A New Genus and Species of Pentatomidae (Hemiptera) from the Upper Pliocene "Kabutoiwa Formation" in Gunma Prefecture, Japan

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A new genus and species of Pentatomidae (Hemiptera) from the Upper Pliocene "Kabutoiwa Formation" in Gunma Prefecture, Japan

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Abstract. The Upper Pliocene Motojuku Group (*ca*. 3.5 Ma) is a well-known Japanese insect fossil locality distributed in the border area between Gunma and Nagano prefectures. Here, we report *Tetrapentatoma nishizawai* gen. et sp. nov., a new fossil genus and species of the true bug or heteropteran family Pentatomidae from the "Kabutoiwa Formation" of the Motojuku Group. The specimen exhibits morphological characteristics typical of the subfamily Pentatominae of the family except for its distinct four-segmented antennae. The new genus is asserted to be a member of the *Pentatoma*-complex (included in the tribe Pentatomini of Pentatominae) and is distinguished from the other pentatomid genera by the following characteristics: body approximately 25 mm, broadly ovate; head tongue-shaped; mandibular plates reaching a level of apex of clypeus; antenna four-segmented; antennal segment II longest among segments, 1.4 times as long as segment III; scutellum subtriangular, reaching posterior margin of abdominal tergite VI; hemelytral vein inconspicuous; and connexivum with dark spots. This discovery is the oldest fossil record of the *Pentatoma*-complex.

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Keywords: Kabutoiwa Formation, Motojuku Group, *Pentatoma*-complex, Pentatomidae, Pliocene, Stink bug

Introduction

Pentatomidae is the third largest family in the suborder Heteroptera Latreille, 1810 of the insect order Hemiptera, with 4,948 species, 940 genera, and nine subfamilies (Schuh and Weirauch, 2020). Its members, commonly called stink bugs, are terrestrial and mostly phytophagous insects known to be pests of crops and forests. Their fossil record is less rich and includes approximately 73 species restricted to the Cenozoic (Mitchell, 2013). Most of them are from the Eocene to Miocene lacustrine deposits distributed in Europe and North America. However, paleontological literatures on this family generally consists of old studies, and the majority of those fossil specimens have not been described (Scudder, 1890, 1891; Carpenter, 1992). Recently, Poinar and Thomas (2012) described *Edessa protera* Poinar and Thomas, 2012 from the Lower Miocene in Mexico. Petrulevičius and Popov (2014) described *Acanthocephalonotum martinsnetoi* Petrulevičius and Popov, 2014, from the Middle Eocene in Patagonia, Argentina. Wedmann *et al*. (2021) described *Eospinosus peterkulkai* Wedmann, Kment, Campos and Hörnschemeyer, 2021 from the Middle Eocene in Germany and *Eospinosus greenriverensis* Wedmann, Kment, Campos and Hörnschemeyer, 2021 from the Early Eocene in the USA. The fossil record from the Pliocene comes mostly from Germany, where 12 fossil species have been described (Piton and Théobald, 1935; Jordan, 1967). However, those specimens are poorly preserved and difficult to interpret morphologically. Moreover, Aiba (2019a, 2019b, 2020, 2021) described eight pentatomid fossils from the Middle Pleistocene Shiobara Group in Japan: *Pentatoma semiannulata* (Motschulsky, 1860), *Okeanos quelpartensis* Distant, 1911, *Dinorhynchus dybowskyi* Jakovlev, 1876, *Lelia decempunctata* Motschulsky, 1860, *Homalogonia grisea* Josifov and

