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A morphology-based revision and phylogenetic analysis of the *Pterostichus macrogenys* species group (Coleoptera, Carabidae) and implications for differentiation of the species group

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Abstract

The *Pterostichus macrogenys* species group is an endemic subterranean Japanese carabid clade that provides intriguing material for studying morphological differentiation, speciation and interspecific relationships. However, its diversity remains not fully explored. We investigated specimens from northern Tohoku District, an area where knowledge of this species group is notably limited. Our research led to the description of three new species: *P. namahage* **sp. nov.**, *P. kamurosanus* **sp. nov.** and *P. atsumidakensis* **sp. nov.** We also updated distribution records for three known species: *P. asahinus* Habu & Baba, 1960; *P. kitakamisanus* Sasakawa, 2005; and *P. chokaisanus* Sasakawa, 2009. This report includes both the expanded distribution ranges of the known species and the discovery of a new sympatric species pair (*P. chokaisanus* and *P. asahinus*). We conducted a morphological phylogenetic analysis of all but one species, for which no male specimens were available, accounting for a total of 42 species within the group. The resulting phylogenetic tree implies that the initial differentiation of this species group originated on the Sea of Japan side, in the northern part of their current distribution, followed by dispersion to other areas and subsequent differentiation. Additionally, our findings indicate that sympatric species of varying body sizes are distantly related phylogenetically. These insights into the differentiation process align with regional distribution patterns of species-level diversity and sympatric sites.

Key Words

character evolution, cryptic species, endophallus, Japan, male genitalia, morphological phylogeny, *Nialoe*, sympatric occurrence, synapomorphy, taxonomy

Introduction

The *macrogenys* species group is an endemic subterranean Japanese carabid clade belonging to the *Pterostichus* subgenus *Nialoe* Tanaka, 1958 (s. lat. i.e. *Nialoe* sensu Sasakawa 2021). Members of this species group are medium to large (body length 12–20 mm) and characterised by a large head with long mandibles, a flattened body and relatively simple secondary sexual characteristics on the male last abdominal segment (Sasakawa 2009; Sasakawa et al. 2020). All species have atrophied hind wings, limiting their dispersal ability. Marked regional differentiation is recognised and about 40 species-group taxa with limited distributions are known in mountainous areas north of the Kinki District, Honshu. These species appear very similar externally and are mainly distinguished by the genital morphology of males. Sympatric occurrences, consistent with reproductive isolation, have been confirmed amongst some species and differences in body and/or male genital size are observed amongst species in sympatry (Sasakawa et al. 2020). Hence, the *macrogenys* species group is of interest for studying morphological differentiation, speciation and interspecific relationships.

On the other hand, several fundamental aspects regarding the diversity of this species group, crucial for comprehensive study, remain unresolved. One such aspect is the insufficient knowledge about species-level diversity in certain regions. Particularly since Sasakawa (2009), there have been no new species discoveries or new reports on the distribution of known species from the northern Tohoku District, located in the northern part of the group's range (Fig. 1). This situation contrasts with other areas, where new species and new distributions of known species are being reported (southern Tohoku District: e.g. Sasakawa and Itô (2017, 2022); Sato (2021); Kanto District: e.g. Morita et al. (2013); Sato et al. (2014); Ohkawa (2018); Chubu District: e.g. Morita and Ohkawa (2010); Toda (2012); Ito and Ogai (2015); Sasakawa and Inoue (2021)).

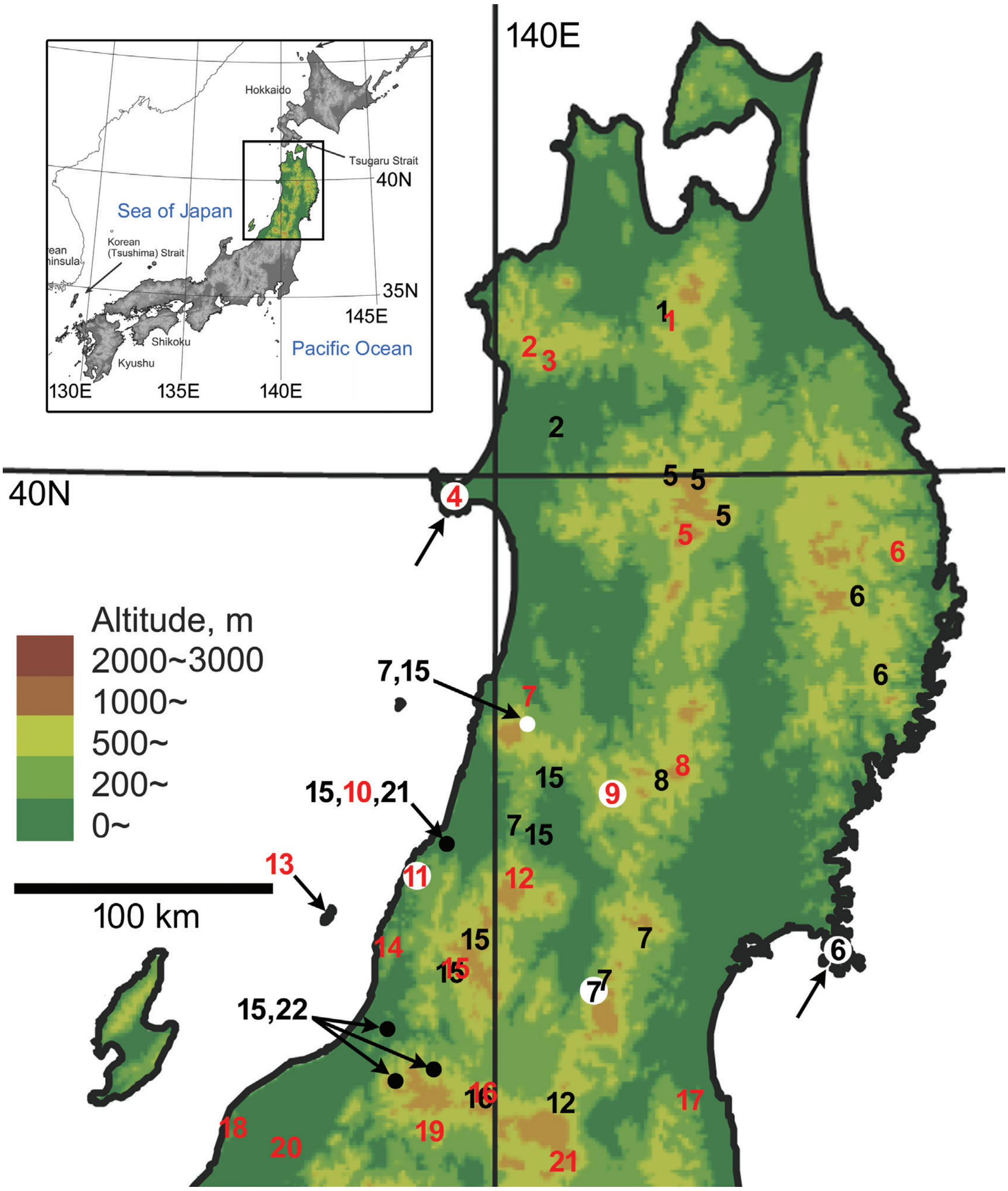

Figure 1. Distribution of the *macrogenys* species group in the Tohoku District and northern part of Niigata Prefecture (the Chubu District), based on collection sites of type specimens and specimens identified by the endophallus. 1. *Pterostichus orionis* Jedlička, 1962; 2. *P. shirakamisanus* Sasakawa, 2005; 3. *P. shirakamisan* Sasakawa, 2009; 4. *P. namahage* sp. nov.; 5. *P. tanakai* Ishida, 1964; 6. *P. kitakamisanus* Sasakawa, 2005; 7. *P. chokaisanus* Sasakawa, 2009; 8. *P. kurikomasanus* Sasakawa, 2005; 9. *P. kamurosanus* sp. nov.; 10. *P. takadateyamanus* Sasakawa, 2009; 11. *P. atsumidakensis* sp. nov.; 12. *P. gassanus* Sasakawa, 2009; 13. *P. awashimaensis* Sasakawa & Itô, 2022; 14. *P. shinbodakensis* Sasakawa & Itô, 2017; 15. *P. asahinus* Habu & Baba, 1960; 16. *P. eboshiyamanus* Sasakawa, 2009; 17. *P. monolineatus* Sasakawa, Mitsuduka & Itô, 2020; 18. *P. yahikosanus* Sasakawa, 2009; 19. *P. tateishiyamanus* Sasakawa & Itô, 2017; 20. *P. ohsawacavus* Sasakawa, 2005; 21. *P. adatarasanus* Sasakawa, 2005. Red letters denote the type localities of each species. White circles indicate where the specimens examined in this study were collected.

Another unresolved aspect involves the incomplete understanding of phylogenetic relationships amongst species. Within the subgenus *Nialoe* (s. lat.), which includes the *macrogenys* species group, phylogenetic relationships amongst species groups have been examined both morphologically (Sasakawa 2005a) and molecularly (Sasakawa and Kubota 2009). However, the phylogenetic understanding within each species group is only partial. To date, within-group phylogenetic relationships have been examined only for two species groups (the *asymmetricus* and *raptor* species groups; Sasakawa (2005b) and Sasakawa et al. (2017), respectively), based on morphological data. The inference of sister-species relationships, based on morphology, has also been examined in only a few species.

In this paper, we describe new species of the *macrogenys* species group and report updated distribution records of known species, based on specimens recently collected from the northern Tohoku District. As mentioned earlier, no reports on the species group have been published from this area since Sasakawa (2009). These findings serve to bridge a gap in our understanding of the species group's diversity and, although preliminary, allow for an analysis of the overall diversity of the species group for the first time. We, therefore, conducted a morphological phylogenetic analysis of nearly all members of the species group and evaluated the regional distribution of species-level diversity. We discuss these results in the context of the species group's differentiation process.

Materials and methods

Sample collection and comparative morphology

Of the specimens examined, one was hand-collected alive during a field survey and the others were collected using subterranean baited traps similar to those in Yoshida (2012). Silkworm pupa powder was used as an attractant. Saturated salt brine, which is suitable for preserving samples for taxonomic studies (Sasakawa 2007), was used as a preservative. For each collection site, the Military Grid Reference System (**MGRS**) and lat/log values are provided. Holotypes of the new species are deposited in the collection of the National Museum of Nature and Science, Tsukuba, Japan (**NSMT**). The other specimens are in the authors' collection.

Male specimens were primarily identified by the morphology of the endophallus, which was everted and fully inflated by injecting toothpaste from the base of the aedeagus. Females were identified by matching their external morphological features with those of identified males from the same collection site. Information on the morphology of related species was obtained from Sasakawa (2005c, 2009), Sasakawa and Itô (2017 and 2022), Sasakawa et al. (2020) and scaled photos of the *Pterostichus kitakamisanus* holotype male, which were taken during a study by Sasakawa (2005c).

The homology and terminology of the endophallus followed Sasakawa et al. (2020). Following Sasakawa et al. (2020), three body lengths were measured: those from the mandible apices (**BLm**), anterior margin of the labrum (**BLl**) and clypeal apex (**BLc**) to the elytral end. The Japanese names of some species reported here are given in of Suppl. material 1: table S1.

