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Abstract

Ten Odonata fossil larvae from the Middle Pleistocene Shiobara Group in Nasushiobara City, Tochigi Prefecture, are described in this study, and identified as *Sieboldius albardae*. Every stage of instars from middle to final larvae is represented in the collection of *S. albardae* in the current and previous studies, but fossils of earlier stages are missing. Such preservation possibly reflects the difference of cuticle strength between larval stages. Habitats of living individuals of the various species of aquatic insects yielded from the Shiobara Group suggest the presence of river(s) in the Paleo-Shiobara Lake.

Keywords: insect fossils, Odonata, Pleistocene, paleoenvironment, larval instar

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1. Introduction

The Middle Pleistocene Miyajima Formation of Shiobara Group[1,2] in Nasushiobara City, Tochigi Prefecture, Japan (Figures 1-A, B, 2) is a well-known Konservat-Lagerstätte[3], which has yielded abundant well-preserved fossils such as plants, vertebrates, and insects[4,5,6,7]. The rocks including fossil leaves are commonly known as "Konoha-ishi" in Japanese, meaning "stones bearing tree leaves". The number of insect fossils from this Group have remained few for many years compared with that of plant fossils, but their studies have been recently conducted actively[8,9]. In addition, these fossils are utilized as teaching material in elementary school[8,10].

Odonata fossils including adult and larva from Japan have been reported frequently, and about 40 specimens had been reported in Japan[4,8,11,12,13,14,15]. The oldest literature on Odonata fossils is by Asahina[4], who described

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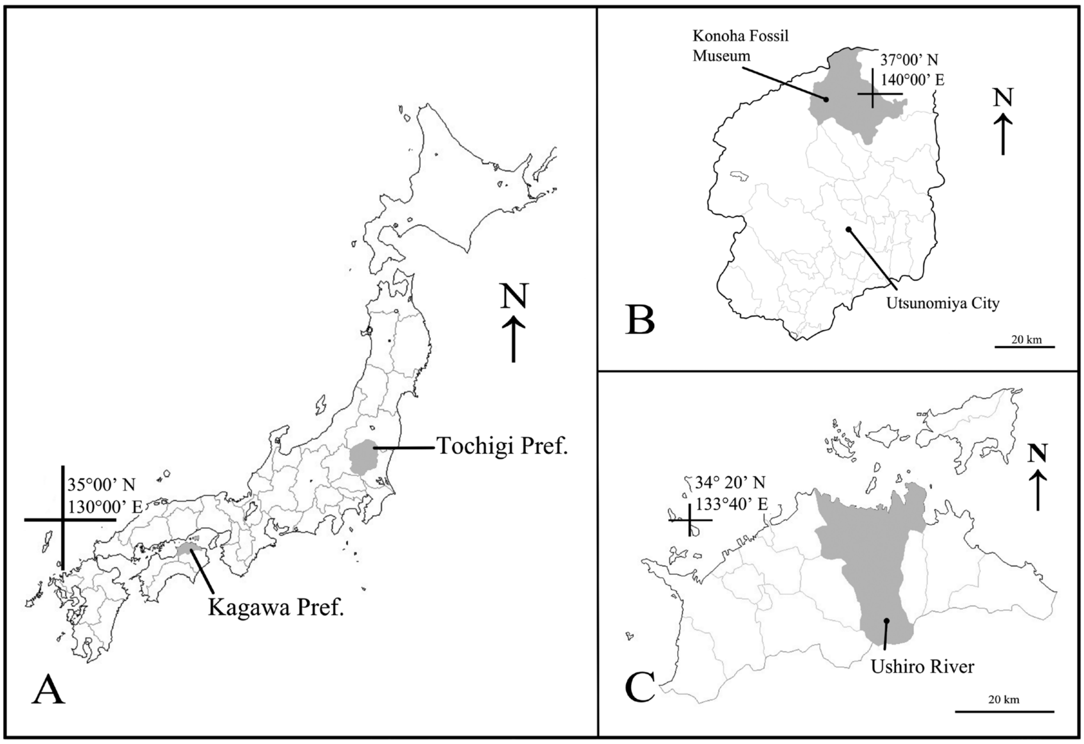