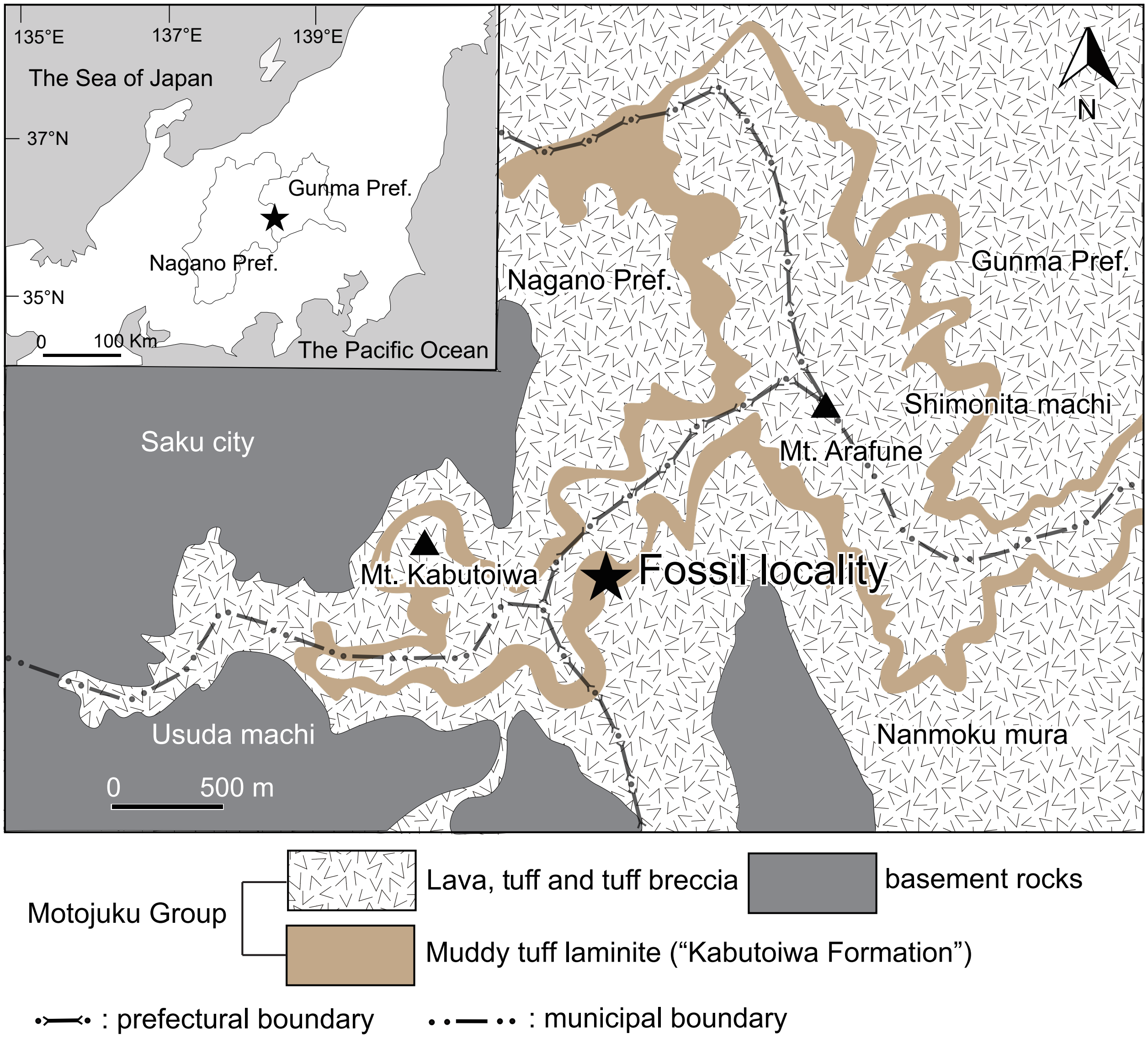

Figure 1. Fossil locality: Location of the border between Nagano and Gunma prefectures, Japan. The star represents the locality, near Mt. Kabutoiwa (after Geological Survey of Japan, 1969).

Kerzhner, 1978, *Pentatoma metallifera* (Motschulsky, 1860), *Pentatoma rufipes* (Linnaeus, 1758), and *Menida disjecta* (Uhler, 1860). All these fossils are extant species.

In this study, we describe a well-preserved pentatomid fossil from the Upper Pliocene "Kabutoiwa Formation" of the Motojuku Group in Gunma Prefecture, Japan. The results indicate that the fossil belongs to a new genus and species of the Pliocene *Pentatoma*-complex.

