka (1985): 114 (part?).

Pterostichus (Nialoe) asahinus: Bousquet (2017): 724.

Pterostichus (Nialoe) falcispinus: Sasakawa (2005): 75 (original description), holotype ♂: “Cave Ishikiri, Nakajo-Machi, N-Echigo” [Ishikiri Cave, Mt. Ishikiriyama, Haguro, Tainai-shi, Niigata Prefecture, Japan]; Bousquet (2017): 724; Sasakawa et al. (2020): 7. Syn. nov.

Specimen examined. 1♂, Miomote, alt. 276 m, on the right bank of Miomotegawa River, Murakami-shi, Niigata Prefecture, Japan (38.273211°N, 139.779922°E), 12.vi.–17.vii.2021, Hirotarô Itô leg., in the collection of HI.

Notes. Sasakawa et al. (2020) suggested that *P. asahinus* and *P. falcispinus* might be conspecific. However, this hypothesis remained untested because males from the type locality of *P. asahinus* have not been examined. The male specimen examined here was obtained from a valley southwest of Mt. Dôrokujinpô, which can virtually be regarded as the type locality (Fig. 1). The structures of the endophallus and right paramere of this specimen are identical to those of the eastern type of *P. falcispinus* in Sasakawa et al. (2020). Its body length is intermediate between that of the eastern and western types of *P. falcispinus* as follows: body length from mandible apices to elytral end (BLm) 16.32 mm, that from anterior margin of labrum (BLl) 14.72 mm, and

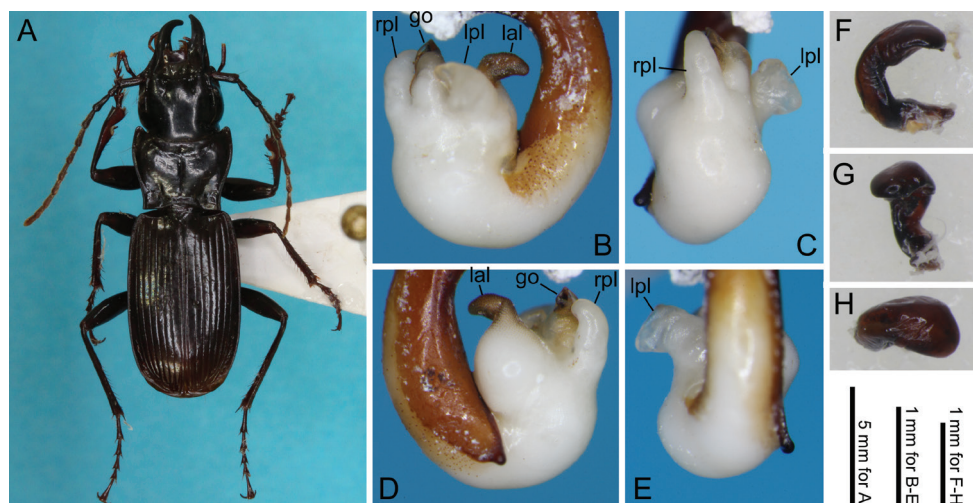


Figure 2. *Pterostichus asahinus* male from Miomote, on the right bank of the Miomotegawa River **A** habitus dorsal view **B–E** Endophallus left lateral (**B**) ventral (**C**) right lateral (**D**) and dorsal (**E**) views **F–H** right paramere left lateral (**F**) apical (**G**) and dorsal (**H**) views. **go**, gonopore; **lal**, left apical lobe; **lpl**, left preapical lobe; **rpl**, right preapical lobe.