Morphological phylogeny and regional species-level diversity

Phylogenetic trees were constructed using maximum parsimony analysis with TNT version 1.6 (Goloboff and Morales 2023). All but one of the 42 members of the species group were included as the ingroup taxa. The exception was *P. awashimaensis* Sasakawa & Ito, 2022, for which no male specimens have been obtained to date. *Pterostichus* (*Nialoe*) *micropoides* Yin, Shi & Liang, 2021 was used as the outgroup taxon; this species is a member of the *opacipennis* species group (= *Koreonialoe* sensu Yin, Shi & Liang, 2021), which is thought to be the sister clade to the *macrogenys* species group. Twelve adult morphological characters (ten male genital, one female genital and one female external) were examined (Tables 1 and 2). The evaluation and coding of character states were based on morphological descriptions in this study, published literature and some unpublished data. Character states without available data were coded with "?". The analysis was performed with the following parameter settings: Analyze > "Traditional search"; Starting trees > "Wagner trees" with "random seed" = 1 and 100 replicates; Swapping algorithm > "tree bisection reconnection (TBR)" with 10 trees saved per replication; default parameter settings for all other factors. All characters were, thus, treated as "non-additive" (unordered as per PAUP*) and given equal weight. Bootstrap values were calculated using 'standard' and 'absolute frequencies' options with 1000 replicates.

Synapomorphies and autapomorphies were mapped on the strict consensus tree derived from the obtained trees, based on the list of these character state changes (found under Optimize > Synapomorphies > List common synapomorphies in the TNT output). Each synapomorphy was designated as "some trees" or "all trees" in the TNT output and they are here referred to as "possible" and "unambiguous" synapomorphies, respectively. In addition, maximum and minimum values of BLc, serving as an index of body size, which is considered to contribute to sympatric occurrence, were shown on the consensus tree for each species. For most species, the values of males were used, but in seven species, *P. akitai*, *P. koheii*, *P. momuranus*, *P. nagasawai*, *P. nakamiyorinus*, *P. omiensis* and *P. shojii*, the values of pooled male and female data were used due to the unavailability of sex-specific values. Maximum and minimum BLc values of male, female and pooled male and female of each taxon were given in of Suppl. material 1: table S2.

Table 1. Character evaluation and coding.

Character ID: Character: Evaluation and coding
1: Right paramere: (0) almost straight, short; (1) with apical part strongly bent ventrally; (2) with apical part strongly bent ventrally and large in size; (3) with apical part strongly bent ventrally, large in size, wide in dorsal view.
2: Basal half of aedeagus: (0) uniformly arcuate, rather than sharply bent; (1) sharply bent at aedeagal basal 1/3.
3: Apical half of aedeagus: (0) not swollen at ventral side of central part, with apical part wide and weakly protruding in dorsal view; (1) not swollen at ventral side of central part, with the apical part narrow and strongly protruding in dorsal view; (2) swollen at ventral side of central part, with apical part narrow and strongly protruding in dorsal view.
4: Left pigmented band: (0) not sclerotised; (1) weakly sclerotised; (2) strongly sclerotised.
5: Right pre-apical lobe: (0) not distinctly protruding, virtually absent; (1) small in size, conical or hemispherical in shape, directed dorsally or dorso-apically, with dorsal contour not continuous with that of connected part of endophallus; (2) large in size, cylindrical-shape, directed apically, with dorsal contour continuous with that of connected part of endophallus; (3) large in size, apically hooked cylindrical-shape, directed apically, with dorsal contour continuous with that of connected part of endophallus.
6: Basal part of left pre-apical lobe: (0) not protruding; (1) weakly protruding; (2) largely protruding.
7: Apical part of left preapical lobe: (0) simple, without protrusions; (1) with one protrusion directed apically; (2) bifidly protruding apically; (3) largely protruding laterally, with the apex bifurcated or T-shaped.
8: Middle part of left apical lobe: (0) almost straight, not bent; (1) uniformly bent, not forming a corner outwards of bending part; (2) sharply bent, forming a distinct corner outwards of bending part.
9: Apical part of left apical lobe: (0) simple, not bifurcated; (1) bifurcated, with two apices different in size; (2) bifurcated, with two apices same size.
10: Surface of left apical lobe: (0) not sclerotised; (1) weakly sclerotised; (2) strongly sclerotised.
11: Vaginal pigmentation: (0) absent; (1) present.
12: Adhesive hairs on female tarsal segment 1: (0) absent; (1) present.

Table 2. Character matrix for phylogenetic analysis.

Taxon	Characters[†]	Source
P. adatarasanus	`000210000?0`0	Sasakawa (2005c); Sasakawa et al. (2020)
P. akitai	012?????????	Morita (2004)
P. asahinus	300a30310200	Sasakawa (2005c)[‡]; Sasakawa et al. (2020)[‡]
P. atsumidakensis	100130110100	this study
P. chokaisanus	000a121220?0	Sasakawa (2009); Sasakawa et al. (2020); this study
P. eboshiyamanus	000210001 0?0	Sasakawa (2009); Sasakawa et al. (2020)
P. fukube	012?????????	Sugimura (2005)
P. gassanus	000210211 0?1	Sasakawa (2009); Sasakawa et al. (2020); Itô, unpublished data (character 12)
P. gujoensis	012?????????	Toda (2012)
P. isolatus	0110000000??	Sasakawa (2005c); Morita et al. (2013)
P. iwakiensis	000110200000	Sasakawa (2009); Sasakawa et al. (2020)
P. kamurosanus	000110100010	this study
P. kitakamisanus	000a10200010	Sasakawa (2005c); this study
P. koheii	0020100020?0	Sasakawa (2005c); Morita and Hirasawa (1996)
P. kuraiyamanus	012?10???0??	Morita and Ohkawa (2010)
P. kurikomasanus	000210000010	Sasakawa (2005c); Sasakawa et al. (2020)
P. macrogenys	000212210011	Sasakawa (2005c); Sasakawa and Itô (2018)
P. miyazawai	012?003100??	Morita and Ohkawa (2009)
P. momuranus	01200????0??	Morita et al. (2013)
P. monolineatus	0002100000?0	Sasakawa et al. (2020)
P. nagasawai	002??????0??	Ito and Ogai (2015)
P. nakamiyorinus	01100????0??	Morita et al. (2013)
P. namahage	0002010200??	this study
P. ohosawacavus	0000102100?0	Sasakawa (2005c); Sasakawa and Itô, unpublished data (character 12)
P. omiensis	0120????????	Sekine and Nakase (2022)
P. orionis	000110100000	Sasakawa (2005c)
P. shikatai	012?????????	Toda (2012)
P. shinbodakensis	2002303102??	Sasakawa and Itô (2017)
P. shirakamisan	000110111000	Sasakawa (2009)
P. shirakamisanus	000110100010	Sasakawa (2005c)
P. shojii	012?????????	Sugimura (2006)
P. sumondakensis	000210210011	Sasakawa (2005c)
P. takadateyamanus	100120110100	Sasakawa (2009); Sasakawa and Itô (2015); Sasakawa et al. (2020)
P. tanakai	000110100010	Sasakawa (2005c)
P. tateishiyamanus	0001102220?0	Sasakawa and Itô (2017)
P. todai todai	0110???????0	Morita and Kanie (1997); Sugimura (2002)
P. todai toyoshimai	012?????????	Sugimura (2002)
P. toyodai	012????????0	Morita and Kurosa (1998)

Taxon	Characters[†]	Source
P. uedaorum	012????????0	Morita and Hirasawa (1996)
P. yahikosanus	000210100010	Sasakawa (2009); Sasakawa and Itô (2015)
P. yamizosanus	000110200010	Sasakawa (2005c)
P. yorikoae	0120???????0	Sugimura (2007)
P. micropoides	00000010000?	Yin et al. (2021)

[†] a: polymorphic character state, 1 and 2, which is coded as "(12)" in date for TNT.

[‡] as *P. falcispinus* Sasakawa, 2005.

Regional species-level diversity was assessed by the number of species per Prefecture. This was achieved by compiling collection records from published literature and one unpublished data source.

Results

New species descriptions

Three species described here are similar and share the following adult morphology:

Dorsal habitus. Medium-sized (ca. 13–17 mm) macrocephalic species. Surface glossy, not opaque; head reddish-black; pronotum and elytra reddish-brown, with pronotum darker; appendages dark brown to reddish-brown.

Head. Large, widest at tempora. Mandibles long, hooked at apex, left mandible larger and more hooked than right. Frontal grooves shallow. Tempora strongly swollen, widest part wider than pronotal posterior margin, anterior–posterior length more or less longer than anterior–posterior length of eye. Surfaces of labrum, frons and tempora smooth. Antennal segment 1 with one seta; segment 2 with one or more setae; segment 3 with apical ring of six or seven setae; pubescence absent on segments 1–3, but present on other segments. Eyes weakly convex, with anterior–posterior length exceeding half-length of antennal segment 1. Mentum with pair of medial setae and pair of longitudinal depressions; mentum tooth bifid; submentum with two setae on each side.

Pronotum. Cordate-shaped, widest slightly behind apical 1/5. Anterior angles produced, with widely rounded apices. Hind angles with apices narrowly rounded, not denticulate. Posterior margin more or less emarginated medially and arcuate laterally. Median line distinctly impressed in middle area. Laterobasal impression single each side, shallow, as both impressions connected by transverse grooved area. Anterior marginal setae at widest pronotal point; posterior marginal setae near hind angles.

Elytra. Almost parallel-sided, less convex. Basal margin at interval 3–5 concave; shoulders distinct, not denticulate. Apices rounded. Basal transverse line connecting anterior ends of elytral intervals distinct; scutellar-stria present; striae distinct; intervals less convex. One setigerous puncture on stria 1 at level of posterior end of scutellum. Two setigerous punctures on interval 3, anterior one slightly in front of middle, posterior one between posterior almost 1/4 to posterior 1/5, both adjoining stria 2. Hind wings completely atrophied.

Abdominal ventral sides. Sterna 4–6 with pair of setae; sternum 7 with pair of setae in male, two pairs of setae in female. Sternum 7 of male more or less concave, forming secondary sexual characteristic.

Legs. Ventral side of first tarsomere of female forelegs without adhesive hairs in species for which female specimens were available for examination. Fifth tarsomere of hind legs without setae on the ventral side.

Male genitalia. Aedeagus stout, bent at basal 1/3, without tubercles. Endophallus short, stout, strongly bent ventrally. Left paramere subquadrate.

Female genitalia. Vagina almost spherical. Apophyses of seminal canal and median oviduct fully sclerotised.

***Pterostichus* (*Nialoe*) *namahage* Sasakawa & Mitsuduka, sp. nov.**

https://zoobank.org/589C7C23-CC4B-4DC7-B92A-473A42F766B3

Figs 2A, 4A–D, 6A

Type material. ***Holotype***, ♂, Haraikawa, Honzanmonzen, Funagawaminato, Oga-shi, Akita Prefecture, Japan (MGRS: 54SUK92241 16384; 39.89067718°N, 139.73961047°E), 28. v–30. vi. 2022, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2A).

Description. ***Body length* (*mm*).** ♂ (n = 1), BLm 13.15, BLl 12.32, BLc 11.96.

Head. Mandibular surface with several short wrinkles at middle. Anterior–posterior length of tempora slightly longer than anterior–posterior length of eye. Surface of clypeus smooth. Antennal segment 2 with two setae. Mentum tooth shallowly bifid; width between paired apices three times anterior–posterior length between level of mentum apices to level of innermost part of median notch.