Figure 1. Locality of fossils and living specimens in this study. A, Prefectures where the insect specimens were collected. Fossil specimens came from Tochigi Prefecture and living specimens came from Kagawa Prefecture. B, Location of Konoha Fossil Museum (black point) in Nasushiobara City (gray) of Tochigi Prefecture. C, Locality where living specimens were collected in Takamatsu City (gray), Kagawa Prefecture. Filled circle indicates collection spots. These maps are based on CraftMAP (http://www.craftmap.box-i.net/).

one wing of *Macromia amphigena amphigena* from the Shiobara Group. In recent years, Tanaka[11, 12] had reported a hind wing of *Anax* and a larva of Coenagrionide from the Late Pliocene Kabutoiwa Member of Honjuku Formation in Gunma Prefecture. A forewing and a larva of *Macromia amphigena amphigena*, a larva of *Sieboldius albardae*, and hindwing of Gomphidae gen. et sp. indet. have been reported[4, 8, 13] in the same group. Most Odonata fossil larvae from Japan are reported as only one specimen per species at each formation [8, 14, 15], and Odonata fossil larvae representing different larval stages have not been described yet. In this paper, we describe 10 Odonata fossil larvae including various size from Shiobara and estimate the paleoenvironment at that time.

2. Geological background

All specimens described in this study were collected from the Middle Pleistocene Miyajima Formation of the Shiobara Group exposed in the backyard of Konoha Fossil Museum in Nasushiobara City of Tochigi Prefecture, Japan[1, 2] (Figures 1-A, B). This group is distributed in the center of Shiobara Basin (Figures 2) and considered to be composed of caldera lake deposits[1, 2]; the lake at that time is commonly known as the Paleo-Shiobara Lake. Onoe [1] suggested the group unconformably covers the basement rocks and is overlain by terrace gravels, talus deposits and lava flows of Takahara Volcano.

Various previous studies have divided the Shiobara Group into several stratigraphic units[1, 2, 16, 17, 18] etc.. Among of them, this study follows stratigraphic units of Tsujino and Maeda [2]. The Kamishiobara Formation is distributed on the eastern, western, and northern margins of the Shiobara Basin (Figure 2). The formation is mainly composed of subangular to rounded gravels and sand, and represents to the proximal terrigenous marginal facies of Paleo-Shiobara Lake. On the other hand, the Miyajima Formation is situated in center to eastern areas of the basin[2, 19] (Figure 2). The formation is characterized by laminated mudstone and siltstone and indicates deep profundal, hemipelagic and stagnant condition. The age of sediments in these formations are dated as about 300 Ka by comparing tephra around the Shiobara Basin and the K-Ar dating of several andesite lavas, derived from the Takahara Volcano, are interbedded with or covering sediments of the group[20, 21].

The Miyajima Formation has yielded abundant insect

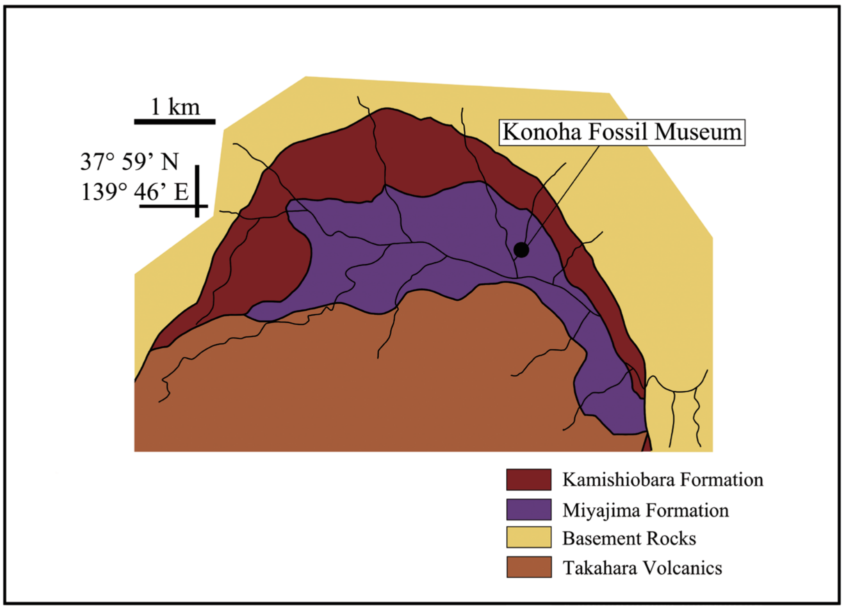

Figure 2. Geological map of the Shiobara area, based on Tuzino et al.[21]. A black circle indicates location of Konoha Fossil Museum where the fossil specimens were collected.

fossils[8, 22, 23, 24, 25]. Diptera are the most common fossils, then those of Ephemeroptera and Hymenoptera follow. This formation also contains insect fossils of other orders (e.g. Coleoptera[8], Heteroptera[5]).

