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Source: Paleontological Research, 27(4) : 441-450

Published By: The Palaeontological Society of Japan

URL: <https://doi.org/10.2517/PR220018>

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A new species of fossil Nymphalidae (Lepidoptera, Papilionoidea) from the Upper Pliocene Motojuku Group, Gunma Prefecture, Japan

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Received May 27, 2022; Revised manuscript accepted September 22, 2022; Published online March 1, 2023

Abstract. In this study, we describe and illustrate a new fossil species of Nymphalidae (Lepidoptera, Papilionoidea), *Neptis kabutoiwaensis* sp. nov., based on an impression fossil from the Upper Pliocene Motojuku Group, Gunma Prefecture, central Japan, which is the first fossil representative belonging to the subfamily Limenitidinae of Nymphalidae. In addition, our study is the first to report the discovery of a named Papilionoidea fossil from the Pliocene Series. The fossil shares characteristics, such as the reduced forelegs, open discal cell in the forewing, and short Sc+R1 vein in the hindwing, with the tribe Neptini of Limenitidinae. However, the presence of the CuP vein in the forewing suggests that the studied fossil is clearly different from known species of tribe Neptini. This is an important discovery that can assist us in exploring the evolution of the tribe Neptini during the Pliocene, because this new species has the possible ancestral characteristic of a CuP vein in its forewing.

ZooBank registration: urn:lsid:zoobank.org:pub:5D268512-5CBD-4C9B-BA71-474876011BF6

Keywords: Fossil insect, Late Pliocene, Limenitidinae, Motojuku Group, *Neptis*, Nymphalidae

Introduction

Nymphalidae is the most diverse family in the superfamily Papilionoidea, consisting of 541 genera and more than 6000 species belonging to 13 subfamilies (Wahlberg *et al.*, 2009). This family comprises medium or large-sized butterflies that are distributed in Holarctic, Indo-Australian, Neotropical, and Afrotropical regions (Teshirogi, 2015). Nymphalids are characterized by small or reduced forelegs and antennae that always have two grooves on the underside (Khyade *et al.*, 2018). Nymphalid fossils are quite limited because of their fragile bodies. To date, only 35 species have been described from Cenozoic strata, and Sohn *et al.* (2015) reviewed these fossil records in detail. The oldest nymphalid fossil is from the Lower Eocene Green River Formation in Colorado, USA (Durden and Rose, 1978), but its classification within the family is unclear. Other Eocene records consist of 10 species discovered in the Florissant Formation, Colorado, USA (Scudder, 1889; Emmel *et al.*, 1992; Grimaldi and Engel, 2005). Two Oligocene examples from the Lower Oligocene were found in the Calcaires de Montfuron and

Calcaires de Vachères Formations in France (Nel *et al.*, 1993; Nel and Descimon, 1994), while six species were found in the Upper Oligocene Aix-en-Provence Formation, France (Scudder, 1872; Nel and Nel, 1986). Additionally, two species were found in Miocene Dominican amber (Peñalver and Grimaldi, 2006). In the Pliocene, only one example, with partially preserved forewing and thorax, was described as *Limenites* sp. from deposits at Willershausen, Germany (Branscheid, 1977). Another uncertain fossil, *Aporia?* sp., was described from the same locality (Brauckmann *et al.*, 2001). Thus far, no named Papilionoidea fossils have been reported from the Pliocene. The fossil records of an extant species, *Hestina japonica* (Felder and Felder, 1862), were described from the Shiobara Group (Middle Pleistocene, 0.3 Ma), Tochigi Prefecture, Japan (Fujiyama, 1983). The species *Charaxes candiope* (Godart, 1824) was described from the East African Copal in unconsolidated sediments (Late Pleistocene) from Zanzibar Island, Tanzania (Skalski, 1976).

Notably, Pliocene records on the Papilionoidea are lacking because of the limited distribution of the Konservat-