Pronotum. Lateral margin arcuate on apical 4/5, only slightly sinuate on basal 1/5. Anterior margin emarginated, with contour arched more strongly than curvature of apical 4/5 of lateral margin. Posterior margin slightly emarginated at median area and slightly arcuate at lateral areas, with curvatures of both the same as curvature of basal 1/5 of lateral margin. Hind angles slightly acute. Median line absent near anterior margin and in front of transverse grooved area between laterobasal impressions. Transverse grooved area between laterobasal impressions concave to same degree as laterobasal impressions. Surface including laterobasal impressions smooth.

Elytra. Scutellar-stria not connected to stria 1. One setigerous puncture in front of level of posterior end of scutellum. Posterior setigerous punctures on interval 3 slightly in front of posterior 1/4.

Abdominal ventral sides. Sternum 7 of male moderately concave, with degree of concavity greater than that

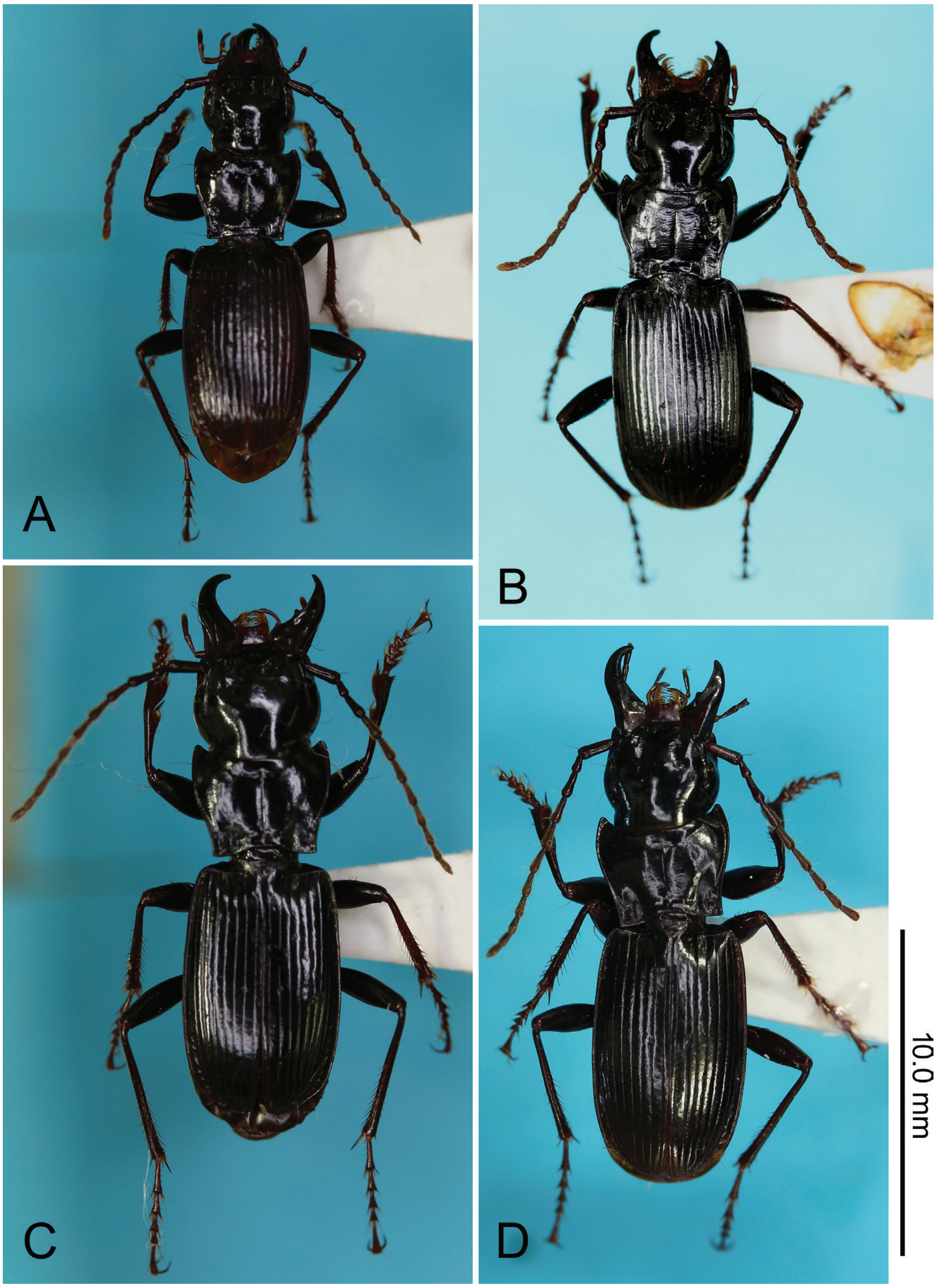

Figure 2. Habitus dorsal view of the *macrogenys* species group. **A**. *Pterostichus namahage* sp. nov. holotype male from Haraikawa; **B**. *P. kamurosanus* sp. nov. holotype male from Ariya; **C**. *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi; **D**. *P. asahinus* male from Momoyake.

of convexity of median area of sterna; shape of concave area transverse ellipse; posterior margin of ellipse corresponding to posterior margin of sternum; anterior–posterior length of concave area slightly longer than 1/2 anterior–posterior length of sternum 7; transverse, major axis of ellipse about 1.4 times that of longitudinal minor axis; area corresponding to minor axis of ellipse posterior to major axis slightly raised.

Male genitalia. Endophallus with gonopore directed basal-ventrally; left pigmented band weakly sclerotised; distinct right preapical lobe absent, but corresponding area slightly swollen; left preapical lobe with basal part protruding left-laterally; left apical lobe short, not bent, bifurcated (Fig. 4A–D). Relative sizes of lobes: right apex of bifurcated left apical lobe apex ≈ basal protrusion of left preapical lobe >> left apex of bifurcated left apical lobe apex. Right paramere short, straight, with apex rounded (Fig. 6A).

Female. Unknown.

Etymology. The specific name is a noun in apposition and derives from Namahage, which is a famous folk event held on the Oga Peninsula, where the type specimen was collected.

***Pterostichus* (*Nialoe*) *kamurosanus* Sasakawa & Mitsuduka, sp. nov.**

https://zoobank.org/EC64C14A-C5A7-4161-BA26-77958C62BD19

Figs 2B, 4E–H, 6B, 7A, B

Type materials. ***Holotype***, ♂, Ariya, alt. 403 m, Kaneyama-machi, Yamagata Prefecture, Japan (MGRS: 54SVJ49358 06377; 38.90482277°N, 140.41594335°E), 18. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2B). ***Paratypes***, 4♀, same data as the holotype; 2♂2♀, Kamuro Forest Road, alt. 416 m, Ariya, Kaneyama-machi, Yamagata Prefecture, subterranean baited trap, Y. Mitsuduka leg. (1♂, 15–29. ix. 2015; 1♂2♀, 5. vii–21. viii. 2017).

Description. ***Body length* (*mm*).** ♂ (n = 3), BLm 14.46–15.97, 15.19 ± 0.64, BLl 13.15–14.43, 13.84 ± 0.54, BLc 12.70–13.95, 13.37 ± 0.52; ♀ (n = 6), BLm 14.19–15.08, 14.58 ± 0.46, BLl 13.10–13.63, 13.34 ± 0.27, BLc 12.60–13.21, 12.89 ± 0.31.

***Head*.** Mandibular surface wrinkled with individual variation: short rudimentary wrinkles on both lateral sides, wrinkles on one lateral side, no wrinkles on either lateral side. Anterior–posterior length of tempora 1.7–1.8 times anterior–posterior length of eye. Surface of clypeus smooth in females, but irregular and slightly uneven in males. Antennal segment 2 with one or two setae, varying individually. Mentum tooth deeply bifid; width between paired apices apparently less than three times anterior–posterior length between level of mentum apices to level of innermost part of median notch.

***Pronotum*.** Lateral margin arcuate for apical 3/4, only slightly sinuate for basal 1/4; anterior margin emarginated, with contour arched more strongly than curvature of apical 3/4 of lateral margin; posterior margin emarginated at median area and arcuate at lateral areas, with curvature of median area distinctively greater than that of basal 1/4 of pronotal lateral margin and that of lateral areas same or only slightly greater than basal 1/4 of pronotal lateral margin; hind angles right-angled to slightly acute. Median line disappearing near pronotal anterior margin; in holotype male, posterior end disappears in front of transverse grooved area between laterobasal impressions, while in paratype female, posterior end reached pronotal posterior end. Transverse grooved area between laterobasal impressions concave to same degree as laterobasal impressions. Surface including laterobasal impressions smooth in most specimens; in some specimens, several punctations sparsely present near posterior ends of laterobasal impressions.

***Elytra*.** Scutellar-stria connected smoothly to stria 1 in most specimens; in some specimens, scutellar-stria disappears before connecting with stria 1, but its hypothetical extension smoothly connects to stria 1. One setigerous puncture on stria 1 at level of posterior end of scutellum. Posterior setigerous punctures on interval 3 at posterior 1/5–1/4.

***Abdominal ventral sides*.** Sternum 7 of male very shallowly concave, with degree of concavity matching that of median area of sterna; shape of concavity transverse ellipse, but indistinct due to shallowness; posterior margin of ellipse aligns with sternum posterior margin; anterior–posterior length of concavity about 0.6 times anterior–posterior length of sternum 7; transverse, major axis of ellipse about 1.5 times that of longitudinal minor axis; area corresponding to minor axis very weakly raised, except near anterior and posterior ends.

***Male genitalia*.** Endophallus with gonopore directed basal-ventrally; left pigmented band weakly sclerotised; right pre-apical lobe indistinct, only weakly swollen; left pre-apical lobe protrudes apically at apical part; left apical lobe short, not bifurcated (Fig. 4E–H). Relative sizes of lobes: apical protrusion of left preapical lobe > left apical lobe apex >> right pre-apical lobe. Right paramere short, straight, with rounded apex (Fig. 6B).

***Female genitalia*.** Innermost part of vagina with pigmentation (Fig. 7A, B).

Etymology. The specific name is an adjective, derived from the Japanese noun Kamurosan, which refers to Mt. Kamuro, where the type specimens were collected and the Latin adjectival suffix -*anus* (m), which means, when attached to a noun, "pertaining to".

***Pterostichus* (*Nialoe*) *atsumidakensis* Sasakawa & Mitsuduka, sp. nov.**

https://zoobank.org/76E0733E-1D9A-472E-BBFC-6BEFAD64DBD2

Figs 2C, 4I–L, 6C–E, 7C, D

Type material. ***Holotype***, ♂, Take-no-koshi, Yuatsumi, Tsuruoka-shi, Yamagata Prefecture, Japan (MGRS: 54SUH79821 75877; 38.62327968°N, 139.61944580°E), 2–24. vi. 2022, subterranean baited trap, Y. Mitsuduka leg., in the collection of NSMT (Fig. 2C). ***Paratype***, 1♀, same data as the holotype.

Description. ***Body length* (*mm*).** ♂ (n = 1), BLm 16.54, BLl 14.91, BLc 14.36; ♀ (n = 1), BLm mm, BLl 14.62, BLc 14.09.