3. Material and Method

When necessary, the specimens are prepared under a digital microscope (Leica DMS 1000) at Tokyo Gakugei University, using an insect pin. Photographs were taken by Nikon D850 with a Macro-NIKKOR lens (120 mm F 46.3, 55 mm f 2.8, and 65 mm f 4.5), and the images

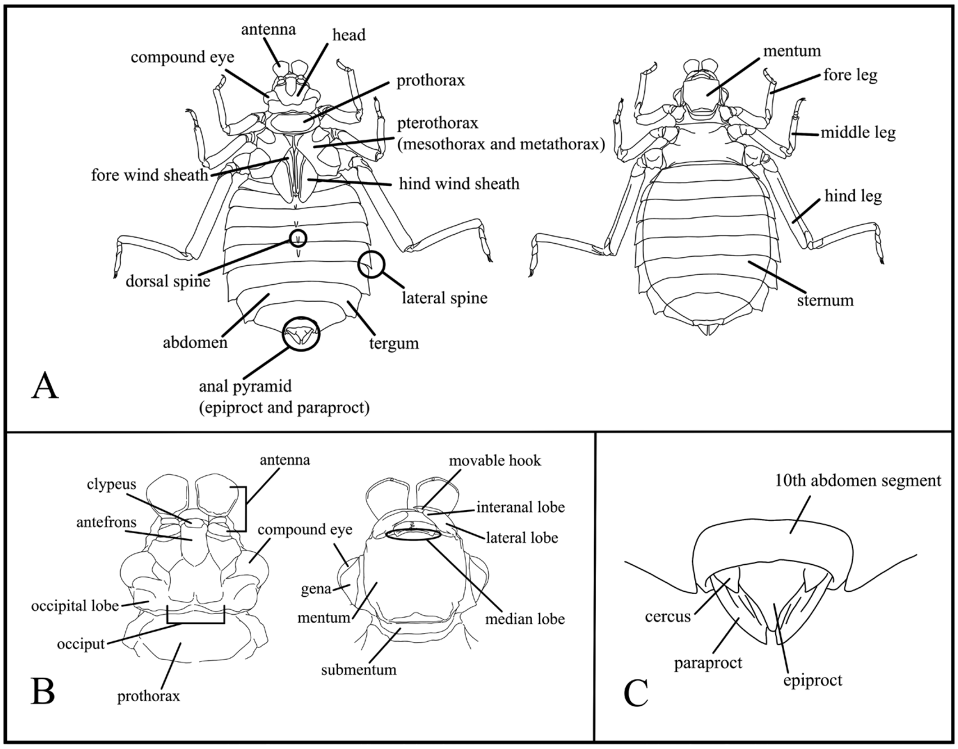

Figure 3. Anatomical illustrations of *Sieboldius albardae*. A, general view in dorsal (left) and ventral (right) views. B, head in dorsal (left) and ventral (right). C, anal pyramid. Based on Sugimura et al.[27] and Ozono et al.[28].

are processed with CLIP STUDIO PAINT Ver 1.11.14 (CELSYS, Inc.). Anatomical terms and diagnosis used in this study follow Ozono et al.[26] and Sugimura et al.[27]. Moreover, we made anatomical illustrations based on this literature (Figure 3). In this study, classification of Odonata employs that of Ozono et al.[28]. Anatomical abbreviations and measurement definitions are shown in Table 1 and Figure 4. All specimens were measured by Nikon Profile Projector V-12B at the Kyusyu University Museum. The habitats of fossil insects are estimated based on the data of living species in Kawai and Tanida[29].

For the comparison with fossil specimens, the extant specimens of *Sieboldius albardae* are collected from Ushiro River, Takamatsu City, Kagawa Prefecture, Shikoku, Japan (Figures 1-A, C), 28 August 2021 and 4 September 2021 by Y. Sato (Figures 5-B, 6-B, 7-E, F).

