Koleopterologische Rundschau	93	1–11	Wien, October 2023

Identities of two macrocephalic *Pterostichus* BONELLI, 1810 species from continental Far East as revealed by the examination of type material (Coleoptera: Carabidae)

K. SASAKAWA

Abstract

Pterostichus syleus KIRSCHENHOFER, 1997 and *P. ompoensis* JEDLIČKA, 1932 (Coleoptera: Carabidae: Pterostichini) from continental Far East were studied including type specimens. For *P. syleus*, specimens treated as this species by previous authors without type examination are confirmed to be true *P. syleus*, and supplemental morphological descriptions of the external and male genitalia (including the sufficiently inflated endophallus) are provided. For *P. ompoensis*, detailed external and male genital characters (including the sufficiently inflated endophallus) are described for the first time, based on the lectotype, which is designated herein. The observed characters imply that *P. ompoensis* is related to the *P. macrogenys* species group of the subgenus *Nialoe* TANAKA, 1958 sensu lato.

Key words: Coleoptera, Carabidae, Pterostichini, *Nialoe*, lectotype designation, endophallus, male genitalia, China, Korea.

Introduction

The genus *Pterostichus* BONELLI, 1810 is currently one of the most extensively studied carabid genera in East Asia, and new discoveries are ongoing at not only the species level but also the subgenus level (e.g., SHI et al. 2013, TIAN et al. 2019, JIA et al. 2021). Many of these findings are the product of new collecting methods (e.g., subterranean traps), new techniques allowing more precise morphological observations (e.g., preparation of the endophallus), and improved sampling efforts (e.g., JANOVSKA et al. 2013, SASAKAWA & ITÔ 2017, SASAKAWA et al. 2020). Nonetheless, problems remain, some of which are attributable to insufficient examination of type specimens. This is particularly the case in groups composed of species of similar morphology, such that insufficient type specimen examination can call into question the scientific names of all members of the group.

The main purpose of this study was to resolve outstanding issues related to the taxonomy of the macrocephalic *Pterostichus syleus* KIRSCHENHOFER, 1997, originally described from a mountain in Liaoning Province, China. The taxonomy of this species is controversial at both the subgenus and species levels. KIRSCHENHOFER (1997) described this species under the subgenus *Nialoe* TANAKA, 1958 but did not discuss the supraspecies classification within it. Based on examinations of a male specimen from the type locality (but not part of the type material), SASAKAWA et al. (2013) included this species in the *P. opacipennis* species group of the subgenus *Nialoe* (s.l.). In their redescription of *P. syleus*, YIN et al. (2021) supported the supraspecies classification by SASAKAWA et al. (2013); however, they concluded that the specimen examined by SASAKAWA et al. (2013) was not *P. syleus* but rather an undescribed species, given the deviation in the external and genital morphology, judging from the descriptions provided by KIRSCHENHOFER (1997). However, the identification of *P. syleus* by YIN et al. (2021) is also questionable, because their specimens did not include a male from the type locality, which is necessary for precise species identification of taxa characterized by marked regional differentiation, such as members of the *P. opacipennis* species group. Consequently, the specimens that SASAKAWA et al. (2013) and YIN et al. (2021) treated as *P. syleus* both may have been

incorrectly identified. If so, this would necessitate a species-level rather than a supraspecies-level revision of the taxonomy of the material thus far treated as *P. syleus*. Therefore, in this study I have examined the type specimens of *P. syleus* and *P. ompoensis* JEDLIČKA, 1932. The latter species was described from a locality near the distribution of *P. syleus* and, according to the morphological characteristics presented to date, may be related or identical with the specimen examined by SASAKAWA et al. (2013) and/or to *P. syleus*.

Material and methods

YIN et al. (2021) pointed out the morphological differences between the specimen described by SASAKAWA et al. (2013) and the original description, including the presence of setae on the ventral side of the fifth tarsomere in specimen of SASAKAWA et al. (2013), which are lacking in the type specimens and in the specimens described by YIN et al. (2021). Differences in the male genitalia were also noted. To address these conflicts, the following specimens were examined:

(i) Male specimen treated as *Pterostichus syleus* in SASAKAWA et al. (2013).

(ii) Holotype male and one male paratype of *Pterostichus syleus*: neither SASAKAWA et al. (2013) nor YIN et al. (2021) compared their specimens with the type specimens of *P. syleus*. Additionally, the endophallus preparation methods used by the authors obviously differed. Furthermore, YIN et al. (2021) based their morphological comparison on the low-resolution photographs of SASAKAWA et al. (2013). Thus, the observed morphological differences may have been artifactual, due to methodological differences. To address these issues, the endophallus of the type specimens of *P. syleus* was prepared using the same method as described in SASAKAWA et al. (2013) and then compared with the specimen of SASAKAWA et al. (2013) and the photographs of the endophallus published by YIN et al. (2021).