***Head*.** Mandibular surface smooth, except for right mandible of the paratype female, which has several short wrinkles at middle. Anterior–posterior length of tempora about twice anterior–posterior length of eye. Surface of clypeus irregularly uneven. Antennal segment 2 with four setae in the holotype male, with one seta on left and two on right in the paratype female. Mentum tooth deeply bifid; width between paired apices apparently less than three times anterior–posterior length between level of mentum apices to level of innermost part of median notch.

***Pronotum*.** Lateral margin arcuate on apical 3/4, only slightly sinuate on basal 1/4. Anterior margin emarginated, with contour arched more strongly than curvature of apical 3/4 of lateral margin. Posterior margin emarginated at median area and arcuate at lateral areas, with curvature of median area distinctly greater than that of basal 1/4 of pronotal lateral margin and with that of lateral areas to same degree or slightly stronger than basal 1/4 of pronotal lateral margin. Hind angles right-angled to slightly acute. Median line absent near pronotal anterior margin and in front of transverse grooved area between laterobasal impressions. Concavity of transverse grooved area between laterobasal impressions weaker than that of laterobasal impressions. Surface smooth, except for laterobasal impressions; laterobasal impressions sparsely punctate.

Elytra. Scutellar-stria not connected to stria 1. One setigerous puncture on stria 1 at level of posterior end of scutellum in the holotype male, slightly in front of posterior end in the paratype female. Posterior setigerous punctures in front of posterior 1/4.

Abdominal ventral sides. Sternum 7 of male fairly concave, with degree of concavity obviously greater than the convexity of median area of sterna; shape of concavity transverse ellipse; posterior margin of ellipse corresponding to posterior margin of sternum; anterior–posterior length of concavity 0.7 times anterior–posterior length of sternum 7; transverse, major axis of ellipse about 1.7 times that of longitudinal minor axis; middle of minor axis slightly raised for half the length of minor axis.

Male genitalia. Endophallus with gonopore directed basally; left pigmented band slightly sclerotised; right pre-apical lobe short, stout, hooked at apex; left pre-apical lobe small, protruding left laterally; left apical lobe slender, slightly bent, with weakly sclerotized surface (Fig. 4I–L). Relative sizes of lobes: right pre-apical lobe > left apical lobe; and right pre-apical lobe > left pre-apical lobe (size difference between left apical and pre-apical lobes could not be determined unambiguously because of shape difference). Right paramere bent at acute angle at apical 1/3 (Fig. 6C–E).

Female genitalia. Innermost part of vagina without pigmentations (Fig. 7C, D).

Etymology. The specific name is an adjective and derives from the Japanese noun Atsumidake, which refers to Mt. Atsumi, where the type specimens were collected and the Latin adjectival suffix *-ensis* (m), which means, when attached to a locality name, "from the locality".

New distribution records

***Pterostichus* (*Nialoe*) *asahinus* Habu & Baba, 1960**

Figs 2D, 4M–P, 6F–H

Materials examined. 1♂, Momoyake, alt. 1030 m, Yurihonjô-shi, Akita Prefecture, Japan (MGRS: 54SVJ26680 29227; 39.1091115°N, 140.15197046°E), 24. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg.

Notes. The body lengths (mm) of the specimen are BLm 16.38, BLl 14.60 and BLc 14.06. This specimen was collected together with *P. chokaisanus*, which is to be recorded below. This is the first report of the sympatric occurrence of this species pair and provides evidence that they are reproductively isolated distinct species. Although the comparison was based on a single male for each species, a body-size difference was observed between the two species, with *P. asahinus* larger than *P. chokaisanus*. This collection record is the northernmost distribution record of the species and the first record for Akita Prefecture.

***Pterostichus* (*Nialoe*) *chokaisanus* Sasakawa, 2009**

Figs 3A, B, 5A–H, 6I, J

Materials examined. 1♂2♀, Momoyake, alt. 1030 m, Yurihonjo-shi, Akita Prefecture, Japan (MGRS: 54SVJ26680 29227; 39.1091115°N, 140.15197046°E), 24. vi–15. vii. 2021, subterranean baited trap, Y. Mitsuduka leg. (Figs 3A, 5A–D, 6I); 1♂, Zaô-chûô-kôgen, Zaô-onsen Spa, Yamagata-shi, Yamagata Prefecture, Japan (MGRS: 54SVH49227 23449; 38.15750459°N, 140.42046179°E), 1–6. ix. 2020, subterranean baited trap, Y. Mitsuduka leg. (Figs 3B, 5E–H, 6J).

Notes. The endophallus of the Zaô-chûô-kôgen specimen could not be inflated sufficiently due to changes in the membranous part (Fig. 5E–H), but the specimen was identified unambiguously as *P. chokaisanus*, based on species-specific structures of the endophallus. The body lengths (mm) of the Momoyake specimens (♂/♀/♀) are BLm 14.91/14.24/14.94, BLl 13.65/13.08/13.68 and BLc 13.18/12.56/13.21; and those of the Zaô specimen are BLm 14.20, BLl 12.83 and BLc 12.40. The Zaô-chûô-kôgen specimen is the southernmost distribution record of this species.

***Pterostichus* (*Nialoe*) *kitakamisanus* Sasakawa, 2005**

Figs 3C, D, 5I–N, 6K–M

Material examined. 1♂, Ôdateminami, Ayukawahama, Ishinomaki-shi, Miyagi Prefecture, Japan (MGRS: 54SWH45274 40885; 38.31492752°N, 141.51788663°E), 28. vii. 2022, hand-collected from soil, Y. Mitsuduka leg (Figs 3C, 5I–L, 6K, L).

Notes. The identification was based on comparison with the *P. kitakamisanus* holotype male, which is labelled "JAPAN; Iwate-ken/Miyako-shi/Genbeidaira/ 30.VIII–10.IX. 2002/Y. Kawahara leg" (Figs 3D, 5M, N, 6M). Although the apex of the left pre-apical lobe was not confirmed to be the same structure as that of the holotype due to failure to evert it, all other structures of the endophallus, parameres and external morphology were identical to those of the holotype. In particular, the left pre-apical lobe directed left laterally is a character state found only in *P. kitakamisanus* amongst the known taxa of the *macrogenys* species group and provides definitive evidence for our species identification. The body lengths (mm) of the specimen are BLm 15.11, BLl 14.13 and BLc 13.63. This collection record is the southernmost record of the species. Judging from its known collection sites, *P. kitakamisanus* is likely distributed widely in the Kitakami Mountains.

Morphological phylogeny

Eighty most-parsimonious trees with a score of 40 were obtained. The strict consensus tree had many unresolved nodes with low bootstrap values, but some relationships were still recognised (Fig. 8). The species

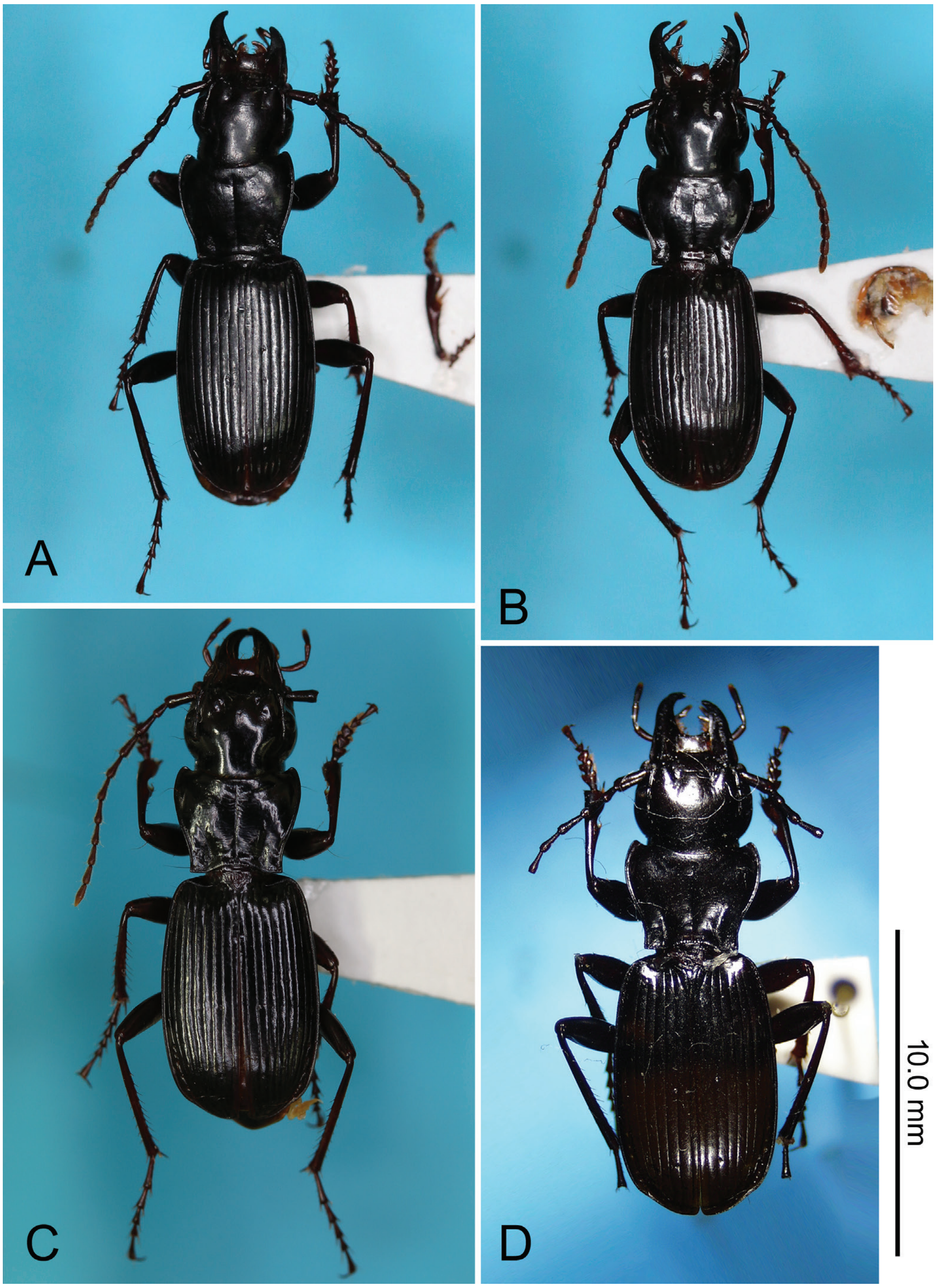

Figure 3. Habitus dorsal view of the *macrogenys* species group. **A**. *Pterostichus chokaisanus* male from Momoyake; **B**. *P. chokaisanus* male from Zaô-chûô-kôgen; **C**. *P. kitakamisanus* male from Ôdateminami; **D**. *P. kitakamisanus* holotype male from Genbeidaira.

P. takadateyamanus, *P. atsumidakensis*, *P. shinbodakensis* and *P. asahinus* formed a clade, supported by three possible synapomorphies. Within this clade, *P. shinbodakensis* and *P. asahinus* were sister taxa, supported by one unambiguous and one possible synapomorphy. A polytomy was formed by *P. shinbodakensis* + *P. asahinus*, *P. atsumidakensis* and *P. takadateyamanus*. *Pterostichus chokaisanus* and *P. tateishiyamanus* were sister taxa, supported by one unambiguous and one possible synapomorphy.

Pterostichus ohsawacavus, *P. sumondakensis*, *P. gassanus* and *P. macrogenys* formed another clade, supported by two possible synapomorphies. Within this clade, *P. sumondakensis*, *P. gassanus* and *P. macrogenys* formed a polytomic clade, supported by one unambiguous synapomorphy and was sister to *P. ohsawacavus*.