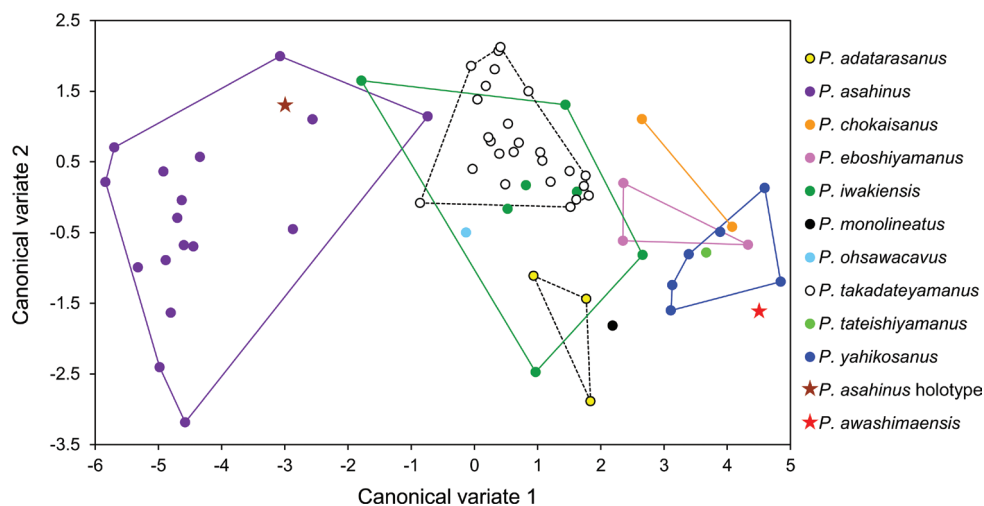


Figure 3. Scatterplot of the first two canonical variates obtained from the discriminant analysis of four measurements of the female pronotum.

that from clypeal apex (BLc) 14.26 mm. Based on these results, we regard *P. asahinus* and *P. falcispinus* as conspecific. The results of the discriminant analysis support this conclusion. The *P. asahinus* holotype was classified in this newly defined *P. asahinus* in the discriminant function analysis, and was within the area of *P. asahinus* on the scatterplot of the first two canonical variates (Fig. 3).

***Pterostichus (Nialoe) awashimaensis* Sasakawa & Itô, sp. nov.**

<http://zoobank.org/77C1F12B-3E95-4058-92B8-AA57D4F76D02>

Fig. 4

Pterostichus (Paralianoe) macrogenys macrogenys: Habu and Baba (1972): 19 (part).

Pterostichus macrogenys: Tanaka (1985): 114 (part?); Shimizu (2001): 23.

Type specimen. Holotype: ♀, Mt. Koshibayama, alt. 235 m, Awashima Island, Awashima-mura, Niigata Prefecture, Japan, 24.v.–14.vi.2015, Hirotarô Itô leg., deposited in the Laboratory of Zoology, Department of Science Education, Faculty of Education, Chiba University, Chiba, Japan.

Notes. In the discriminant function analysis, the Awashima specimen was classified as *P. yahikosanus*. On the scatterplots of the first two canonical variates, the specimen was located outside of, but close to, the area of *P. yahikosanus* (Fig. 3). These results suggest that the Awashima specimen is most similar in external morphology to, but different from, *P. yahikosanus*. Differences between the Awashima specimen and *P. yahikosanus* were also observed in other morphological features: the body length of the Awashima specimen (see below) is smaller than that of *P. yahikosanus* (n=6 from Mt. Yahikosan; BLm 15.32–14.35, mean 14.94 mm; BLl 14.22–13.46, mean 13.73 mm; BLc 13.64–12.89, mean 13.18 mm) (Fig. 4A, B); in the pronotum, anterior angles are barely produced, hind angles are obtuse, and posterior margin is arcuate posteriorly behind the laterobasal impressions in the Awashima specimen (Fig. 4C), whereas in *P. yahikosanus*, anterior angles are notably produced, hind angles are right-angled to acute, and the posterior margin behind the laterobasal impressions is almost straight (Fig. 4D); the body of the Awashima specimen is darker than that of *P. yahikosanus* (Fig. 4A–D); and pigmentation on the innermost part of vagina is smaller in the Awashima specimen, less than half the size of median and seminal apophyses (Fig. 4E), while it is larger than these apophyses in *P. yahikosanus* (Fig. 4F). In the *macrogenys* species group, pronotum shape and the pigmentation on the innermost part of vagina differ distinctly among species and are used as important species-level diagnostic characters (e.g., Sasakawa 2005; Sugimura 2005; Morita et al. 2013). Because these characters differ distinctly between the Awashima specimen and *P. yahikosanus*, we describe the Awashima specimen as a new species. Based on information on the morphological features of the pronotum and female genitalia in related species (Sasakawa et al. 2020 and references therein), notably produced pronotal anterior angles and developed vaginal pigmentation are limited to some species and considered to be derived character states in the *macrogenys* species group. Therefore, the Awashima species is considered more ancestral than *P. yahikosanus* with respect to the pronotal and genital features.