(iii) Lectotype male of *Pterostichus ompoensis*: the setae on the ventral side of the fifth tarsomere are also a feature of another macrocephalic pterostichine, *P. ompoensis*, described from a nearby locality (North Korea) (JEDLIČKA 1932). Thus, it is possible that the specimen of SASAKAWA et al. (2013) refers in fact to *P. ompoensis*. To address this issue, the external and genital characters of *P. ompoensis* were examined and compared with those of *P. syleus*.

The endophallus was fully inflated by injecting toothpaste from the base of the aedeagus. The homology and terminology of the endophallus structures follow YIN et al. (2021). As in SASAKAWA (2021), all species are treated as members of the subgenus *Nialoe* (s.l.). For label data, a back slash (\) was used to separate lines on the same label, and a double back slash (\\) to separate different labels. Depositories of the examined specimens are abbreviated as follows: NMW, Natural History Museum Vienna, Austria; NMP, National Museum, Prague, Czechia; NSMT, National Museum of Nature and Science, Tsukuba, Japan.

Results

The morphological comparisons have shown that the specimens of SASAKAWA et al. (2013) and YIN et al. (2021) are true *Pterostichus syleus*, and that *P. ompoensis* is distinct from *P. syleus*. Although not the main purpose of this study, the results also provide new insights into the supraspecies classification of *P. ompoensis*. Explanations for these taxonomic assignments, a supplemental morphological description of *P. syleus*, and a redescription of *P. ompoensis* are provided below.

Pterostichus (*Nialoe*) *syleus* KIRSCHENHOFER, 1997
(Figs. 1–25)

Pterostichus (*Nialoe*) *syleus* KIRSCHENHOFER 1997: 694; BOUSQUET 2013: 502; SASAKAWA et al. 2013: 430; BOUSQUET 2017: 726; SASAKAWA 2021: 211.
Pterostichus (*Koreonialoe*) *syleus*: YIN et al. 2021: 10.

TYPE LOCALITY: Shi-Fang-Ding, the highest peak of Baishilazi Nature Reserve, Liaoning Province, China (YIN et al. 2021).

MATERIAL EXAMINED:
C H I NA: Holotype ♂ (NMW): "CHINA, LIAONING prov. \ DANDONG City, Mt.SHI- \ FANG-DING, 3.-4. 08. 1996 \ leg. Li Jingke" \\ HOLO. \ TYPUS \\ Pterostichus \ (Nialoe) \ syleus m. \ det. Kirschenhofer 96" (NMW); paratype ♂: "CHINA, LIAONING prov. \ DANDONG City, Mt.SHI- \ FANG-DING, 3.-4. 08. 1996 \ leg. Li Jingke \\ Lianoe \ sp. \ Paratypus \ Pterostichus (Nialoe) \ syleus m. \ det. Kirschenhofer 1996"; 1 ♂ (NSMT): "Mt.Shi-Fang-Ding \ Dan Dong – city \ Liao Ning Prov \ China \ 1996.VIII.17" (specimen already examined by SASAKAWA et al. 2013).

COMMENT: The conclusion that the specimens of SASAKAWA et al. (2013) (Figs. 1–4) and YIN et al. (2021) are true *Pterostichus syleus* (Figs. 5–10) is based on the morphological comparisons presented below. Although the difference in the fifth tarsomere was confirmed (Figs. 2–3, 6–7), the other characters of all specimens matched. Based on the following three reasons, the difference in the tarsomeral setae can be considered as a rare individual variation that does not justify treating the specimen of SASAKAWA et al. (2013) as a species distinct from *P. syleus*.

(i) Other congeneric species with tarsomeral setae usually have more than five setae on both the left and the right ventrolateral margins on the middle and hind legs (thus, a total of more than ten setae on a tarsomeral ventral side), but the setae in the specimen of SASAKAWA et al. (2013) are present only on the hind legs, with only one on the left and two on the right (Figs. 2–3).