Eighteen taxa, including *P. nagasawai*, *P. koheii*, *P. isolatus*, *P. nakamiyorinus*, *P. todai todai*, *P. momuranus*, *P. omiensis*, *P. shikatai*, *P. shojii*, *P. todai toyoshimai*, *P. miyazawai*, *P. toyodai*, *P. uedaorum*, *P. kuraiyamanus*, *P. gujoensis*, *P. fukube*, *P. yorikoae* and *P. akitai*, formed a clade, supported by one unambiguous and two possible synapomorphies. Within this clade, 16

Figure 4. Endophallus of *Pterostichus namahage* sp. nov. holotype male from Haraikawa (**A–D**), *P. kamurosanus* sp. nov. holotype male from Ariya (**E–H**), *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi (**I–L**) and *P. asahinus* male from Momoyake (**M–P**). Fully inflated endophallus in left lateral (**A, E, I, M**), apical (**B, F, J, N**), right lateral (**C, G, K, O**) and basal part in dorsal and apical part in ventral (**D, H, L, P**) views. Abbreviations: go – gonopore; lal – left apical lobe; lpb – left pigmented band; lpl – left pre-apical lobe; rpl – right pre-apical lobe.

species, except for *P. nagasawai* and *P. koheii*, formed a clade supported by one unambiguous synapomorphy, with *P. isolatus*, *P. nakamiyorinus* and *P. todai todai* forming another clade supported by one unambiguous synapomorphy.

Regional species-level diversity

The highest number of species, totalling nine, was observed in Yamagata and Niigata Prefectures, followed by six in Akita, Nagano and Gifu Prefectures. There were

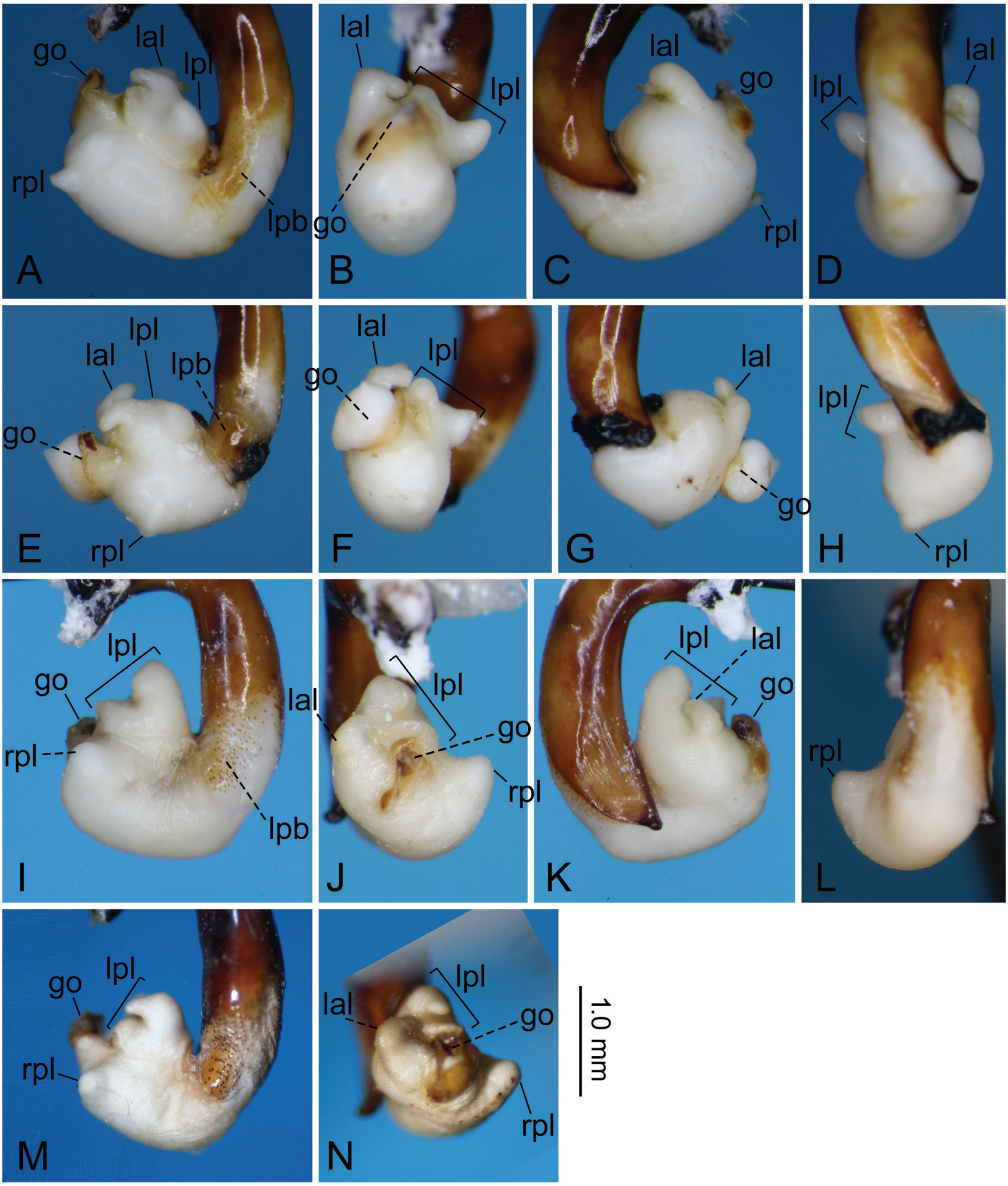

Figure 5. Endophallus of *Pterostichus chokaisanus* male from Momoyake (**A–D**), *P. chokaisanus* male from Zaô-chûô-kôgen (**E–H**), *P. kitakamisanus* male from Ôdateminami (**I–L**) and *P. kitakamisanus* holotype male from Genbeidaira (**M, N**). Fully inflated endophallus in left lateral (**A, E, I, M**), apical (**B, F, J, N**), right lateral (**C, G, K**) and basal part in dorsal and apical part in ventral (**D, H, L**) views.

four in Fukushima and Tochigi Prefectures, three in Miyagi Prefecture and one or two in the remaining Prefectures. Overall, there were more species on the Sea of Japan side than on the Pacific side and the central part had a higher number of species than the northern and southern regions of the distribution (Fig. 9).

Discussion

We describe three new species and report new distribution records for three known species, thereby updating their distribution ranges and documenting a new sympatric species pair. Together with the first morphological

Figure 6. Right paramere of *Pterostichus namahage* sp. nov. holotype male from Haraikawa (**A**), *P. kamurosanus* sp. nov. holotype male from Ariya (**B**), *P. atsumidakensis* sp. nov. holotype male from Take-no-koshi (**C–E**), *P. asahinus* male from Momoyake (**F–H**), *P. chokaisanus* male from Momoyake (**I**), *P. chokaisanus* male from Zaô-chûô-kôgen (**J**), *P. kitakamisanus* male from Ôdateminami (**K, L**) and *P. kitakamisanus* holotype male from Genbeidaira (**M**). Left lateral (**A–C, F, I–K**), right lateral (**L, M**), apical part in apical and basal part in ventral (**D, G**) and apical part in dorsal (**E, H**) views.

phylogenetic analysis performed in this study, these findings provide important insights into the diversification process of this species group.

Despite many unresolved nodes in the resultant strict consensus tree, several notable species relationships were unveiled. For instance, in the two clades—one consisting of *P. takadateyamanus*, *P. atsumidakensis*, *P. shinbodakensis* and *P. asahinus* and the other comprising *P. ohsawacavus*, *P. sumondakensis*, *P. gassanus* and *P. macrogenys*—the basal clade species (*P. takadateyamanus* and *P. atsumidakensis* in the former and *P. ohsawacavus* in the latter) exhibited fewer apomorphic traits and were localised to a narrow area on the Sea of Japan side. Conversely, species with more apomorphic traits had a wider distribution across various mountains. This pattern implies that initial differentiation of these clades occurred on the Sea of Japan side, followed by dispersal to other regions and geographical differentiation. A similar pattern was observed in the clade composed of western 18 species, although at the supraspecific level rather than at species level. Members of this clade are allopatrically distributed over a wide area to the west of the species group's distribution. Considering that the two species of the basal clades—*P. nagasawai* and *P. koheii*—are distributed more towards the east than most other members of the clade, it is assumed that this clade of 18 species dispersed from the east and subsequently differentiated.

Our assumptions regarding the differentiation and dispersal processes of these three clades align with the overall distribution patterns of the species group. Higher species diversity was observed on the Sea of Japan side than on the Pacific side and the highest diversity was in the central part of the distribution on the Sea of Japan side. Even though prefectural boundaries do not necessarily align with geographical barriers (such as mountain ranges or rivers) and are thus artificial, the spatial distribution of species diversity would not significantly change the observed distribution pattern. Interpreting the number of species in Nagano and Gifu Prefectures requires caution. This is because some species pairs that are close in distribution and very similar in morphology have not had their endophallus structure compared—a procedure that is critical for confirming their status as distinct species. Therefore, the actual number of species in these two Prefectures might be less than currently recognised. Considering the species' phylogeny, character evolution and distribution of diversity, it appears the *macrogenys* species group initially differentiated on the Sea of Japan