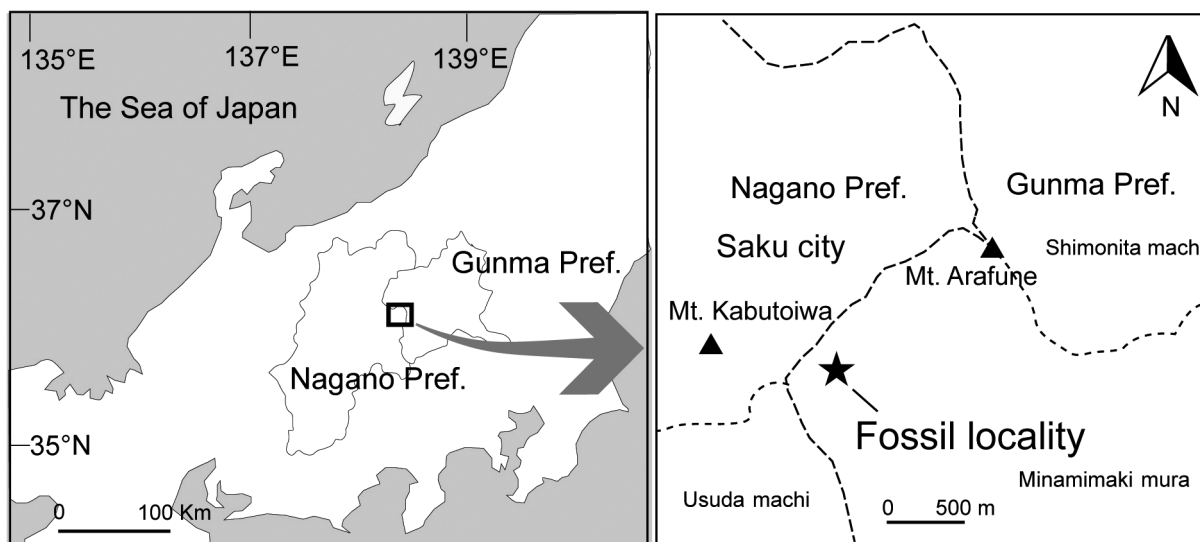


Figure 1. Map of the study area. The star represents the location of the fossil discovery on the eastern slope of Mt. Kabutoiwa, Gunma Prefecture, Japan.

Lagerstätten. Here, we describe a new fossil species of the genus *Neptis* belonging to a family Nymphalidae from the Upper Pliocene Motojuku Group, Gunma Prefecture, central Japan.

Geological setting

The Motojuku Group, distributed the prefectural border area between Gunma and Nagano pefs. (Figure 1), comprises the Maisawa and Monogatariyama Formations, in ascending order (Motojuku Collapse Research Group, 2018). The lower part of the Maisawa Formation includes lake deposits consisting of fine-grained muddy tuff. The lake deposits, named the “Kabutoiwa Formation,” after Mt. Kabutoiwa, contain many fossils of plants (Yagi, 1931; Ozaki, 1984), frogs (Hasegawa *et al.*, 1993; Nokariya and Hasegawa, 1998), and diatoms (Tanaka and Nagumo, 2019). Among the insect fossils, 11 orders and 43 families have been reported (e.g., Koshimizu, 1983; Tanaka and Mano, 2017; Tanaka, 2021); however, most of these have only been identified up to the order or family levels. Among Lepidoptera, only a fossil leaf miner from the Nepticulidae family has been reported (Kuroko, 1987). Frog and diatom fossils have been belonging to extinct taxa. Sato (2007) used K–Ar dating to estimate the numerical age of the “Kabutoiwa Formation” to be 3.5 Ma (the Late Pliocene). The specimen studied herein was obtained on the eastern slope of Mt. Kabutoiwa, toward the Gunma Prefecture (Figure 1).

Material and methods

The specimen was collected by Hikaru Nishizawa and entrusted to the author by Ken’ichi Saiki of the Natural History Museum and Institute, Chiba, Japan. As shown in Figure 2, the specimen was preserved in grayish, fine-grained muddy tuff and included the head (lateral view), left and right antennae, proboscis, thorax (lateral view), basal part and costal margin of the left forewing, and costal margin and apex of the right hindwing. The abdomen was not preserved. The counterpart of this fossil has not been discovered. The studied specimen was deposited in the Gunma Museum of Natural History under repository number GMNH-PI-6321. The fossil was observed under a Leica M205 C microscope (Leica Corporation, Wetzlar, Germany). Photographs were captured using a Leica MC170HD microscope running Leica Application Suite Version 4.1.3. (Leica Corporation). The images were sharpened, and their contrast and tonality were adjusted using Adobe Photoshop TM Version CS6 (Adobe Systems Incorporated, San Jose, CA). The nomenclature of the veins followed Nielsen and Common (1991), and terminology for morphological characters followed Leite *et al.* (2013).