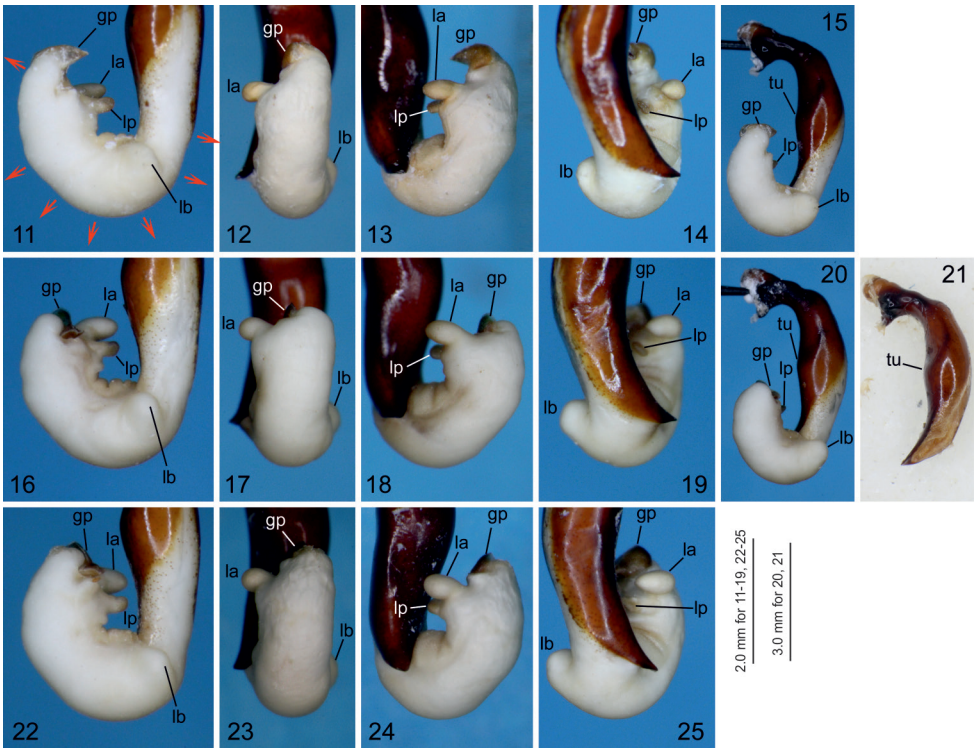
(ii) Additional setae on the ventral side of the fifth tarsomere were also reported as an individual variation in a closely related species, *P. woongbii* PARK & KWON, 1996 (PARK & KWON 1996).

(iii) The same individual variation was also found in another closely related species, *P. bellatrix* (TSCHITSCHÉRINE, 1895); during the course of this study, one male of this species from Korea (Jumbongsan, Mt. Seoraksan, Yangyang County, Gangwon-do, 11.–12.VII.2002, leg. K. Kubota, J-K. Kim, Y. Takami & T. Sota) with additional setae was discovered, but there were no other morphological differences compared to a simultaneously collected conspecific male without additional setae.

In the specimen studied by SASAKAWA et al. (2013) (Figs. 11–15), the endophallic and other aedeagal structures are perfectly consistent with those of the type specimens of *P. syleus* (Figs. 16–25). The differences noted by YIN et al. (2021) could not be confirmed and probably resulted from methodological deviations. Regarding the endophallus, YIN et al. (2021) did not describe the preparation method but instead cited the method of SHI et al. (2013). However, the latter authors did not examine the endophallus. Judging from their photographs, YIN et al. (2021) used a preparation method that clearly differed from the method used herein, such that the endophalli were probably not sufficiently inflated, which may have resulted in inadequate morphological evaluations. Regarding the aedeagus, the figures used in the shape comparisons by YIN et al. (2021) differed in their observation angles. In SASAKAWA et al. (2013), the aedeagus was photographed using dorsolateral rather than lateral views to show the lateral side of the inflated endophallus (figure caption: "endophallus (right and left lateral views)"). In the present comparisons, based on lateral views, there are no differences between the specimen of SASAKAWA et al. (2013) (Fig. 15), the type specimens (Figs. 20–21), and the photos of YIN et al. (2021).

Figs. 1–10: *Pterostichus syleus* male, specimen studied by SASAKAWA et al. (2013) (1–4), holotype (5–8), and paratype (9–10): 1, 5, 9) habitus in dorsal view; 2, 3, 6, 7) fifth tarsomeres of left (2, 6) and right (3, 7) hind legs in left (2, 3, 7) and right (6) lateral views; 4, 8, 10) labels. Abbreviation:se, seta(e).