Institutional abbreviation. SFM, Shiobara Fossil Museum ("Konoha-kaseki-en" in Japanese)

Table 1. Definition of the dimensions used in this study.

Abbreviation	Dimension	Definition in this study
BL	Body length	The longitudinal length from the anterior margin of the head except for the antenna to the apex of the anal pyramid
TOL	Total length	The distance from anterior end to posterior end of the fossil
HL	Head length	The longitudinal length from anterior margin the head except for the antenna to posterior of the occipt
HW	Maximum width of head	
ATL	Antenna length	The visible antennal length
TL	Thorax length	The longitudinal length from anterior margin of the prothorax to posterior of the pterothorax
TW	Maximum width of thorax	
HWL	Hind wing length	The longitudinal length from anterior margin of the hind sheath to posterior
FL	Hind femur length	
AL	Abdomen length	The longitudinal length from the anterior margin of abdomen to the posterior of anal pyramid
AW	Maximum width of abdomen	
EL	Epiproct length	The longitudinal length along median line from the posterior edge of 10th abdomen segment to the apical part of the epiproct
PL	Paraproct length	The longitudinal length along median line from the posterior edge of 10th abdomen segment to the apical part of the paraproct
APW	Maximum width of anal pyramid	

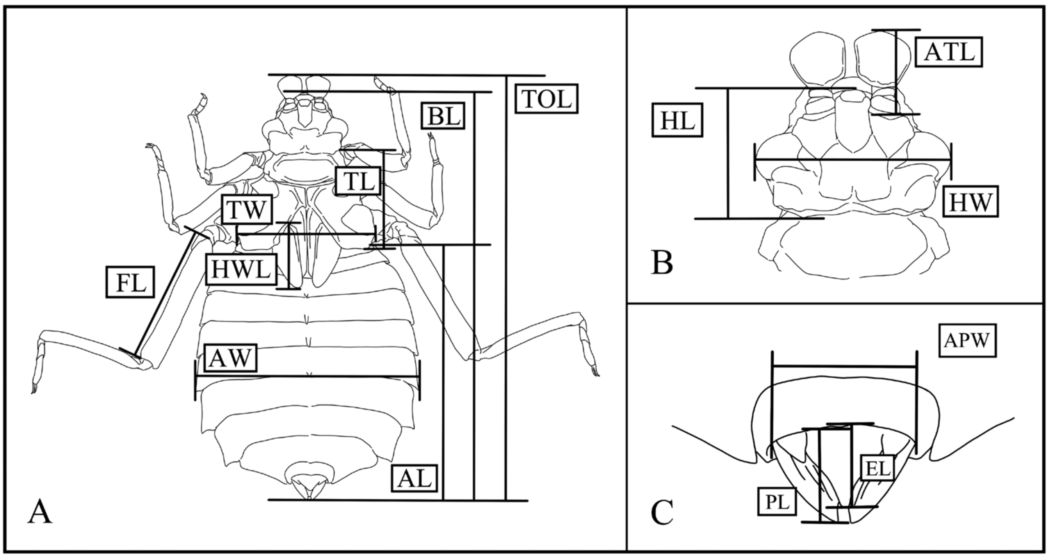

Figure 4. Measured locations of *Sieboldius albardae*. A, *Sieboldius albardae* of dorsal view. B, head. C, anal pyramid. Each black bar on the illustrations indicates measured intervals. See Table 1 for anatomical abbreviations and definitions of the measured sections.