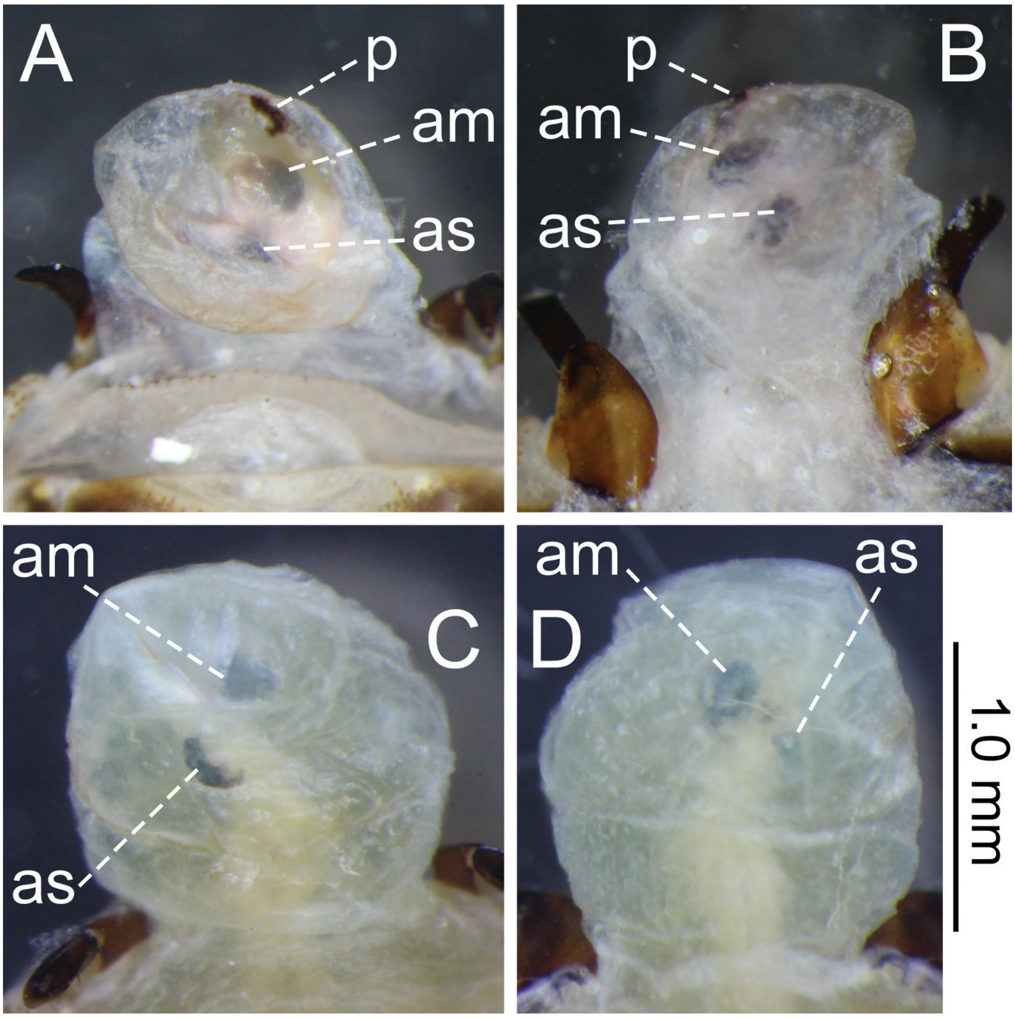

Figure 7. Genital membranous part of a *Pterostichus kamurosanus* sp. nov. paratype female from Ariya (**A, B**) and the *P. atsumidakensis* sp. nov. paratype female from Take-no-koshi (**C, D**). Dorsal (**A, C**) and ventral (**B, D**) views in everted condition of the vagina. Abbreviations: am – apophysis of the median oviduct; as – apophysis of the seminal canal; p – pigmentation on the innermost part of the vagina. Note that the two apophyses (am and as) are viewed through the membranous vagina.

side, likely near Yamagata and Niigata prefectures and, subsequently, dispersed and diverged in other areas. This hypothesis aligns with the fact that most species in the basal clades of the *opacipennis* species group, thought to be the sister clade to the *macrogenys* species group (Sasakawa 2005a; Sasakawa and Kubota 2009), are found in north-eastern China, the northern part of the Korean Peninsula and Russian Primorye (Yin et al. 2021). These regions are located almost directly across the Sea of Japan from the presumed initial differentiation area of the *macrogenys* species group (around Yamagata and Niigata Prefectures). This distribution pattern implies that the presence/formation of the Sea of Japan may have been associated with the origin of the *macrogenys* species group.

The obtained phylogenetic tree revealed that sympatric species of different body sizes were not sister taxa. In almost all instances, the sympatric species belonged to separate clades and were phylogenetically distant. The exception to this pattern is *P. asahinus* and *P. takadateyamanus*, which belong to the same clade, but these two species were not sister taxa within that clade. These patterns imply an ancient origin of body-size differences that contribute to species sympatry. This hypothesis is supported by the fact that all known sympatric sites are located on or near the Sea of Japan side in the northern part of the current distribution, which is considered the initial differentiation area of the species group.

Key to species of the *macrogenys* species group (for males)

Currently, it is virtually impossible to identify species based solely on female specimens. Usually, females are identified, based on conspecific males from the same collection site. Therefore, a key is presented here for males only. Information about species that have not been covered in our previous studies was obtained from the

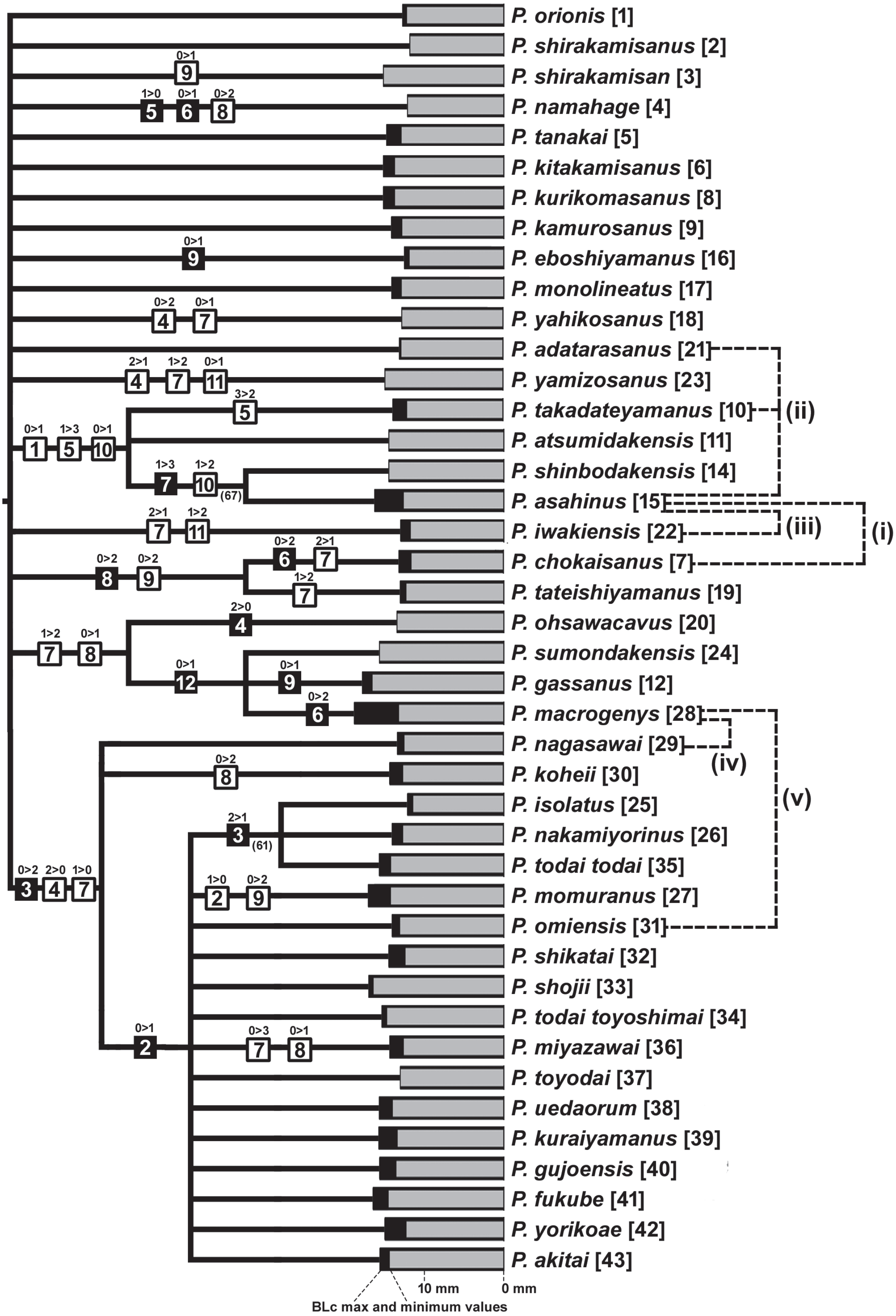

Figure 8. The strict consensus tree of 80 most parsimonious trees. Syn- and autapomorphies are indicated by the squares on branches, where the numbers in the squares indicate character ID and numbers above the squares indicate character-state change. Black and white squares indicate "unambiguous" and "possible" apomorphies, respectively. Numbers in parentheses below the branches indicate bootstrap values (where > 50%). Horizontal bars at tips of the tree indicate body length of each species. Numbers in the square brackets after species name indicate that the species were collected at site coded as the same number in Figs 1 and 9. Dashed lines, which connect species and have the code (i)–(v), indicate that the species occur sympatrically at sites with the same code in Fig. 9.

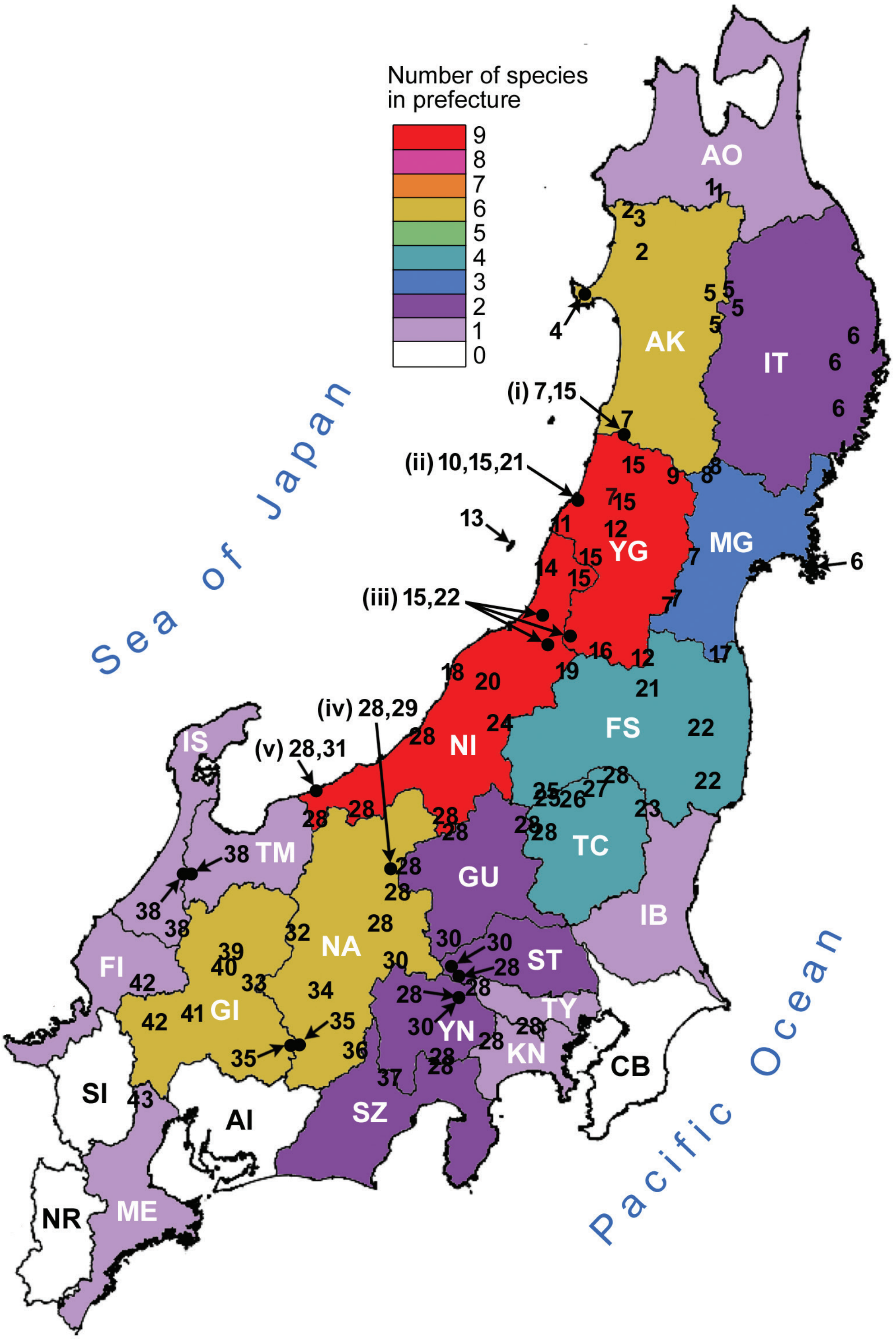

Figure 9. Distribution of species diversity of the *macrogenys* species group, based on collection records. Collection sites for each species are indicated by the numbers used as species identifiers in Figs 1, 8. The codes (i)–(v) for sympatric sites are the same as those used in Fig. 8. Two uppercase letters indicate the following abbreviations for prefectures in Japan: AI – Aichi; AK – Akita; AO – Aomori; CB – Chiba; FI – Fukui; FS – Fukushima; GI – Gifu; GU – Gunma; IB – Ibaraki; IS – Ishikawa; IT – Iwate; MG – Miyagi; NA – Nagano; NI – Niigata; NR – Nara; SI – Shiga; ST – Saitama; SZ – Shizuoka; TC – Tochigi; TY – Tokyo; TM – Toyama; YG – Yamagata; YN – Yamanashi.

original description of each species. For body lengths, male values are given, except for *P. akitai*, *P. koheii*, *P. momuranus*, *P. nagasawai*, *P. nakamiyorinus*, *P. omiensis* and *P. shojii*; values of pooled male and female data are provided for these seven species. Abbreviations: BLc, body lengths measured from the clypeal apex to the elytral; PW/PA, pronotum width at widest part / pronotum anterior margin width.