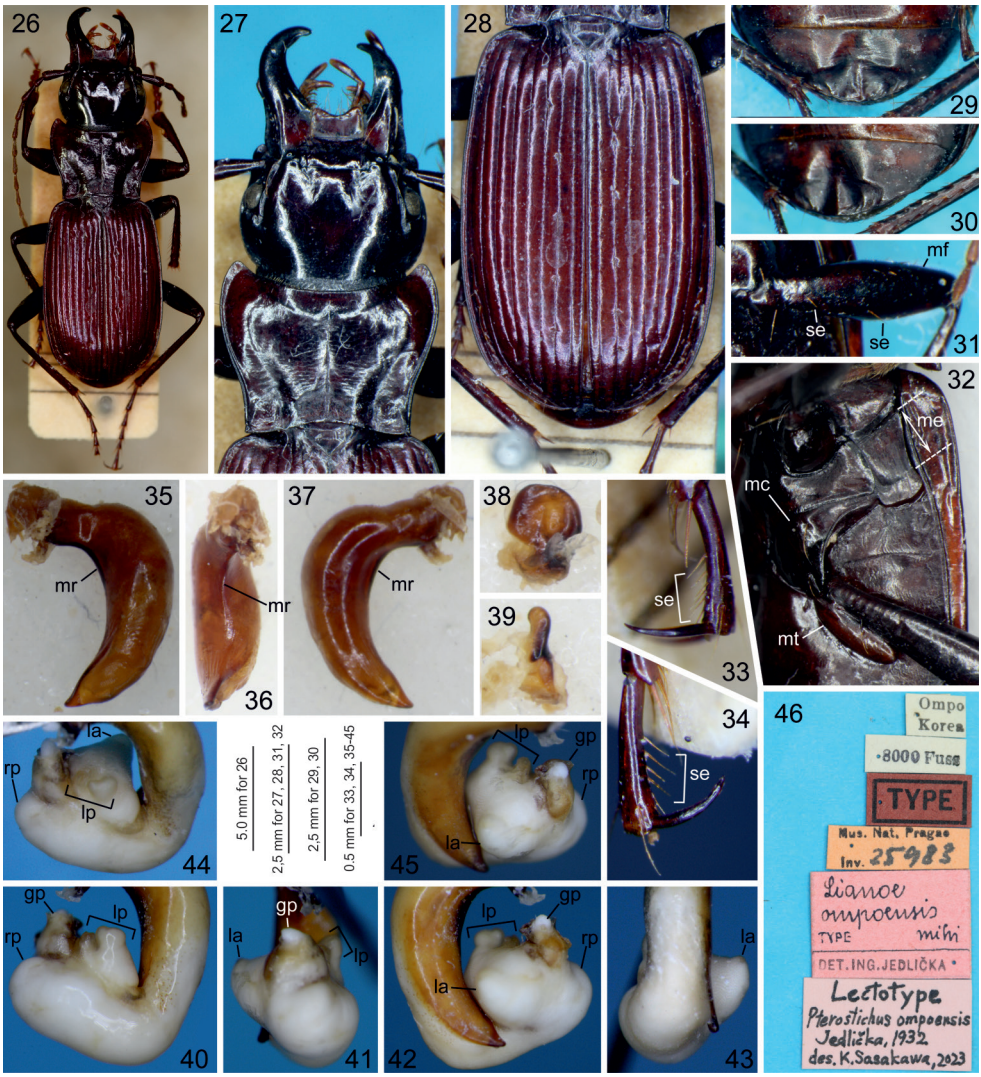
Finally, although the specimen of SASAKAWA et al. (2013) and *P. ompoensis* are identical in terms of the presence of setae on the ventral side of the hind tarsus, the position and number of setae, other external characters, and the genitalia are completely different, thus unambiguously indicating that they are distinct species.



Figs. 11–25: *Pterostichus syleus* male, specimen studied by SASAKAWA et al. (2013) (11–15), holotype (16–21), and paratype (22–25): fully inflated endophallus in left lateral (11, 16, 22), apical half in dorsal (12, 17, 23), in right lateral (13, 18, 24), and dorsal part in basal and apical half in ventral (14, 19, 25) views; 15, 20) aedeagus with fully inflated endophallus in left lateral views; and 21) aedeagus with endophallus not everted in left lateral view. Abbreviations: gp, gonopore; la, left apical lobe; lb, left basal swelling; lp, left preapical lobe; tu, tubercle. Red arrows indicate dorsal side of bending endophallus in Fig. 11.

SUPPLEMENTAL DESCRIPTION: Mandibles wrinkled on the middle of the dorsal side. Mesofemur with two setae on the ventral surface along the posterior margin, but three setae in the paratype male. Fifth tarsomere of the hind legs usually without setae on the ventral side (Figs. 6–7), but rarely with 1–2 setae (Figs. 2–3). Endophallus (Figs. 11–25) with left apical and preapical lobes near gonopore, with left basal swelling on the basal part; right apical lobe virtually absent; left apical lobe semi-prolate spheroid, apex not hooked; left preapical lobe weakly sclerotized, plate-shaped, and apparently smaller than that of the left preapical lobe; left basal swelling widely swollen and larger than the left apical lobe. The other external and genital characters of the three specimens examined herein are consistent with the description by YIN et al. (2021).

DISTRIBUTION: Qianshan Mountains, and Shedao Island, Liaoning Province, China (YIN et al. 2021).



Figs. 26–46: *Pterostichus ompoensis* lectotype male: 26–28) dorsal views of habitus (26), head and pronotum (27), and elytra (28); 29, 30) male sternum 7 in ventral (29) and left ventrolateral (30) views; 31) left mesofemur in ventroproximal view; 32) metepisternum, metacoxa, metatrochanter, and surrounding part in left ventrolateral view; 33, 34) fifth tarsomeres of left middle leg in left lateral view (33) and of right hind leg in right lateral view (34); 35–47) aedeagus in left lateral (35), ventral (36), and right lateral (37) views; 38) left paramere in left lateral view; 39) right paramere in left lateral view; 40–45) fully inflated endophallus in left lateral (40), apical part in dorsodistal (41), in right lateral (42), basal part in dorsal and apical part in ventral (43), in left ventrolateral (44), and in right ventrolateral (45) views; and 46) labels. Abbreviations: gp, gonopore; la, left apical lobe; lp, left preapical lobe; mc, metacoxa; me, metepisternum; mf, metafemur; mr, mountain-folded ridge; mt, metatrochanter; rp, right preapical lobe; se, seta(e).