Systematic paleontology

Order Lepidoptera Linnaeus, 1758
 Superfamily Papilionoidea Latreille, 1802
 Family Nymphalidae Rafinesque, 1815
 Subfamily Limenitidinae Behr, 1864
 Tribe Neptini Newman, 1870

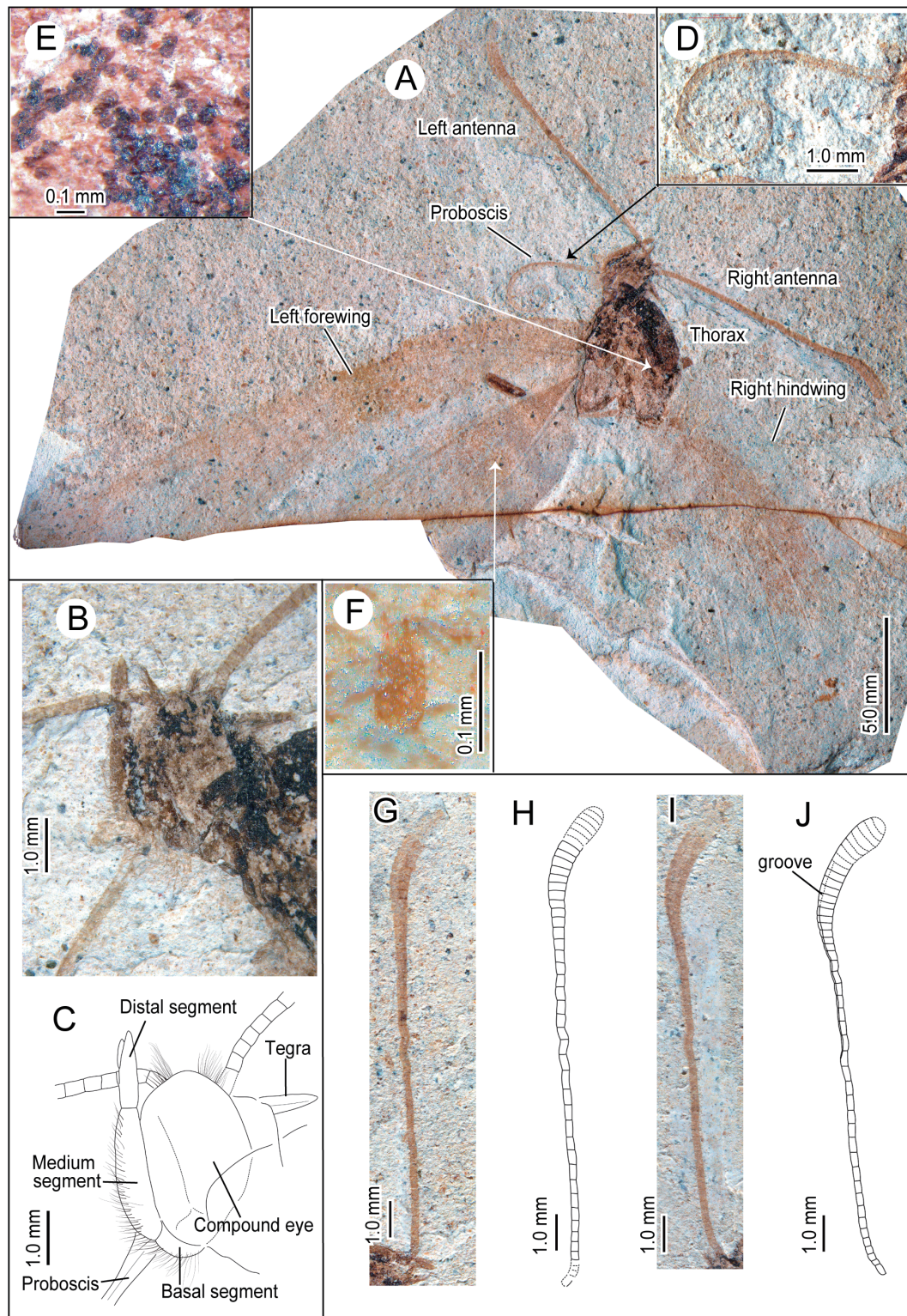


Figure 2. Photographs and diagrams of the morphology of *Neptis kabutoiwaensis* sp. nov., holotype, GMNH-PI-6321. A, Photograph of the specimen in rock; B, C, details of its head; D, enlarged proboscis; E, thorax (enlarged scale); F, forewing; G, H, left antenna; I, J, right antenna.

Genus *Neptis* Fabricius, 1807
Neptis kabutoiwaensis sp. nov.
 [Japanese name: Kabutoiwa-misujityo]

Figures 2, 3, 4A and 4B

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Holotype.—GMNH-PI-6321: Impression of a head, thorax in lateral view, and incomplete forewing and hindwing (Figure 2A) were preserved in grayish, fine-grained muddy tuff. Sample dimensions were 45 × 43 × 10 mm.