1 Right paramere strongly bent at apical 1/3, forming C-shape in left lateral view (e.g. Fig. 6C, F) 2

– Right paramere almost straight in lateral view; even if curved, not forming C-shape in left lateral view (e.g. Fig. 6A,B) 5

2 Width at widest part of apical 1/3 of right paramere in dorsal view > 1.5 times width of basal 1/3 of right paramere in lateral view (e.g. Fig. 6F, H). Left apical lobe hooked, distinctly sclerotised (e.g. lal in fig. 4O) 3

– Width at widest part of apical 1/3 of right paramere in dorsal view < 1.5 times width of basal 1/3 of right paramere in lateral view (e.g. Fig. 6C, E). Left apical lobe only weakly sclerotised (e.g. lal in Fig. 4K) 4

3 Widest part of apical 1/3 of right paramere in dorsal view located behind half of dorsal view of right paramere apical 1/3 (Sasakawa and Itô 2017: fig. 16). BLc 14.3 mm. Mount Shinbodake .... *P. shinbodakensis* Sasakawa & Itô

– Widest part of apical 1/3 of right paramere in dorsal view located before half of dorsal view of right paramere apical 1/3 (Fig. 6H). BLc 12.5–16.1 mm. Asahi and Iide Mountains, Mount Chokaisan and adjacent areas .... *P. asahinus* Habu & Baba

4 Right paramere with dorsum of apical margin concave (Sasakawa et al. 2020: 7 in fig. 5C); left ventrolateral margin of apical part almost straight in left lateral view (Sasakawa et al. 2020: 5 in fig. 5C). Right pre-apical lobe straight, not hooked (Sasakawa et al. 2020: rpl in fig. 5C). BLc 12.0–13.9 mm. Mount Takadateyama .... *P. takadateyamanus* Sasakawa

– Right paramere with dorsum of apical margin not concave (Fig. 6E); left ventrolateral margin of apical part sinuate in left lateral view (Fig. 6C). Right pre-apical lobe hooked apically (rpl in Fig. 4I–K). BLc 14.36 mm. Mount Atsumidake .... *P. atsumidakensis* sp. nov.

5 Left lateral margin of aedeagus constricted at subapical part, forming narrow apical part in ventral view (e.g. Sugimura (2005): fig. 2b) 6

– Left lateral margin of aedeagus not constricted but slightly arcuate at subapical part (e.g. Morita and Hirasawa (1996): figs 10a and 11a) 23

6 Apical part of right paramere without modification and simply, widely rounded (e.g. Fig. 6A) 7

– Apical part of right paramere more or less modified, i.e. narrowed apically (e.g. Morita and Hirasawa (1996): fig. 12a), truncate with sharp corner(s) (e.g. Toda (2012): fig. 12) or with a small projection on apical margin (Sekine and Nakase 2022: fig. 9) 15

7 Right paramere not bent in lateral views; contour of ventral side in lateral view almost straight (e.g. Morita and Ohkawa (2009): fig. 5). Aedeagus with tubercle on ventral side near middle (e.g. Morita and Ohkawa (2009): fig. 3). Posterior margin of sternum 7 with small, shallow notch at middle (e.g. Morita and Ohkawa (2009): fig. 2) 8

– Right paramere weakly, but distinctly bent at apical 1/2–1/3 in lateral views (e.g. Morita et al. (2013): fig. 8) 9

8 Pronotal laterobasal impressions shallow, with deep, wide transverse wrinkles; PW/PA < 1.15. BLc 12.5–14.2 mm. Shirabiso-tôge Pass, on ridgeline between Mounts Odakayama and Oikeyama .... *P. miyazakii* Morita & Ohkawa

– Pronotal laterobasal impressions rather deep, with shallow transverse wrinkles; PW/PA > 1.15. BLc 12.9 mm. Abe-tôge Pass, on south-eastern ridgeline of Mount Hakkôrei .... *P. toyodai* Morita & Kurosa

9 Right paramere strongly constricted at bending part; in lateral view, width at bending part less than half that of widest part of basal part (Ito and Ogai 2015: rp in fig. 5). Posterior margin of sternum 7 with emargination, width of which is more than half that between pair of setae near posterior margin (Ito and Ogai 2015: as in fig. 6). Aedeagus with tubercle on ventral side near middle; in lateral view, curvature of contour of tubercle greater than that of dorsal contour of aedeagal bending part (Ito and Ogai 2015: l and r in fig. 5). BLc 12.4–13.2 mm. Sugadaira-kôgen Highland, on the north-western slope of Mount Azuyamasan .... *P. nagasawai* Ito & Ogai

– Right paramere not conspicuously constricted at bending part, with width at bending part more than half that of widest part of basal part. Posterior margin of sternum 7 weakly emarginated or not emarginated; even if emarginated, width of emargination less than half that between pair of setae near posterior margin (e.g. Morita et al. (2013): fig. 11c). Aedeagus without tubercle on ventral side (e.g. Morita et al. (2013): fig. 11b); or with tubercle, curvature of which is less than that of dorsal contour of aedeagal bending part (e.g. Sugimura (2005): fig. 2a) 10

10 Pronotum widest at apical < 1/10 (Morita et al. 2013: fig. 11a). BLc 12.57–13.85 mm. Nakamiyori, i.e. Mount Shibakusayama and neighbouring mountain slopes .... *P. nakamiyorinus* Morita, Ohkawa & Kurihara

– Pronotum widest at apical 1/6–1/5. BLc > 13.87 m 11

11 Contour of aedeagal apical 2/3 in dorsal view bent to right (Morita et al. 2013: fig. 10). Ventral contour of aedeagal apical 2/3 in lateral views bent at apical 1/4 of total length of aedeagus, rather than uniformly bent throughout apical 2/3 (Morita et al. 2013: fig. 5). Posterior margin of sternum 7 simply rounded, not emarginated (Morita et al. 2013: fig. 4). BLc 14.14–16.86 mm. Mount Momurayama and neighbouring areas .... *P. momuranus* Morita, Ohkawa & Kurihara

– Contour of aedeagal apical 2/3 in dorsal view not bent, directed posteriorly (e.g. Morita and Hirasawa (1996): fig. 18b). Ventral contour of aedeagal apical 2/3 in lateral views uniformly bent throughout (e.g. Morita and Hirasawa (1996): fig. 18a) 12

12 Ventral side of aedeagal subapical part with transverse wrinkles (e.g. Sugimura (2005): fig. 2b). Sternum 7 weakly and transversely raised near middle (e.g. Sugimura (2005): fig. 2h) 13

– Ventral side of aedeagal subapical part without transverse wrinkles (e.g. Morita (2004): fig. 7). Sternum 7 not raised transversely near middle (e.g. Morita (2004): figs 1, 2) 14

13 Apical margin of left paramere widely emarginate (Sugimura 2005: fig. 2d). Pronotum widest at apical 1/6 (Sugimura 2005: fig. 3a). BLc 14.4–16.3 mm. Mounts Fukubegatake and Kôkasan .... *P. fukube* Sugimura

– Apical margin of left paramere slightly arcuate (Sugimura 2007: fig. 2d). Pronotum widest at apical 1/4 (Sugimura 2005: figs 1a, b). BLc 12.2–14.8 mm. Midori-dani Valley on north-western foot of Mount Ioganayama and Mount Shagatateyma .... *P. yorikoae* Sugimura

14 Terminal lamella of aedeagus shorter, with length less than twice width of base (Morita 2004: fig. 6). Elytral marginal setigerous punctures 12 or more. Sternum 7 weakly concave (Morita 2004: figs 1, 2). BLc 14.25–15.43 mm. Mount Oikedake .... *P. akitai* Morita

– Terminal lamella of aedeagus longer, with length more than twice width of base (Morita and Hirasawa 1996: figs 18b , 19b). Elytral marginal setigerous punctures 11 or less. Sternum 7 deeply concave (Morita and Hirasawa 1996: figs 16, 17). BLc 13.87–15.53 mm. Mounts Iwôzen and Hakusan .... *P. uedaorum* Morita & Hirasawa

15 Apex of right paramere gradually narrowed along mid-line (e.g. Morita and Hirawasab (1996): fig. 12d). Ventral contour of aedeagal apical 2/3 in lateral views bent at apical 1/4 of total length of aedeagus, rather than uniformly bent throughout apical 2/3 (e.g. Morita et al. (2013): fig. 12c) 16

– Apex of right paramere not gradually narrowed along mid-line, but either bent ventrally with narrow apex (e.g. Morita and Ohkawa (2010): fig. 9), with a small projection (Sekine and Nakase 2022: fig. 9) or truncate (e.g. Toda (2012): fig. 12) 17

16 Right lateral contour of aedeagal apical part in dorsal view straight (Morita et al. 2013: fig. 12d). PW/PA > 1.1. BLc 11.35–12.00 mm. Mount Tashiroyama .... *P. isolatus* Sasakawa

– Right lateral contour of aedeagal apical part in dorsal view more or less bent to right (Morita and Hirasawa 1996: figs 12b, 13b). PW/PA < 1.1. BLc 12.54–14.15 mm. Mounts Yatsugatake, Daibosatsurei, Akagunayama and Hakutai .... *P. koheii* Nakane

17 Right paramere with a small projection on apical margin (Sekine and Nakase 2022: fig. 9). Aedeagus with tubercle on ventral side near middle (Sekine and Nakase 2022: figs 6, 7). Elytral marginal setigerous punctures 15. BLc 13.0–13.9 mm. Ômi, a low mountain on right bank of downstream of Ômigawa River .... *P. omiensis* Sekine & Nakase

– Right paramere without projection on apical margin and either bent ventrally with narrow apex (e.g. Morita and Ohkawa (2010): fig. 9) or truncate (e.g. Toda (2012): fig. 12) 18

18 Right paramere apical 1/3 bent ventrally; apical 1/3 directed approximately perpendicular to mid-line of basal 2/3, gradually narrowed apically (Morita and Ohkawa 2010: fig. 9). BLc 13.28–15.57 mm. Mount Kuraiyama .... *P. kuraiyamanus* Morita & Ohkawa

– Right paramere truncate apically, forming two (ventral and dorsal) corners in lateral views (e.g. Toda (2012): fig. 12) 19