Pterostichus (*Nialoe*) *ompoensis* JEDLIČKA, 1932
(Figs. 26–46)

Pterostichus (*Lianoe*) *ompoensis* JEDLIČKA 1932: 46; JEDLIČKA 1962: 273.
Pterostichus (*Nialoe*) *ompoensis*: BOUSQUET 2013: 502; BOUSQUET 2017: 725; SASAKAWA 2021: 211.

TYPE LOCALITY: According to the label data: "Ompo [Onpho], 8000 Fuss [8000 feet, ≈ 2440 m], Korea", the type specimens were probably collected somewhere in the high mountains of southwestern Kyŏngsŏng County, Hamgyŏngbukdo, North Korea. The elevation data in the original description (JEDLIČKA 1932: 46: "Corea: Ompo (3000 m hoch) [altitude of 3000 m]" are obviously wrong, because the highest mountain in the Korean Peninsula has an elevation of 2,744 m.

MATERIAL EXAMINED:

NORTH KOREA: Lectotype ♂ (NMP), by present designation: "Ompo \ Korea \\ 8000 Fuss \\ TYPE \\ Mus. Nat. Pragae \ Inv. 25983 \\ Lianoe ompoensis \ TYPE mihi \ DET.ING.JEDLIČKA \\ Lectotype \ Pterostichus ompoensis \ Jedlička, 1932 \ des. K. Sasakawa, 2023". According to the original description (JEDLIČKA 1932), there should be four syntypes (all males and all from the type locality). According to J. Hájek (pers. comm.), only one paralectotype ("Ompo \ Korea \\ 8000 Fuss \\ Mus. Nat. Pragae \ Inv. 25984 \\ COTYPE \\ ompoensis mihi \\ det. ing. Jedlička") is deposited in the NMP. The whereabouts of the remaining two paralectotypes is unknown.

COMMENT: Unlike other *Nialoe* species, this species has setae on the ventral side of the fifth tarsomere (Figs. 33–34). The absence of tarsomeral setae is the only currently recognized autapomorphy of *Nialoe* (SASAKAWA 2005), and many species of the *Platysma* group (sensu DORJDEREM et al. 2020), which is sister to *Nialoe* (SASAKAWA & KUBOTA 2007), have tarsomeral setae. Thus, with respect to its tarsomeral setae, *Pterostichus ompoensis* is more similar to the *Platysma* group than to *Nialoe*. JEDLIČKA (1932, 1962) examined only the superficial external morphology, not the taxonomically important external morphology or genital morphology of *P. ompoensis*. Consequently, the traditional treatment of *P. ompoensis* as a member of *Nialoe* (e.g., KASAHARA 1988, BOUSQUET 2017, SASAKAWA 2021) lacks supporting evidence.

The present results show that *Pterostichus ompoensis* belongs to *Nialoe* not to the *Platysma* group, for the following reasons:

(i) *Pterostichus ompoensis* lacks the most reliable autapomorphy of the *Platysma* group, i.e., more than four setae on the ventral side of the mesofemur along the posterior margin; the reliability of this autapomorphy is supported by the monophyly of the *Platysma* group in molecular phylogenies: SASAKAWA & KUBOTA (2007), RAUPACH et al. (2020) (Fig. 32).

(ii) The structure of the endophallus of *Pterostichus ompoensis* seems more close to the *P. macrogenys* species group of *Nialoe* (SASAKAWA et al. 2020) rather than to the *Platysma* group (BERLOV & BERLOV 1997, 1999, BERLOV & TILLY 1998; DORJDEREM et al. 2020, SASAKAWA unpublished data) (Figs. 40–45).

(iii) The mandibular surface in *Pterostichus ompoensis* is smooth, it completely lacks wrinkles (Fig. 27); this and similar character states are found in most species of the *P. macrogenys* species group of *Nialoe*, but other *Nialoe* species and species of the *Platysma* group usually have distinct wrinkles on the mandibular surface.

(iv) The male sternum 7 of *Pterostichus ompoensis* is fairly concave (Figs. 29–30) and thus clearly different from the unmodified male sternum 7 of the *Platysma* group but similar to that of some species of the *P. macrogenys* species group of *Nialoe* (e.g., HABU 1977, MORITA & KANIE 1997, SUGIMURA 2002).

(v) The head and pronotum are very similar to those of the *Pterostichus macrogenys* species group of *Nialoe* (SASAKAWA et al. 2020) (Figs. 26–27).

If *Pterostichus ompoensis* is regarded a member of *Nialoe*, its tarsomeral setae are interpreted as a species autapomorphy re-acquired within *Nialoe*. In addition to this trait, three traits were considered autapomorphies:

(i) A very weakly impressed elytral basal transverse line and scutellary stria (Fig. 28); both are distinctly impressed in other *Nialoe* and most *Pterostichus* species.