Geological setting

The Motojuku Formation, characterized by the Miocene to Pliocene collapse basin-fill deposits, is distributed in the Arafuneyama area, northwestern part of Kanto Massif, and border area between Gunma and Nagano prefectures. The formation is mainly composed of andesitic lava, ignimbrite, and volcaniclastic rocks with minor intercalations of lake deposits (Motojuku Collapse Research Group, 1970). Due to the recent discovery of additional caldera collapse in the formation, the Motojuku Collapse Research Group (2018) granted the Motojuku Formation "group" status (the Motojuku Group) and divided it into two formations, i.e., the lower Maisawa and upper Monogatariyama formations (Figure 1). The lake deposits, called "Kabutoiwa Formation," belong to the Maisawa Formation and are famous for yielding well-preserved fossils (e.g. Koshimizu, 1982; Ozaki, 1991). Sato (2007) reported that the *ca*. 3.5 Ma age (Late Pliocene) of the fossiliferous lake deposits was obtained based on K–Ar dating of overlying lava in the Maisawa Formation.

The "Kabutoiwa Formation" consists of muddy tuff laminite. Plant fossils were first reported by Yagi (1921), who later listed 33 species (Yagi, 1931). Subsequent studies have revealed 111 species of Kabutoiwa flora in 45 families and 75 genera (Suzuki, 1967; Ozaki, 1984, 1987, 1991). Ozaki (1991) suggested that the flora is characterized by typical cool temperate elements and is composed of the following two habitat communities: valley forest and slope forest. The deposits yielded well-preserved fossil leaves, which were sometimes associated with fossil insects. Yagi (1931) formed the oldest record of fossil insects, which also included photographs. Koshimizu (1982) listed 116 species of fossil insects belonging to 28 families and 13 genera of 10 orders and described 48 of these species. Kuroko (1987) reported a fossil leaf with a nepticulid mine. Recently, Tanaka and Mano (2017) and Tanaka (2021) evaluated unclassified collections of fossil insects, which are called the "Mogi collection," deposited in the Shimonita Town Natural History Museum. Aiba *et al*. (2023) described a new fossil butterfly species. They concluded that the insect fauna of the "Kabutoiwa Formation" consisted of 44 families of 11 orders.

Materials and methods

The studied specimen was collected by Mr. Hikaru Nishizawa during a bachelor's thesis approximately 40 years ago. The specimen was preserved in grayish fine muddy tuff. However, its counterpart is missing. The studied specimen is deposited in the Gunma Museum of Natural History under repository number GMNH-PI-6322. The material was examined using a Leica M205 C microscope (Leica Corporation, Wetzlar, Germany). Photographs were taken using a Leica MC170HD Macroscope and measurements with the Leica Application Suite version 4.1.3. Photographs were sharpened and adjusted in contrast and tonality using Adobe Photoshop^{TM} version CS6 (Adobe Systems Incorporated, San Jose, CA, USA). The terminology used to describe the specimen followed that of Tsai *et al*. (2011).

Systematic paleontology

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Pentatomomorpha Leston, Pendergrast and Southwood, 1954
Superfamily Pentatomoidea Leach, 1815
Family Pentatomidae Leach, 1815
Subfamily Pentatominae Leach, 1815
Tribe Pentatomini Leach, 1815

Genus ***Tetrapentatoma*** **gen. nov.**

[New Japanese name: Mukashi-ashiaka-kamemushi-zoku]
ZooBank lsid: urn:lsid:zoobank.org:act:2619A67C-D1EC-4040-853D-7F91984199A7

Type species.—***Tetrapentatoma nishizawai*** **sp. nov.**

Etymology.—Latin Tetrapentatoma (female) genus name from tetra + pentatoma, in reference to tetra (from the Greek τετρα- which means four) and denotes four jointed antennae, and pentatoma from the genus name *Pentatoma* Oliver, 1789, type genus of Pentatomidae.

Diagnosis.—Recognized from other pentatomid genera by the following characteristics: body approximately 25 mm, broadly ovate; head tongue-shaped; mandibular plates reaching a level of apex of clypeus; antenna four-segmented; antennal segment II longest among segments, 1.4 times as long as segment III; scutellum subtriangular, reaching posterior margin of abdominal tergite VI; hemelytral vein inconspicuous; and connexivum with dark spots.