Type locality and horizon.—The eastern slope of Mt. Kabutoiwa, on the Gunma Prefecture side, Japan (Figure 1); Upper Pliocene Motojuku Group, Maisawa Formation.

Etymology.—Kabutoiwa, named after the mountain near the fossil locality.

Diagnosis.—Medium-sized nymphalid butterfly. The forewing has a distinct discal streak, with vein R2 arising from the common stalk of veins R3–R5, a short and thin sclerotized CuP vein, and a relatively thick CuA vein. The distal segment of the labial palpus is short and slender (Figure 3).

Description.—Body preserved in lateral view. Head and thorax sclerotized. Actual forewing length approximately 32 mm. Head and thorax dark brown. Antennae, forewing, and hindwing light brown in color.

Head (Figure 2B and C) preserved in lateral view and 2.56 mm long and 2.12 mm wide with large compound eyes; vertex with thin bristles near the base of antennae. Left labial palpus completely preserved; short basal segment (0.71 mm) with thin long hairs (1.97 mm long). Second segment elongated, and widest at middle with thin hairs. Distal segment short and slender (1.12 mm long), approximately half the length of the medium segment, with no hairs. Proboscis (Figure 2D) 9.13 mm long, pale brown in color, and two-thirds the length of antennae.

Antennae (Figure 2G, H, I and J) preserved entirely, although slightly obscured; clavate shape, moderately long, and brown throughout but lighter apically, with 46 segments. Right and left antennae 13.25 and 13.28 mm long, respectively. Antennomere 1 (scape) approximately twice the length of antennomere 2. Antennomere 2 short, but not swollen. Successive antennomeres gradually lengthened towards middle of antenna, and then shortened towards the apex. Antennomeres gradually swelled in apical third of antenna. One groove slightly visible in right antenna, but the other groove not visible (Figure 2J).

Thorax (Figure 3E) 5.63 mm long and 4.52 mm wide. Terga preserved at base of head, 1.00 mm long, elongated and triangular, pointed at apex. Dorsal surface of mesothorax loosely curved. Scutum II and scutellum II

dark brown and sclerotized with numerous circular scales (60–70 µm in diameter) (Figure 2E); hairs not preserved. Femur of foreleg thin.

Forewing (Figure 3A and B): basal part and costal margin of left forewing preserved. Apex and outer margin absent. Preserved part of forewing 28.59 mm long; actual wing length estimated to be approximately 32 mm. Forewing light brown; cells M2 and R5 not colored. Discal cell open; vein CuA thick and almost straight; vein 1A+2A thick but slightly curved; vein CuP obscured, short, thin (Figure 3F), slightly sclerotized, and 5.12 mm long; veins M1 and M2 straight; veins Sc, R1, and R2 almost parallel with vein R2, arising from common stalk of veins R3–R5. Some scales (Figure 2F) preserved in cells 1A+2A, and CuA2 elongated with a rectangular shape (approximately 100 µm long and 50 µm wide), different from that observed in the thorax. The length of visible veins: Sc (13.80 mm), R (8.78 mm), R1 (9.49 mm), R2 (10.39 mm), and CuA (9.23 mm).

Hindwing (Figure 3C and D): Costal margin and apex of right hindwing well preserved; basal half light brown in color; cell C not colored. Humeral vein slightly visible, arising from vein Sc+R1; vein Sc+R terminated at the apical third of anterior margin. Length of visible veins: Rs (16.90 mm), M (1.93 mm), and R (0.81 mm).

Discussion

Morphological comparison

We created a reconstruction from preserved fossils (Figure 4A and B). The butterfly was medium sized with a light-colored streak on its forewings; the uncolored part of the wing was presumed to be the discal streak.

Based on the reduced forelegs and the presence of a groove at the base of the antenna, the study specimen undoubtedly belongs to the family Nymphalidae (Khyade *et al.*, 2018). Additionally, this specimen can be placed in the tribe Neptini of this family according to the characteristics of its wing veins and cells: the presence of the open discal cell in the forewing, a short straight humeral vein, and short Sc+R1 veins in the hindwing (Chermock, 1950).