Description. BLm 13.79 mm; BLl 12.66 mm; BLc 12.13 mm. Head, pronotum, and elytra dark brown; appendages reddish brown. Dorsal surface almost smooth except for laterobasal impressions of the pronotum, the anterior half of which bear several transverse wrinkles and the posterior half of which are weakly punctate.

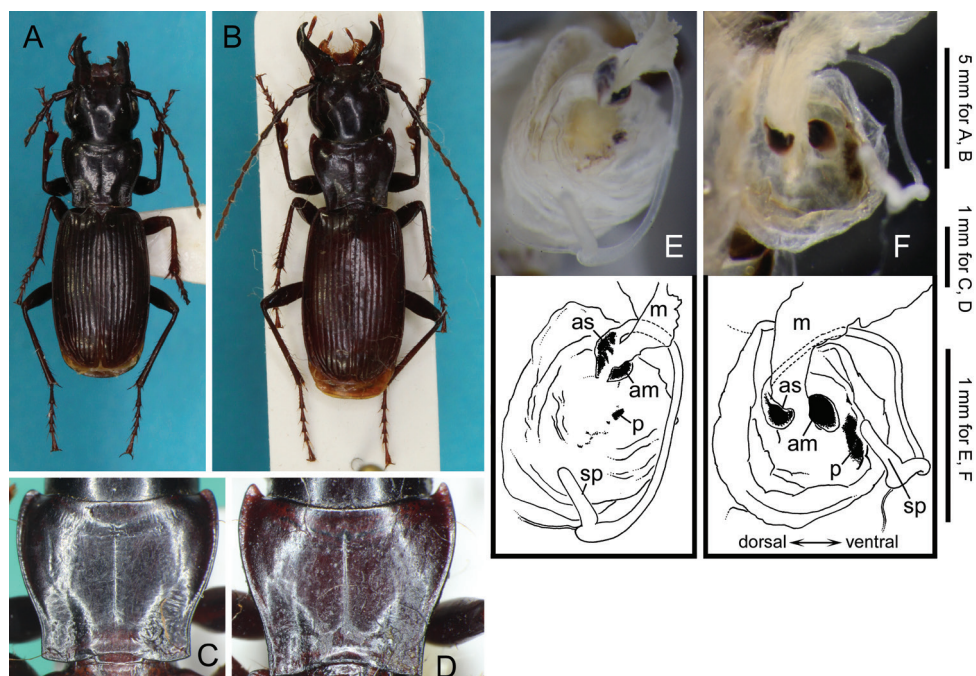


Figure 4. *Pterostichus awashimaensis* sp. nov. holotype female (**A, C, E**) and *P. yahikosanus* female from Mt. Yahikosan (**B, D, F**) **A, B** habitus dorsal view **C, D** pronotum dorsal view **E, F** vagina anterior view. **am**, apophysis of the median oviduct; **as**, apophysis of the seminal canal; **m**, median oviduct; **p**, pigmentation on the innermost part of the vagina; **sp**, spermatheca.

Head large, widest at tempora, which are distinctly swollen; width at the widest point larger than pronotal posterior margin width; length from clypeal apex to neck base longer than pronotum length along the median line. Left mandible larger than the right and curved at the apical 1/4; length between mandible apex and posterolateral end on dorsal side slightly shorter than 2.5 times the anterior width of the clypeus. Eyes weakly convex, with the anterior-posterior length longer than 1/2 length of antennal segment 1. Antennal segment 2 with two setae.