Tetrapentatoma nishizawai **sp. nov.**

[New Japanese name: Mukashi-ashiaka-kamemushi]

Figures 2, 3

ZooBank lsid: urn:lsid:zoobank.org:act:2DEA9E61-ECFC-4509-A696-F2905EF3B76B

Diagnosis.—As for the genus.

Material.—Holotype GMNH-PI-6322 is a nearly complete specimen, strongly compressed body fossils that show remarkably detailed preservation in dorsal view (Figures 2A, 3): head (Figure 2B), antennae (Figures 2F, G), pronotum, scutellum, hemelytron, left and right forelegs, right midleg, left and right hindlegs, abdominal tergites. However, its counterpart has not yet been discovered.

Locality and horizon.—Specimen was discovered from grayish fine muddy tuff belonging to the Upper Pliocene "Kabutoiwa Formation" (lacustrine deposits of Maisawa Formation; *ca*. 3.5 Ma) in the Motojuku Group, Gunma Prefecture, Japan.

Etymology.—After Hikaru Nishizawa, fossil collector.

Description of holotype.—Body, broadly oval, widest at pronotal humeri and abdominal tergite IV (Figures 2A, 3).

Head and cephalic appendages: Head (Figure 2B) api-

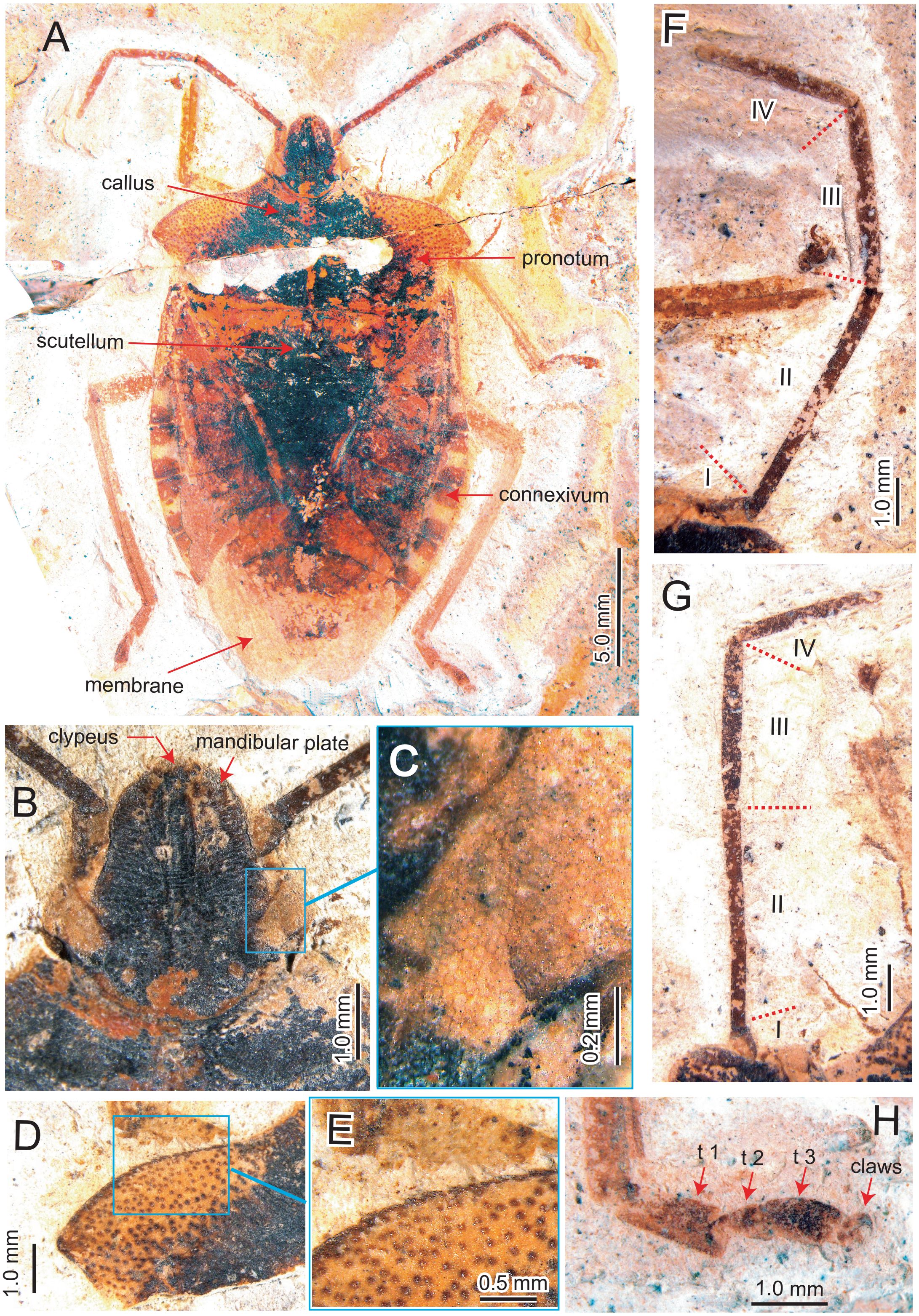

Figure 2. *Tetrapentatoma nishizawai* gen. et sp. nov., holotype. **A,** habitus, dorsal view; **B,** head, dorsal view; **C,** ommatidia of compound eye; **D,** humeral angle; **E,** serrated anterolateral margins of pronotum; **F,** left antenna; **G,** right antenna; **H,** hind tarsus. I–IV: antennomere I–IV; t1–t3: first to third tarsomeres.