The tribe Neptini includes the six genera: *Aldania* Moore (1896), *Lasippa* Moore (1898), *Neptis* Fabricius (1807), *Pantoporia* Hübner (1819), *Phaedyra* Felder (1861), and *Lebadea* Felder (1861) (Wahlberg and Brower, 2007). Only species of the genus *Neptis* are distributed in modern Japan, such as *N. alwina* (Bremer et Grey, 1853), *N. sappho* (Pallas, 1771), *N. hylas* (Linnaeus, 1758), *N. rivularis* (Scopoli, 1763), *N. philyra* Ménétries, 1859, and *N. pryori* Butler, 1871 (Inomata, 1990). The studied fossil is similar to these extant species owing to the presence of a discal streak on its forewings. *N. sappho* resembles the

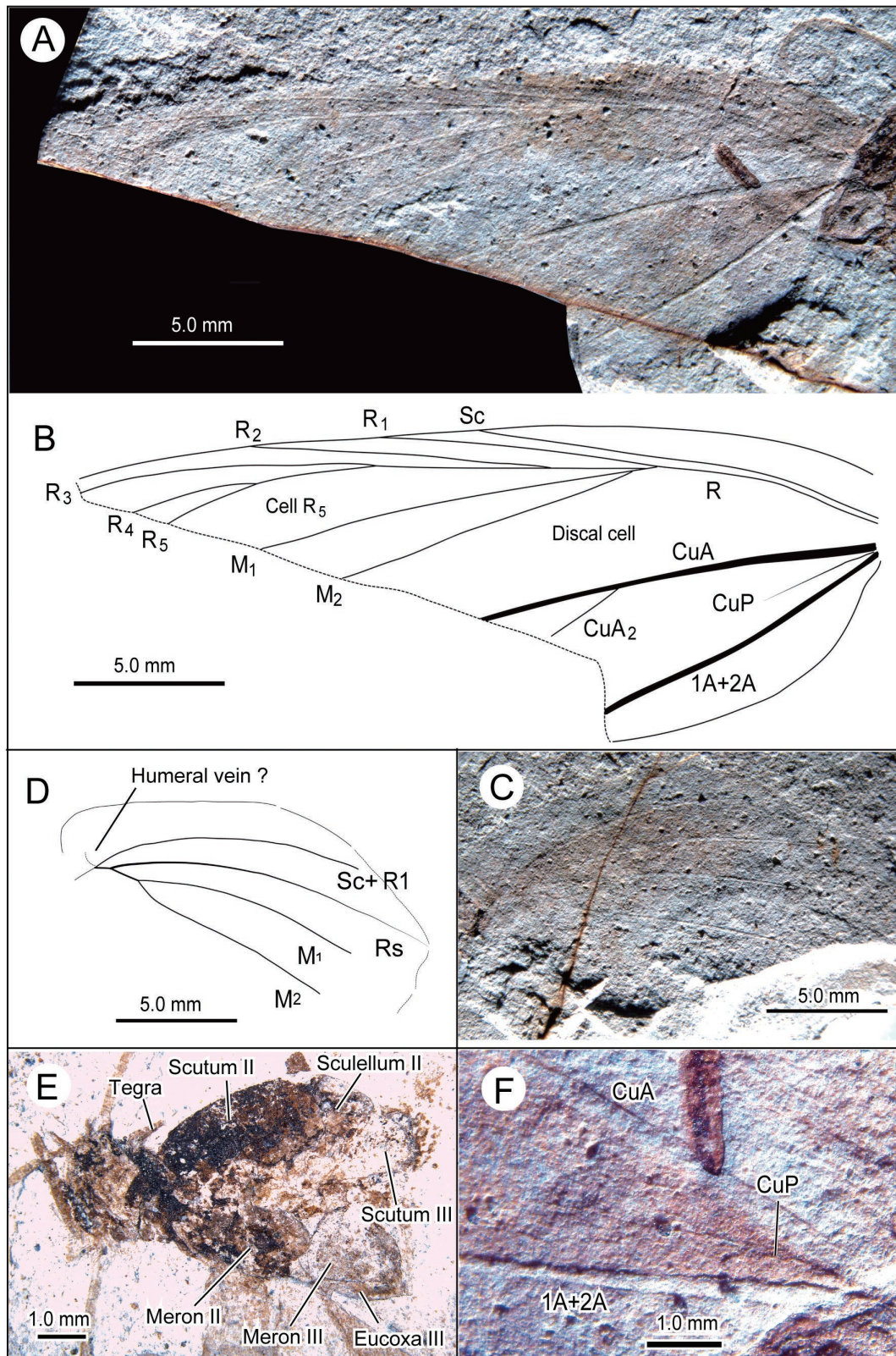


Figure 3. Photographs and diagrams of *Neptis kabutoiwaensis* sp. nov., holotype GMNH-PI-6321. **A, B**, left forewing; **C, D**, right hindwing; **E**, details of thorax in lateral view; **F**, base of the left forewing.