19 Pronotal laterobasal impressions not wrinkled (Toda 2012: fig. 6). Sternum 7 transversely raised near middle (Toda 2012: fig. 7). BLc 13.45–15.46 mm. Sakamoto-tôge Pass and Miyama-shônyûdô Cave in mountainous areas on left bank of Yoshidagawa River .... *P. gujoensis* Toda

– Pronotal laterobasal impressions more or less wrinkled (e.g. Toda (2012): fig. 13). Sternum 7 not raised transversely near middle 20

20 Aedeagus without tubercle on ventral side near middle (Morita and Kanie 1997: fig. 3; Sugimura 2002: fig. 3a). Angles of two corners of truncate apex of right paramere in lateral views differ, with ventral corner acute and dorsal corner obtuse, forming diamond shape in lateral views (Morita and Kanie 1997: fig. 5; Sugimura 2002: fig. 3d). Posterior margin of sternum 7 only slightly or not emarginated at middle; even if emarginated, width of emargination less than 1/3 width between pair of setae near posterior margin (Morita and Kanie 1997: fig. 2; Sugimura 2002: fig. 3f). BLc 14.1–15.6 mm. Mount Enasan .... *P. todai todai* Morita & Kanie

– Aedeagus with tubercle on ventral side near middle (e.g. Sugimura (2002): fig. 4a). Angle of two corners of truncate apex of right paramere in lateral views almost equal, forming square shape in lateral views (e.g. Sugimura (2002): fig. 4d). Posterior margin of sternum 7 with an emargination, width of which more than half that between pair of setae near posterior margin (e.g. Sugimura (2002): fig. 4f) 21

21 Terminal lamella of aedeagus longer, with length more than twice width of base (Toda 2012: figs 9, 10). Pronotum laterobasal impressions with wrinkles at proximal anterior part, but not near base (Toda 2012: fig. 13). BLc 12.30–14.31 mm. Shirahone-onsen Spa and Shirakaba-tôge Pass, on eastern slope of Mount Norikuradake .... *P. shikatai* Toda

– Terminal lamella of aedeagus shorter, with length less than twice width of base (e.g. Sugimura (2002): fig. 4a, b). Pronotum laterobasal impressions with wrinkles near base. BLc > 14.5 mm 22

22 Sternum 7 with several wrinkles near posterior margin on outside of pair of setae (Sugimura 2006: fig. 2g). Pronotum widest at apical 1/5.1. BLc 16.30–16.81 mm. Mount Shirakusayama .... *P. shojii* Sugimura

– Sternum 7 not wrinkled near posterior margin on outside of pair of setae. Pronotum widest at apical 1/6. BLc 14.6–15.2 mm. Mount Kisokomagatake .... *P. todai toyoshimai* Sugimura

23 Aedeagus with middle dorsal side convex (Sasakawa et al. 2020: 1 in fig. 7C, D). Left pigmented band sclerotised from base to apex, with same degree as aedeagus and positioned on exactly left lateral side (Sasakawa et al. 2020: 1, 2, 4

in fig. 7C, D). BLc 12.81–13.98 mm. Northern part of Abukuma Mountains ...... *P. monolineatus* Sasakawa, Mitsuduka & Itô

– Aedeagus with middle dorsal side not convex (e.g. Sasakawa et al. (2020): 1 and 2 in fig. 7B). Left pigmented band, if present, positioned on left ventrolateral rather than lateral side (e.g. Sasakawa et al. (2020): lpb in fig. 7B), with degree of chitinisation varying amongst species 24

24 Base of left pre-apical lobe swollen and protruding left laterally in dorsal view (e.g. lpl in Fig. 5B, D, F, H) 25

– Base of left pre-apical lobe not swollen (e.g. lpl in Fig. 4E–H) 27

25 Left apical lobe smoothly bent near middle, without corner outwards of bending part (Sasakawa and Itô 2018: figs 3, 5). BLc 13.1–18.6 mm. Jôshin'etsukokkyô Mountains, Nikkô Mountains, Nasu Mountains, Okuchichibu Mountains, Tanzawa Mountains, Myôko Mountains, Yatsugatake Mountains and Mount Fuji and their surrounding mountains ...... *P. macrogenys* Bates

– Left apical lobe sharply bent near middle, forming distinct corner outwards of bending part (e.g. lal in Fig. 5B). BLc < 13.0 mm 26

26 Left apical lobe bifid apically (Sasakawa et al. 2020: lal in fig. 3A–C). BLc 11.5–13.1 mm. Mounts Chôkaisan, Gassan, Funagatayama and Zaôsan ...... *P. chokaisanus* Sasakawa

– Left apical lobe not bifid (lal in Fig. 4A–C). BLc 12.0 mm. Oga Peninsula ...... *P. namahage* sp. nov.

27 Left apical lobe large, bifid; length between larger of left apical lobe apices and left pre-apical lobe apex in lateral views longer than width of aedeagus at ostium in lateral views (Sasakawa 2009: lal in fig. 11). BLc 15.0 mm. Shirakami Mountains ...... *P. shirakamisan* Sasakawa

– Left apical lobe with length between left apical lobe apex (or apices) and left pre-apical lobe apex in lateral views shorter than half width of aedeagus at ostium in lateral views (e.g. Fig. 4E, F) 28

28 Apex of right preapical lobe directed left laterally (rpl in Fig. 5I–N). BLc 13.6–15.0 mm. Kitakami Mountains ...... *P. kitakamisanus* Sasakawa

– Apex of right pre-apical lobe not directed left laterally (e.g. Fig. 4E–G) 29

29 Endophallus and gonopore directed ventroposteriorly (Sasakawa et al. 2020: fig. 3D, E). BLc 13.6–15.0 mm. Mount Kurikomayama ...... *P. kurikomasanus* Sasakawa

– Endophallus and gonopore directed ventrally/anteriorly (e.g. Figs 4, 5) 30

30 BLc ≥ 15.5 mm 31

– BLc < 15.0 mm 32

31 Left apical lobe gradually narrows towards apex and moderately bent (Sasakawa 2005c: fig. 10). BLc 15.5 mm. Mount Sumondake ...... *P. sumondakensis* Sasakawa

– Left apical lobe cylindrical, not narrowed towards apex and strongly bent (Sasakawa et al. 2020: lal in fig. 6A, B). BLc 16.4–17.6 mm. Mount Gassan and Azuma Mountains ...... *P. gassanus* Sasakawa

32 Left apical lobe sharply bent near middle, forming distinct corner outwards of bending part; apical part bifid, with two apices same size (Sasakawa and Itô 2017: lal in figs 21, 22). BLc 12.2–12.9 mm. Mount Tateishiyama ...... *P. tateishiyamanus* Sasakawa & Itô

– Left apical lobe bent at the base (not at the middle) (e.g. Sasakawa (2005c): fig. 8) or not bent (e.g. Sasakawa (2005c): fig. 2) 33

33 Left pre-apical lobe bifid apically (e.g. Sasakawa et al. (2020): lpl in fig. 6C–E) 34

– Left pre-apical lobe not bifid (e.g. Sasakawa et al. (2020): lpl in fig. 5D, E) 36

34 BLc < 13.5 mm Left pigmented band absent or weakly sclerotised 35

– BLc 14.7 mm. Left pigmented band weakly sclerotised (Sasakawa 2005c: fig. 9). Mount Yamizosan ...... *P. yamizosanus* Sasakawa

35 Left pigmented band absent (Sasakawa 2005c: fig. 8). Dorsal surface of body reddish-brown. BLc 13.3 mm. Ohsawa-shônyûdô Cave ...... *P. ohsawacavus* Sasakawa

– Left pigmented band weakly sclerotised (Sasakawa et al. 2020: lpb in fig. 6C–E). Dorsal surface of body black. BLc 11.61–12.82 mm. Southern part of Abukuma Mountains and north-western foot of Iide Mountains ...... *P. iwakiensis* Sasakawa

36 Ventral contour of left pre-apical lobe widely emarginate at middle in left lateral view (e.g. Sasakawa et al. (2020): lpl in fig. 5D, E) 37

– Ventral contour of left pre-apical lobe arcuate, not emarginate at middle in left lateral view (e.g. Sasakawa et al. (2020): lpl in fig. 7A, B) 39

37 Left pre-apical lobe with posteriorly directed protrusion at ventroposterior end (e.g. Sasakawa (2005c): lpl in fig. 2). Degree of chitinisation of left pigmented band weaker than that of aedeagus near ostium (e.g. Fig. 4E) 38

– Ventroposterior end of left pre-apical lobe widely rounded, without apically narrowed protrusion (Sasakawa et al. 2020: lpl in fig. 5D, E). Degree of chitinisation of left pigmented band same as that of aedeagus near ostium (Sasakawa et al. 2020: lpb in fig. 5D, E). BLc 12.7–12.9 mm. Mounts Adatarayama and Takadateyama ...... *P. adatarasanus* Sasakawa

38 Right pre-apical lobe about same size as protrusion at ventroposterior end of left pre-apical lobe (Sasakawa 2005c: fig. 2). BLc 12.1–12.6 mm. Mount Hakkôdasan ...... *P. orionis* Jedlička

– Right pre-apical lobe rudimentary, with size apparently smaller than that of protrusion at ventroposterior end of left pre-apical lobe (Fig. 4E–H). BLc 12.7–14.0 mm Mount Kamurosan ...... *P. kamurosanus* sp. nov.

39 Left pre-apical lobe with single, hooked protrusion at ventroposterior end (Sasakawa 2005c: fig. 4). BLc 12.8–14.6 mm. Mounts Akitakomagatake, Iwatesan and Hachimantai .... *P. tanakai* Ishida

– Left pre-apical lobe with simple, unhooked protrusion (e.g. Sasakawa (2009): lpl in fig. 17) or without protrusions (Sasakawa et al. 2020: lpl in fig. 7A and B). BLc ≤ 12.6 mm 40

40 Left pre-apical lobe without protrusions (Sasakawa et al. 2020: lpl in fig. 7A, B). BLc 11.8–12.4 mm. Eboshiyama Hills, located in the north between Iide and Azuma Mountains.. *P. eboshiyamanus* Sasakawa

– Left pre-apical lobe simple, unhooked protrusion (e.g. Sasakawa (2009): lpl in fig. 17)... 41

41 Left pigmented band strongly sclerotised (Sasakawa 2009: lpb in fig. 17). Pronotum less cordate, with PW/PA being 1.15. Dorsal surface of body reddish-brown (Sasakawa 2009: fig. 8). BLc 12.6 mm. Mount Yahikosan .... *P. yahikosanus* Sasakawa

– Left pigmented band weakly sclerotised (Sasakawa 2005c: fig. 3). Pronotum cordate, with PW/PA being 1.24. Dorsal surface of body black. BLc 11.7 mm. Shirakami Mountains ....*P. shirakamisanus* Sasakawa

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Supplementary material 1

Proposed Japanese name for species treated in the present study and BLc (mm) of each taxon, compiled from published literature and the authors' unpublished data

Authors: Kôji Sasakawa, Yoshiji Mitsuduka

Data type: docx

Explanation note: **table S1.** Proposed Japanese name for species treated in the present study. **table S2.** BLc (mm) of each taxon, compiled from published literature and the authors' unpublished data. The value is given as minimum–maximum values, except when the value was from one individual only or was not obtained from the data sources. In these cases, the single value and "NA" instead of value is provided, respectively.

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