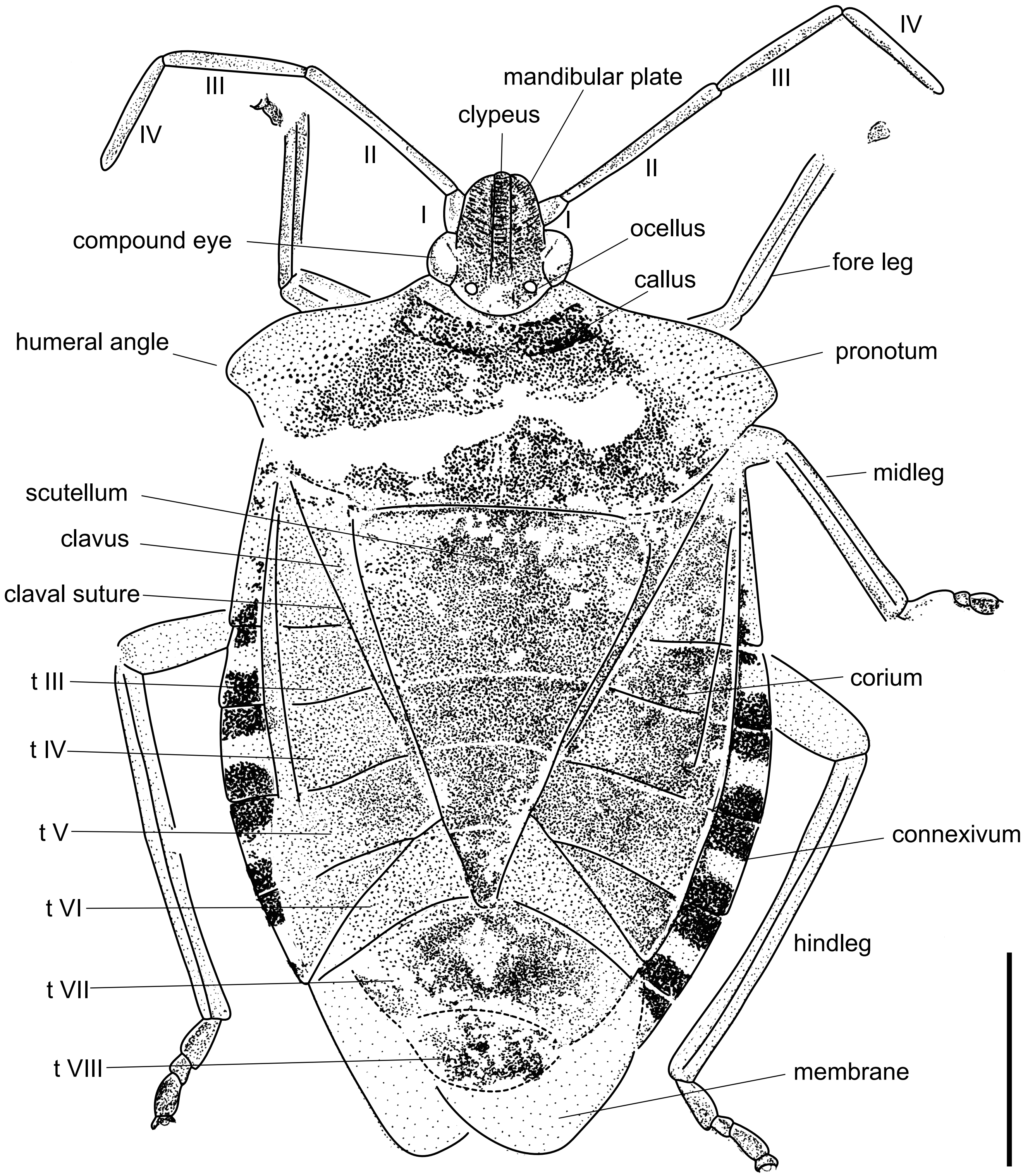

Figure 3. Line drawing of *Tetrapentatoma nishizawai* gen. et sp. nov., holotype. I–IV: antennomere I–IV; tIII–VIII: tergite III–VIII. Scale bar: 5.0 mm.

cally blunt, approximately equal in length to its maximum width across compound eyes, densely punctate, with transverse wrinkles on apical two-thirds. Compound eyes conspicuously protruding laterally (Figure 2C). Ocelli spherical, positioned basal to compound eyes. Antenna (Figure 2F, G) approximately 0.5 times as long as body length; segment I not reaching beyond head apex; segment II longest among all antennal segments, 3.9 times as long as segment I, 1.4 times as long as segment III; segment IV as long as segment III.

Thorax: Pronotum densely punctate; anterolateral margins slightly curved outward, slightly serrate (Figure 2D, E). Calli smooth on surface. Humeral angle (Figure 2D) obtuse at apex; posterolateral margins almost straight; anterolateral and humeral areas with coarse and small punctures. Scutellum subtriangular, coarsely punctate; frena extend beyond abdominal tergite VII. Corium of forewing densely punctate. Legs without pubescence, setae, or spines; hind tibia with distinct longitudinal ridges on dorsal surface; tarsi 3-segmented (Figure 2H); second hind tarsomere shortest among tarsomeres, 0.5 times as long as first hind tarsomere; third hind tarsomere as long as first hind tarsomere.

Abdomen: Abdomen oval, smooth on surface, widest at tergite IV, as wide as pronotum; tergite III–VI almost of equal length; tergite VII longest among abdominal tergites; connexivum well-developed, densely punctate.

Measurements (in mm): Body length 24.67 (from head to apex of hemelytron); length of head 3.62; maximum width across compound eyes of head 3.69; interocular distance 1.18; diameter of ocellus 0.20; lengths of antennal segments I, II, III, IV 1.20, 4.65, 3.42, 3.18, respectively; median length of pronotum 5.57; pronotal width across apices of humeral processes 14.38; median length of scutellum 9.88; maximum width of scutellum 7.19; length of hind tibia 9.36; length of first hind tarsomere 1.19; length of second hind tarsomere 0.55; length of third hind tarsomere 1.04; length of claws 0.15; and maximum width of abdomen 14.38.

Discussion

The studied specimen was identified to belong to the family Pentatomidae as indicated by typical characteristics of the family such as the broadly oval-shaped body, 3-segmented tarsi, ocelli positioned basal to compound eye, developed pronotum, and large scutellum (Schuh and Slater, 1995; Takai and Ishikawa, 2012; Rider, 2015; Schuh and Weirauch, 2020).