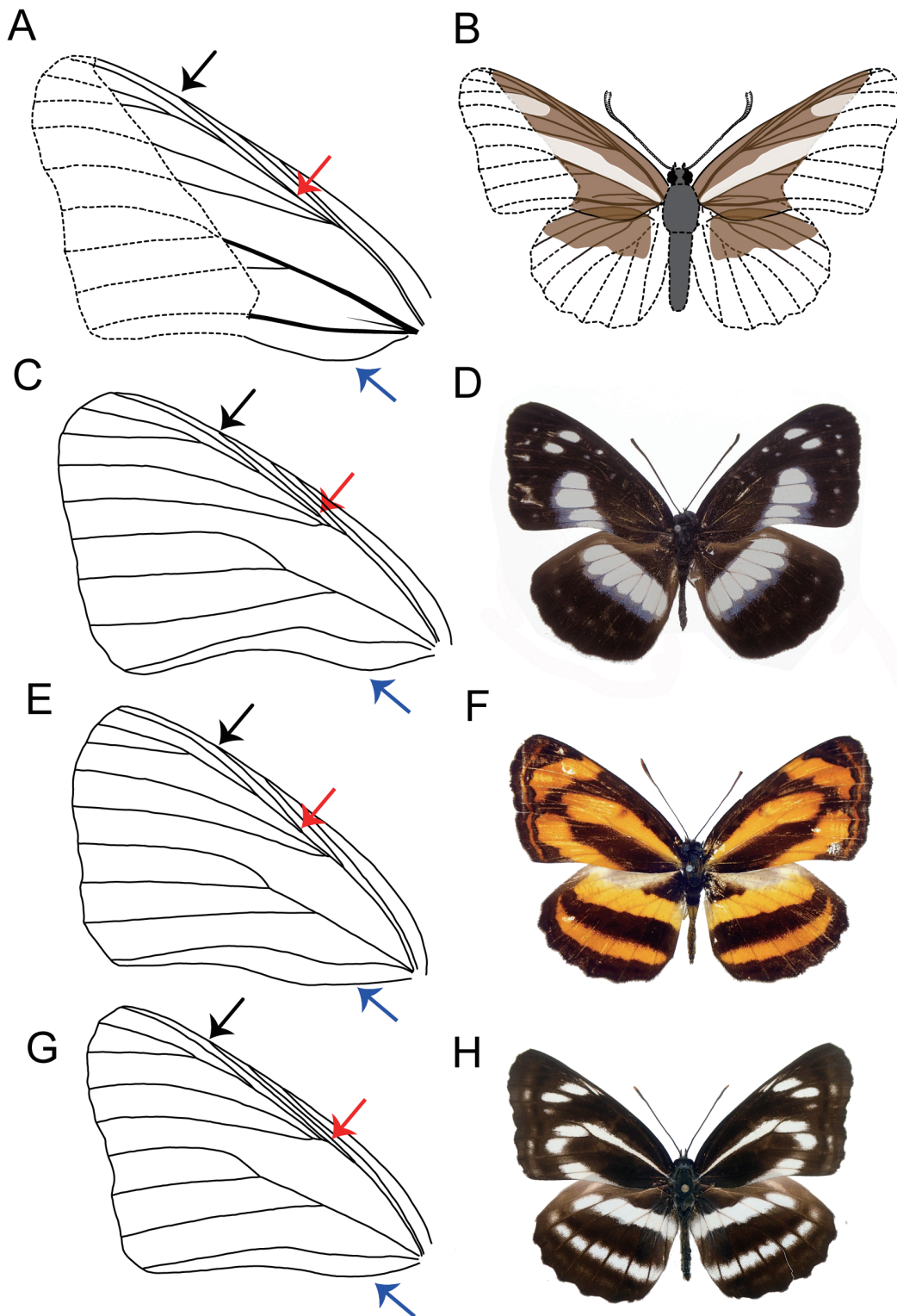


Figure 4. Reconstruction of *Nepti kabutoiwaensis* sp. nov. and comparison with some extant species. **A**, forewing of *N. kabutoiwaensis* sp. nov.; The dotted line area was estimated with reference to the forewing morphology of *Neptis sappho* (type species of the genus *Neptis*); **B**, habitus of *N. kabutoiwaensis* sp. nov.; **C**, forewing of *Pantoporia venilia*; **D**, habitus of *P. venilia*; **E**, forewing of *Pantoporia hordonia*; **F**, habitus of *P. hordonia*; **G**, forewing of *Neptis philyra*; **H**, habitus of *N. philyra*. The black, red, and blue arrows indicate vein R2, the point at which vein R2 arises, and the inner margin of the forewing, respectively.