(ii) Six setigerous punctures on elytral interval 3 (Fig. 28), whereas most species of *Nialoe* have three or fewer setigerous punctures, and only two species, *P. multinodosus* SASAKAWA, KIM & KIM, 2006 and *P. marginellus* SASAKAWA, KIM & KIM, 2006, which are phylogenetically distant from *P. ompoensis* (SASAKAWA 2005), exceptionally have four to six punctures (SASAKAWA et al. 2006).

(iii) A ridge on the ventral side of the aedeagus (Figs. 35–37), a trait not reported in the genus *Pterostichus* and thus an unambiguous autapomorphy.

These four autapomorphies will be useful in the search for the sister species of *P. ompoensis* in future studies.

REDESCRIPTION: Body length from mandible apices to elytral end 17.71 mm, from anterior margin of labrum to elytral end 15.74 mm, and from clypeal apex to elytral end 15.21 mm. Dorsal surface of body shiny, not opaque; head reddish black; pronotum and elytra reddish brown, with pronotum darker; appendages dark brown to reddish brown (Figs. 26–28).

Head (Figs. 26–27) large, widest at tempora. Mandibles long, hooked at the apex, left mandible larger and more hooked than the right one; mandibular surface smooth; a small shallow pore on subapical part, at apical 1/4 on the left, 1/3 on the right. Frontal grooves shallow; tempora strongly swollen, width at the widest part wider than the width at the pronotal posterior margin, anterior-posterior length slightly longer than 1.5 times the anterior-posterior length of the eye; surfaces of labrum, clypeus, frons, and tempora smooth. Antennal segment 1 with one seta; setae on segment 2 not confirmed but, given the presence of discal pores on the ventral side, probably originally present and later lost; segment 3 with five setae; pubescence absent on segments 1–3 but present on the other segments. Eyes weakly convex, small, anterior-posterior length slightly shorter than 1/2 the length of antennal segment 1. Mentum with a pair of setae at the middle part and a pair of longitudinal depressions; mentum tooth bifid; submentum with two setae on each side.

Pronotum (Figs. 26–27) cordate, widest slightly behind apical 1/5; lateral margin arcuate in apical 3/4, only slightly sinuate on basal 1/4; anterior margin emarginate, its contour more strongly arched than the curvature of apical 3/4 of the lateral margin; posterior margin emarginate at the median area and slightly arcuate at lateral areas, curvatures of both slightly more arched than the curvature of the basal 1/4 of the lateral margin. Anterior angles notably produced, with widely rounded apices; hind angles slightly acute, with narrowly rounded apices. Median line distinctly impressed in the middle area, weak near the anterior and posterior margins; area along the anterior margin shallowly grooved, without an impressed line. Laterobasal impressions single, shallow; the anterior part narrowed anteriorly, with the anterior end reaching the apical half of the pronotum; the impressions of both sides connected by very shallow transverse grooved area near the pronotal posterior margin; the middle of the impression only very slightly convex. Pronotal surface smooth except for the laterobasal impressions and an area along the posterior margin; laterobasal impressions slightly punctate at the basal areas; area along the posterior margin slightly wrinkled in the middle. Anterior marginal setae on the widest pronotal point; posterior marginal setae not confirmed but, given the presence of discal pores near the hind angles, probably originally present near the hind angles and later lost.

Elytra (Figs. 26, 28) almost parallel-sided, less convex; basal margin at intervals 3–6 concave; shoulders distinct, but not denticulate; apices rounded; basal transverse line connecting anterior ends of elytral intervals very weakly impressed, markedly shallow but visible at the left, almost invisible at the right; scutellary stria weakly impressed, short, its posterior end slightly anterior of the level of the posterior end of the scutellum; stria distinct, more strongly impressed than basal transverse line and scutellary stria; intervals less convex; microsculpture transverse. One setigerous puncture on stria 1 at the level of the posterior end of the scutellum. Six setigerous punctures on interval 3, anterior (the first) one adjoining stria 3 and the remaining five (second to sixth) adjoining stria 2; first, second, third, fourth, fifth, and sixth puncture on almost anterior 1/6, anterior 1/3, middle, posterior 1/3, posterior 1/5, and posterior 1/8, respectively. Sixteen and 17 marginal setigerous punctures on right and left side, respectively; six punctures on anterior 1/6, almost equally spaced; ten punctures on the posterior half, more densely spaced posteriorly; the remaining puncture of the left side slightly behind anterior 1/4. Hind wings completely atrophied.