Pronotum cordate, notably flat, widest at apical 1/5. Lateral margins arcuate on apical 2/3, slightly sinuate on basal 1/3; two marginal setae on each lateral side, anterior setae near widest pronotal point, and posterior setae near hind angles. Anterior margin emarginated, with curvature approximately the same as that of apical 2/3 of lateral margins; anterior angles widely rounded and barely produced. Hind angles obtuse. Posterior margin only slightly emarginated at median area, weakly but distinctly arcuate posteriorly behind the laterobasal impressions. Median line impressed in the middle, not reaching either the anterior or posterior margins; laterobasal impressions single, shallow.

Elytra sides almost parallel, less convex; shoulder distinct, but not denticulate; apices rounded; scutellar stria present, connected to stria 1 on the right side but not on

the left; 1 setigerous puncture on stria 1 at the level of the posterior end of scutellum; two setigerous punctures on interval 3, anterior one slightly before the middle and posterior one on apical 1/5, both adjoining stria 2. Hind wings completely atrophied. First fore tarsomere no adhesive hairs on ventral side.

Female genital structures identical to those of other consubgenera; apophyses of seminal canal and median oviduct fully sclerotized; pigmentation on the innermost part of the vagina present, but less than half the size of apophyses of seminal canal and median oviduct; other parts of vagina lack conspicuous pigmentation.

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Appendix I

Table A1. Information on specimens examined and the raw data for discriminant analysis.

ID [†]	Species	Collection site [§]	PL	PAW	PW	PPW
mttk071	<i>adatarasanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.82	3.55	3.93	3.08
mttk073	<i>adatarasanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.85	3.64	4.16	2.97
mttk077	<i>adatarasanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.66	3.40	3.91	2.93
cHIT_0004	<i>asahinus</i>	Ishikiri Cave, Tainai-shi, NI	2.83	3.98	4.48	3.44
mttk028	<i>asahinus</i>	Kurosawagawa forest road, Mamurogawa-machi, YG	2.43	3.42	3.94	3.07
mttk079	<i>asahinus</i>	Togawa, Tozawa-mura, YG	2.45	3.42	3.87	2.92
mttk026	<i>asahinus</i>	Ôtori, Tsuruoka-shi, YG	2.60	3.88	4.35	3.23
mttk040	<i>asahinus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.9	4.20	4.72	3.67
mttk070	<i>asahinus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	3.08	4.25	4.83	3.87
mttk072	<i>asahinus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	3.35	4.56	5.20	4.00
mttk033	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.14	4.66	5.08	3.98
mttk055	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.08	4.73	5.13	3.96
mttk056	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	2.98	4.37	4.88	3.71
mttk057	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.10	4.46	4.92	3.90
mttk059	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	2.97	4.35	4.77	3.76
mttk060	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	2.82	4.16	4.65	3.56
mttk061	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.18	4.39	5.19	3.74
mttk062	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.23	5.06	5.43	4.04
mttk063	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.08	4.37	5.00	3.73
mttk064	<i>asahinus</i>	Nukumidaira, Oguni-machi, YG	3.05	4.67	5.04	3.85
mttk030	<i>chokaisanus</i>	Sakunami, Sendai-shi, MG	2.54	3.07	3.61	2.46
mttk080	<i>chokaisanus</i>	Mt. Chokaisan, Yuza-machi, YG	2.25	2.86	3.34	2.40
mttk052	<i>eboshiyamanus</i>	Yunosawa, Iide-machi, YG	2.47	3.02	3.43	2.47
mttk053	<i>eboshiyamanus</i>	Yunosawa, Iide-machi, YG	2.38	3.09	3.47	2.61
mttk054	<i>eboshiyamanus</i>	Yunosawa, Iide-machi, YG	2.63	3.47	3.81	2.83
cHIT_0002	<i>iwakienis</i>	Miyahisa, Tainai-shi, NI	2.53	3.37	3.82	2.84
cHIT_0005	<i>iwakienis</i>	Ishikiri Cave, Tainai-shi, NI	2.38	3.35	3.87	2.93
iwakienisPT [†]	<i>iwakienis</i>	Iritôno, Iwaki-shi, FS	2.95	3.60	4.29	3.07
mttk034	<i>iwakienis</i>	Nukumidaira, Oguni-machi, YG	2.43	3.04	3.65	2.73
mttk058	<i>iwakienis</i>	Nukumidaira, Oguni-machi, YG	2.31	3.06	3.53	2.57
mttk065	<i>iwakienis</i>	Nukumidaira, Oguni-machi, YG	2.60	3.36	3.90	2.75
mttk066	<i>iwakienis</i>	Nukumidaira, Oguni-machi, YG	2.61	3.32	3.75	2.74
mttk037	<i>monolineatus</i>	Aobaminami, Marumori-machi, MG	2.77	3.55	3.94	2.96
cHIT_0053	<i>ohsawacavus</i>	Ohsawa Cave, Gosen-shi, NI	2.79	3.98	4.22	3.26
cHIT_0017	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.37	3.06	3.53	2.64
cHIT_0018	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.52	3.39	3.84	2.79
cHIT_0019	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.60	3.57	4.01	2.88
cHIT_0020	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.59	3.57	3.99	2.98
cHIT_0021	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.56	3.57	3.96	2.93
cHIT_0022	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.60	3.48	3.86	2.86
cHIT_0023	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.34	3.09	3.51	2.69
cHIT_0024	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.80	3.93	4.19	3.02
cHIT_0025	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.63	3.53	4.07	3.05
cHIT_0026	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.31	3.20	3.64	2.69
cHIT_0027	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.60	3.57	4.01	2.92
cHIT_0028	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.50	3.44	3.87	2.87
cHIT_0029	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.46	3.42	3.87	2.83
cHIT_0030	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.40	3.24	3.65	2.78
cHIT_0031	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.61	3.50	3.90	2.82