Table 1. Comparison of antennomere quantities and measurements of the forewing and labial palpus between *Neptis kabutoiwaensis* sp. nov. and some extant species. Note: *, measurements (mm) were estimated with reference to the forewing morphology of *Neptis sappho* (type species of the genus *Neptis*); +, vein R2 arising from the common stalk of veins R3–R5; ++, exact locality and date of collection unknown.

	Antennomere numbers	Forewing					labial palpus			Specimens examined
		Length (FL)	Discal cell length (DL)	DL/FL	CuA thickness	vein R2	Distal segment length (DSL)	Medium segment length (MSL)	DSL/MSL	
<i>Neptis kabutoiwaensis</i>	46	31.97*	9.29	0.29*	0.38	+	1.12	1.97	0.57	This study
<i>Neptis alwina</i> (Bremer et Grey, 1853)	49	41.18	13.92	0.34	0.27	–	1.39	2.02	0.69	Nagano Pref., Koumi machi, Japan. 29. VII. 1992
<i>Neptis sappho</i> (Pallas, 1771)	46	32.64	11.61	0.36	0.16	–	1.49	1.67	0.89	Yamanashi Pref., Yamanakako mura, Japan. 11. VIII. 1996
<i>Neptis hylas</i> (Linnaeus, 1758)	43	32.35	10.11	0.31	0.16	–	1.12	1.62	0.69	Okinawa Pref., Ishigaki city, Japan. 4. VII. 1995
<i>Neptis rivularis</i> (Scopoli, 1763)	40	28.52	9.46	0.33	0.11	–	1.27	1.53	0.83	Tochigi Pref., Nikko city, Japan. 12. V. 1989
<i>Neptis phillyra</i> Ménétries, 1859	49	35.29	14.26	0.40	0.19	–	1.67	2.21	0.76	Tochigi Pref., Awano machi, Japan. 12. V. 1997
<i>Neptis pryori</i> Butler, 1871	43	34.78	12.84	0.37	0.22	–	1.32	1.50	0.88	Hyogo Pref., Hamasaki machi, Japan. 23. V. 2005
<i>Neptis (Aldania) thisbe</i> (Ménétries, 1859)	49	36.50	13.50	0.37	0.32	+	1.40	2.35	0.60	China ++
<i>Pantoporia venilia</i> (<i>Neptis venilia</i>) (Linnaeus, 1758)	53	27.50	9.52	0.35	0.12	+	0.93	1.76	0.53	Papua New Guinea ++
<i>Pantoporia hordonia</i> Stoll, 1790	52	21.54	7.35	0.34	0.11	+	0.95	1.21	0.79	Laos ++
<i>Lasippa heliodore dorelia</i> (Butler, 1879)	48	18.22	6.74	0.37	0.08	–	0.75	1.20	0.63	MacRitchie Reservoir, Singapore. 23. V. 1979.
<i>Lebadea martha martha</i> (Fabricius, 1787)	45	31.03	15.25	0.49	0.20	–	0.78	2.43	0.32	Da Nang City, Vietnam. 16. VIII. 2014
<i>Phaedyma columella mar-tahana</i> (Moore, 1881)	53	29.62	10.29	0.35	0.21	–	1.07	1.63	0.66	Chaing Mai, Thailand. 6. IX. 1996

studied specimen in terms of forewing length and antennomere numbers. However, since the antennomere numbers of butterflies are known to be variable even in the same species (Makibayashi, 1977), we do not consider that the character is good for specific identification. The fossil is distinguished from all of these Japanese species by the short distal segment of the labial palpus, and vein R2 arising from the common stalk of veins R3–R5 (Table 1). These morphological differences suggest that the fossil is not a species closely related on the phylogenetic tree to any of the *Neptis* species distributed in modern Japan.

This specimen resembles the genera *Aldania* and *Pantoporia*, mainly owing to the R2 vein arising from the common stalk of veins R3–R5 (Figure 4C and E). In other genera, such as *Lasippa*, *Neptis*, *Phaedyma*, and *Lebadea*, R2 arises from the discal cell (Figure 4G). The specimen differs from the genus *Aldania* because of the small size of its forewing and the presence of a light-colored streak (Teshirogi, 2015). Kurosawa (1976) regards the *Neptis thisbe* (Ménétries, 1859) as *Neptis (Aldania) thisbe* because of similarities between the species and *Aldania*, as vein R2 arises from the common stalk of veins R3–

R5. The studied fossil is somewhat similar to *N. thisbe*, but can be distinguished based on its smaller wing length (Table 1).