Metepisternum (Fig. 32) subquadrate, medial and lateral margins 1.45 and 1.70 times as long as basal width, respectively; surface smooth. Mesofemur (Fig. 32) with two setae on ventral surface along posterior margin. Metacoxa (Fig. 32) with two setae; medial seta absent. Metatrochanter (Fig. 32) without setae. Sterna 4–7 with one seta on each lateral side; sternum 7 fairly concave (Figs. 29–30); shape of the concavity a combination of a transverse ellipse and a semicircle; the diameter of the semicircle attached to the anterior margin of the ellipse; posterior margin of the ellipse corresponding to the posterior margin of the sternum; transverse, major axis of the ellipse about 2.7 times that of the longitudinal minor axis; diameter of the semicircle 0.6 times the major axis of the ellipse; area corresponding the minor axis of the ellipse raised, forming a middle ridge; lateral ridge on each side of the median ridge, with the posterior end on the sternum posterior margin laterally at the same level as the connection between the ellipse and the semicircle; lateral ridges directed anterolaterally, vanishing at the level of the major axis of the ellipse; setae on sternum 7 present near the lateral ridges.

Aedeagus (Figs. 35–37) stout, straight at the basal 1/4, the remainder uniformly curved; ventral side with a ridge at the basal 1/2; edge of the chitinized part slightly arcuate in both lateral directions at the aedeagal apical 1/4, forming slightly protruding contours from lateral views; apex narrow, rounded-triangular, without a denticulate; left paramere subquadrate (Fig. 38); right paramere short, straight, apex rounded (Fig. 39). Endophallus (Figs. 40–45) short, stout, strongly bent ventrally, gonopore directed anteriad; sclerites on the surface absent; right preapical lobe large, apex widely rounded; left preapical lobe bifurcate, apical sublobe smaller than basal sublobe; left apical lobe large, apex narrowly rounded and weakly bent in the anterior direction.

DISTRIBUTION: The type locality is currently the only reliable locality of this species. PARK & PAIK (2001) listed a male of this species that was collected from Mt. Kwanmobong (North Korea). Due to its proximity to the type locality, this male specimen may belong to *P. ompoensis*. However, the inclusion of this locality in the distribution of *P. ompoensis* awaits confirmation of the identity of the specimen by comparisons with the lectotype.

Acknowledgements

I thank Jiří Hájek (NMP), Harald Schillhammer (NMW), and Shuhei Nomura (NSMT) for loaning specimens under their care. This study was partly supported by JSPS KAKENHI (no. 22K06386).

References

BERLOV, E. & BERLOV, O. 1997: A key to species of the genus *Pterostichus* (Coleoptera, Carabidae) from Sakhalin Island. – Vestnik of the Irkutsk State Agricultural Academy 5: 36–46.

BERLOV, O. & BERLOV, E. 1999: A contribution to the taxonomy of the ground beetles *Pterostichus niger* and *Pterostichus planipennis* (Coleoptera, Carabidae). – Vestnik of the Irkutsk State Agricultural Academy, Irkutsk 14: 64–65. [in Russian]

BERLOV, O. & TILLY, A.S. 1998: A key to species of the genus *Pterostichus* (Coleoptera, Carabidae) from Samara district. – Vestnik of the Irkutsk State Agricultural Academy, Irkutsk 12: 4–13. [in Russian]

BOUSQUET, Y. 2013: Tribe Pterostichini Bonelli, 1810, pp. 469–521. – In Löbl, I. & Smetana, A. (eds.): Catalogue of Palaearctic Coleoptera, Vol. 1, Archostemata–Myxophaga–Adephaga. – Stenstrup: Apollo Books, 819 pp.

BOUSQUET, Y. 2017: Tribe Pterostichini Bonelli, 1810, pp. 675–755. – In Löbl, I. & Löbl, D. (eds.): Catalogue of Palaearctic Coleoptera, Vol. 1, Archostemata – Myxophaga – Adephaga. Revised and updated edition. – Leiden: Brill, 1443 pp.

DORJDEREM, S., SHI, H. & LIANG, H. 2020: The genus *Pterostichus* in China III: a brief review of subgenus *Chinapterus* Berlov (Coleoptera, Carabidae) with descriptions of two new species. – ZooKeys 953: 61–83.

HABU, A. 1977: On two *Pterostichus* species found in caves in Niigata Prefecture, Japan (Coleoptera, Carabidae). – Entomological Review Japan 30: 13–17.

JANOVSKA, M., ANICHTCHENKO, A.V. & ERWIN, T. 2013: Significant new taxonomic tool for Carabidae (Insecta: Coleoptera): Endophallus inflation methods revised. – Caucasian Entomological Bulletin 9 (1): 39–42.

JEDLIČKA, A. 1932: Noví Carabidi z jižní Číny (III. Díl). Neue Carabiden aus Süd-China. (III. Teil). – Časopis Československé Společnosti Entomologické (Acta Societatis Entomologicae Čechosloveniae) 29: 38–48. [in German, with Czech and German title]

JEDLIČKA, A. 1962: Monographie des [der] Tribus Pterostichini aus Ostasien (Pterostichi, Trigonotomi, Myadi) (Coleoptera-Carabidae). – Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden 26: 177–346.

JIA, X., HE, L. & TIAN, M. 2021: A new subgenus and three new cavernicolous species of the genus *Pterostichus* from China (Coleoptera: Carabidae: Pterostichini). – Annales de la Société Entomologique de France (N.S.) 57 (4): 346–358.