Nevertheless, the studied fossil is characterized by four-segmented antennae in contrast to the typical five-segmented antennae of Pentatomidae. Only the subfamilies Cyrtocorinae Distant, 1880 and Serbaninae Leston, 1953 of Pentatomidae have four-segmented antennae (Rider *et al*., 2018) although this fossil is clearly distinguishable from them since the former has two-segmented tarsi and an oddly shaped body, whereas the latter exhibits an armor-like shape (Schuh and Slater, 1995; Rider *et al.*, 2018).

Another exception is *Peromatus* Amyot and Serville, 1843 (Edessinae Amyot and Serville, 1843), which also has four-segmented antennae (Amyot and Serville, 1843; Rider, 2006). The genus *Peromatus* is a small taxon, which is only limited in Central and South America and includes only eight species (Amyot and Serville, 1843; Rider, 2006). The present fossil is somewhat similar to *Peromatus*, which has a broad oval body. *Peromatus* is characterized by a mesosternal carina lower than the metasternal carina (Amyot and Serville, 1843); unfortunately, the fossils were not preserved in the ventral view. However, many other features of this genus do not match those of the present fossil. Based on the observations of Amyot and Serville (1843), Rider (2006), Melo *et al*. (2017), and Stephen (2020), the studied fossil can be distinguished from *Peromatus* by considering the following characteristics:

(1) Head is tongue-shaped with mandibular plates subequal to clypeus (sub-triangle with longer mandibular plate than clypeus in *Peromatus*).
(2) Antennal segment I does not surpass apex of head, and segment II is distinctly long and 1.4 times as long as segment III (segment I slightly surpasses apex of head, and segment II is subequal to segment III in *Peromatus*).
(3) Hemelytral vein inconspicuous (developed and conspicuous in *Peromatus*).
(4) Humeral angles of pronotum obtuse (rounded in *Peromatus*).
(5) Connexivum with dark spots (without dark spots in *Peromatus*).

Therefore, this fossil cannot be classified in *Peromatus*. Based on these results, we conclude that this fossil is not consistent with any other genera and species of Pentatomidae and should thus be defined as a new genus and species of Pentatomidae.

Some of the subfamilies and tribes within Pentatomidae (e.g. Pentatominae and Pentatomini) are polyphyletic, and their classification by morphology is confusing (Roca-Cusachs *et al*., 2022), thus making it difficult to determine the subfamily or tribe of this new genus fossil.

On the other hand, recent studies (Tsai and Rédei, 2014; Rédei and Tsai, 2021) have considered seven genera in Pentatomini, namely *Pentatoma* Olivier, 1789, *Acrocorisellus* Puton, 1886, *Bifurcipentatoma* Fan and Liu, 2012, *Ramivena* Fan and Liu, 2010, *Lelia* Walker, 1867, *Priassus* Stål, 1868, and *Zhengica* Rédei and Tsai, 2021 as *Pentatoma*-complex based on male genital and other morphological characters. These morphological characters, typical for the *Pentatoma*-complex, include large-oblong bodies, possessing anteriorly finely denticulate pronotum, produced humeri and scutellum covering half of the abdomen (Rédei and Tsai, 2021). The fossil's morphology is consistent with the above characteristics; therefore, it is reasonable to consider it as a member of the *Pentatoma*-complex.

Pentatoma-complex is a monophyletic group consisting of species that have been shown to be closely related as revealed by phylogenetic analysis (Roca-Cusachs *et al*., 2022). *Pentatoma*, a representative member of the *Pentatoma*-complex, is the type genus of Pentatomini and Pentatominae. This indicates that the higher taxa of this fossil can be included in Pentatomini and Pentatominae.

Pentatoma-complex is distributed only in East Asia (Tsai and Rédei, 2014; Rédei and Tsai, 2021). The discovery of fossils of *Pentatoma*-complex, *Tetrapentatoma nishizawai* gen. et sp. nov. from the Late Pliocene, is important evidence that *Pentatoma*-complex appeared earlier than the Late Pliocene in East Asia. And this is the oldest fossil record of them.

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Author contributions

Hiroaki Aiba initiated the study, drafted the manuscript, and compiled all figures. Jun Souma revised the manuscript and provided taxonomic input. Yui Takahashi revised the manuscript and provided input on the geological characteristics of the Motojuku Group. All authors contributed to the writing of the paper.