The genus *Pantoporia* consists of 17 species (Teshirogi, 2015). *Pantoporia hordonia* (Stoll, 1790) had a similar forewing venation (Figure 4E), but the fossil differed from *P. hordonia* because of its larger forewings (Table 1). One exceptional species of *Pantoporia*, *P. venilia* (Linnaeus, 1758), has a small forewing of 19–24 mm in length (Murayama, 1989). Ohshima and Yata (2005) regard *P. venilia* (Linnaeus, 1758) as *Acca venilia* (Linnaeus, 1758), as vein R2 arises from the common stalk of veins R3–R5 (Figure 4C). The studied specimen resembles *A. venilia* because of these characteristics. Additionally, the distal segment of the labial palpus is almost half the length of the medium segment. The short distal segment of the labial palpus is a unique feature of *A. venilia* among the genera of the Neptini tribe (Table 1). These characteristics are consistent with those of the studied fossil (Figures 2B and 2C). However, the fossil was distinguishable from *A. venilia* by the more elongated forewing associated with the wing markings (Figures 4A, 4B, 4C, and 4D).

Recently, *A. venilia* was transferred to *Neptis* based on molecular phylogenetic analysis (Dhungel and Wahlberg, 2018; Ma *et al.*, 2020). The results of these studies are inconsistent with the traditional classification by Eliot (1969), and this increased the difficulty of identifying the fossil using only preserved morphologies. Furthermore, several recent phylogenetic studies suggest that the genus *Neptis* is not monophyletic (Chen *et al.*, 2017; Dhungel and Wahlberg, 2018; Ma *et al.*, 2020). Thus, the new species may be transferred to another genus, after taxonomic revision of the big genus *Neptis* in future.

Notably, the fossil is characterized by the presence of the CuP vein, which is not found in extant members of Neptini. Unfortunately, the CuP vein of the fossil species was very short and not well preserved. Thus, we could not establish a new genus based on this. In this study, we tentatively identified the fossil as a new species to the genus *Neptis*.

Remarks on peculiar forewing veins

The fossil is characterized by the presence of a short CuP vein and a thick CuA vein. The CuP vein of the new species is clearly sclerotized and not a remnant of wing folding. The presence of the vein implies that this could be an ancestral feature of family Nymphalidae. For instance, Eocene fossil species *Praepapilio colorado* belonging to Papilionidae and *Riodinella nympha* to the Riodinidae from the Green River Formation have a conspicuous sclerotized CuP vein (Durden and Rose, 1978), and modern species do not. Based on Green River species that are members of the superfamily Papilionoidea,

and Makibayashi (1995) implied that the presence of CuP vein is a possible characteristic of the ancestral group of the superfamily. The fact that *N. kabutoiwaensis* sp. nov. retains the CuP vein may also suggest that this is a primitive form of the superfamily.

Presence of *N. kabutoiwaensis* sp. nov. also provides a milestone for divergence estimation in Nymphalidae. Wahlberg *et al.* (2009) suggested that the Neptini diverged in the early Eocene (*ca.* 54 Ma.), and the first divergence within the Neptini occurs in the middle Eocene (*ca.* 42 Ma). It is, however, unclear when the genus *Neptis* or a closely associated genus appears. The studied fossil is the direct evidence for the their presence in the Late Pliocene, and furthermore the primitive characteristic of the fossil may imply that their divergence occurred not long before the Late Pliocene.

Conclusion

We described a new fossil species of Nymphalidae (Lepidoptera, Papilionoidea), *Neptis kabutoiwaensis* sp. nov., from the Upper Pliocene Motojuku Group, Gunma Prefecture, central Japan. This is the first fossil representative belonging to the subfamily Limenitidinae of Nymphalidae. In addition, our study is the first to report the discovery of a named species of Papilionoidea from the Pliocene Series. Additionally notable forewing veins are discussed. Presence of *N. kabutoiwaensis* sp. nov. may imply that the divergence of the genus *Neptis* or closely associated genus occurred not long before the Late Pliocene.

Acknowledgements

We would like to thank Hikaru Nishizawa for discovering this specimen, and Ken'ichi Saiki of the Natural History Museum and Institute, Chiba, for giving us the opportunity to study it. Additionally, we would like to thank Yuji Takakuwa of the Gunma Museum of Natural History for accepting the specimen. We thank Kotaro Saito for providing specimens for comparison. We thank Kazunari Nicyo and Haruo Fukuda for information about the comparison specimens. Lastly, we are grateful to two reviewers and an editor for their constructive comments.

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Author contributions

H. A. initiated the study and wrote the manuscript and made all figures. Y. T. revised the manuscript and discussed the geology of the Motojuku Group. Y. S. revised the manuscript and taxonomic aspects. All authors contributed to the writing of the paper.