KASAHARA, S. 1988: Distribution pattern and speciation of pterostichine carabid beetles in Japan, pp. 53–65. – In Satô, M. (ed.): The beetles of Japan, with special reference to their origin and speciation. – Tokyo: Tôkai University Press, 209 pp. [in Japanese]

KIRSCHENHOFER, E. 1997: Neue Arten der Gattungen *Pterostichus* Bonelli 1810[,] *Synuchus* Gyllenhal 1810[,] *Lesticus* Dejean 1828 und *Trigonotoma* Dejean 1828 aus Ost- und Südostasien (Coleoptera, Carabidae: Pterostichinae). – Linzer Biologische Beiträge 29 (2): 689–714.

MORITA, S. & KANIE, N. 1997: A new macrocephalic pterostichine (Coleoptera, Carabidae) from central Japan. – Elytra 25: 163–167.

PARK, J.K. & KWON, Y.J. 1996: A new subgenus of the *Pterostichus* from Korea (Coleoptera: Harpalidae). – Korean Journal of Entomology 26 (1): 93–103.

PARK, J.K. & PAIK, J.C. 2001: Family Carabidae. Economic Insects of Korea 12. – Insecta Koreana Suppl. 19: 1–170.

RAUPACH, M.J., HANNIG, K., MORINIÈRE, J. & HENDRICH, L. 2020: A DNA barcode library for ground beetles of Germany: the genus *Pterostichus* Bonelli, 1810 and allied taxa (Insecta, Coleoptera, Carabidae). – ZooKeys 980: 93–117.

SASAKAWA, K. 2005: Phylogenetic studies of the subgenus *Nialoe* (s. lat.) (Coleoptera, Carabidae, genus *Pterostichus*), part 1: Homology of the component parts of male genitalia and higher phylogeny. – Zoological Science 22 (11): 1205–1216.

SASAKAWA, K. 2021: A new species of ground beetle and a revised list of the East Asian endemic subgenus *Nialoe* (s. lat.) (Coleoptera: Carabidae: *Pterostichus*). – Oriental Insects 55 (2): 204–215.

SASAKAWA, K. & ITÔ, H. 2017: Two new species of the *Pterostichus macrogenys* species group (Coleoptera, Carabidae) discovered in shallow subterranean habitats in northern Honshu, Japan. – Subterranean Biology 21: 47–56.

SASAKAWA, K., KIM, J.-L., KIM, J.-K. & KUBOTA, K. 2006: Geographical differentiation of "*Pterostichus audax* (Tschitschérine, 1895)" (Coleoptera, Carabidae) in south Korea, with descriptions of four new species. – Biogeography 8: 17–23.

SASAKAWA, K., KIM, J.-L., KIM, J.-K. & KUBOTA, K. 2013: Notes on the ground beetle *Pterostichus togyusanus* (Coleoptera: Carabidae): Phylogenetic evidence for species status and new distribution record. – Journal of Asia-Pacific Entomology 16 (4): 429–431.

SASAKAWA, K. & KUBOTA, K. 2007: Phylogeny and genital evolution of carabid beetles in the genus *Pterostichus* and its allied genera (Coleoptera: Carabidae) inferred from two nuclear gene sequences. – Annals of the Entomological Society of America 100 (2): 100–109.

SASAKAWA, K., MITSUDUKA, Y. & ITÔ, H. 2020: Unexpected species identities and interspecific relationships in a subterranean beetle lineage, the *Pterostichus macrogenys* species group (Coleoptera, Carabidae), revealed by fine-scale field sampling and detailed morphological comparisons. – Insects 11: 803.

SHI, H., SCIAKY, R., LIANG, H. & ZHOU, H. 2013: A new subgenus *Wraseiellus* of the genus *Pterostichus* Bonelli (Coleoptera, Carabidae, Pterostichini) and new species descriptions. – Zootaxa 3664 (2): 101–135.

SUGIMURA, A. 2002: A new subspecies of *Pterostichus todai* Morita et Kanie (Coleoptera, Carabidae) from Mt. Kisokoma-ga-take, central Japan. – Elytra 30 (1): 91–99.

TIAN, M., HUANG, S., CHEN, M. & DING, K. 2019: Remarkable cave-adapted ground beetles of the tribe Pterostichini from China: a new subgenus and three new species (Coleoptera: Carabidae). – Annales de la Société Entomologique de France (N.S.) 55 (1): 1–16.

YIN, W.-Q., SHI, H.-L. & LIANG, H.-B. 2021: Revision of the Chinese species of subgenus *Koreonialoe* (Coleoptera: Carabidae: *Pterostichus*), with descriptions of two new species. – ZooKeys 1063: 1–21.

Dr. Kôji SASAKAWA
Chiba University, 1-33 Yayoi-cho, Inage-ku, Chiba, 263-8522, Japan (ksasa@chiba-u.jp)