ID [†]	Species	Collection site [§]	PL	PAW	PW	PPW
cHIT_0032	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.52	3.70	4.01	2.94
cHIT_0034	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.72	3.73	4.10	2.90
cHIT_0035	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.46	3.44	3.83	2.77
cHIT_0036	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.51	3.32	3.81	2.84
cHIT_0037	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.25	3.07	3.52	2.67
cHIT_0039	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.46	3.31	3.67	2.80
mttk041	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.67	3.59	3.99	2.88
mttk074	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.59	3.76	4.14	2.89
mttk075	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.50	3.60	3.99	2.82
mttk076	<i>takadateyamanus</i>	Mt. Takadateyama, Tsuruoka-shi, YG	2.55	3.59	3.95	2.90
tateishiyamanusPTf [‡]	<i>tateishiyamanus</i>	Kuratani-sawa, Nishiaizu-machi, FS	2.50	3.07	3.51	2.55
cHIT_0044	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.56	2.98	3.52	2.42
cHIT_0045	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.59	3.18	3.65	2.67
cHIT_0046	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.55	3.15	3.62	2.53
cHIT_0048	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.50	3.10	3.56	2.40
cHIT_0049	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.68	3.29	3.77	2.74
cHIT_0050	<i>yahikosanus</i>	Mt. Yahikosan, Nagaoka-shi, NI	2.62	3.29	3.73	2.66
asahinusHT [‡]	<i>asahinus</i>	Mt. Dōrokujinpō, Murakami-shi NI	2.51	3.51	4.14	3.10
awashima_F01 [‡]	<i>awashimaensis</i>	Awashima Island, Awashimaura-mura, NI	2.50	2.92	3.38	2.48

[†] cHIT_0002–39 and mttk026–77: specimens used in Sasakawa et al. (2020); cHIT_0044–53 in the collection of HI, mttk079–80 in the collection of Y. Mitsuduka (Yamagata), iwakiensisPT, tateishiyamanusPTf, and awashima_F01: specimens newly examined here.

[‡] Type specimens (paratype for *P. iwakiensis* and *P. tateishiyamanus*, and holotype for *P. asahinus* and *P. awashimaensis*).

[§] Prefecture abbreviations: FS, Fukushima Prefecture; MG, Miyagi Prefecture; NI, Niigata Prefecture; YG, Yamagata Prefecture.