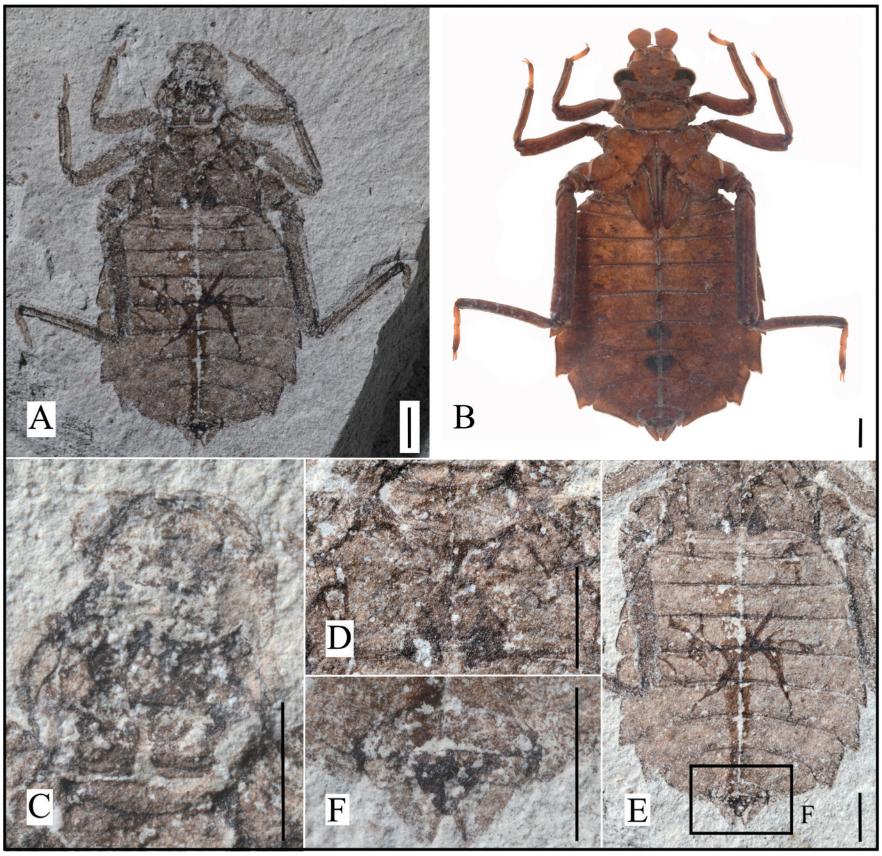

Figure 5. Dorsal view of *Sieboldius albardae* (SFMA0393a from the Shiobara Group and extant specimen). A, SFMA0393a. B, extant specimen. C, head of SFMA0393a. D, thorax of SFMA0393a. E, abdomen of SFMA0393a. F, enlargement of the anal pyramid of E. Scale bar: 2 mm.

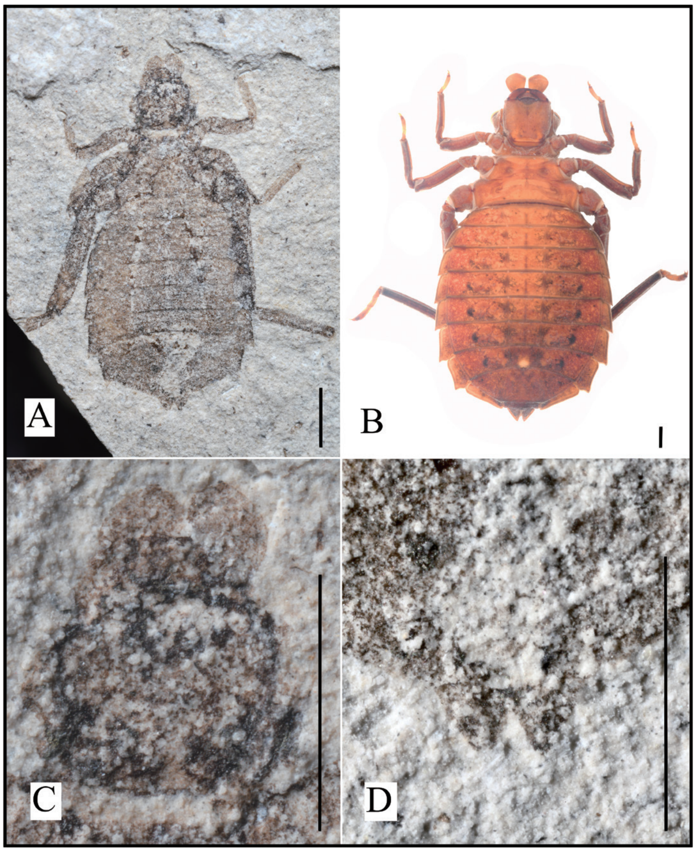

Figure 6. Ventral view of *Sieboldius albardae* (SFMA0398 from the Shiobara Group and extant specimen). A, SFMA0398. B, extant specimen. C, head of SFMA0398. D, anal pyramid of SFMA0398. Scale bar: 2 mm.

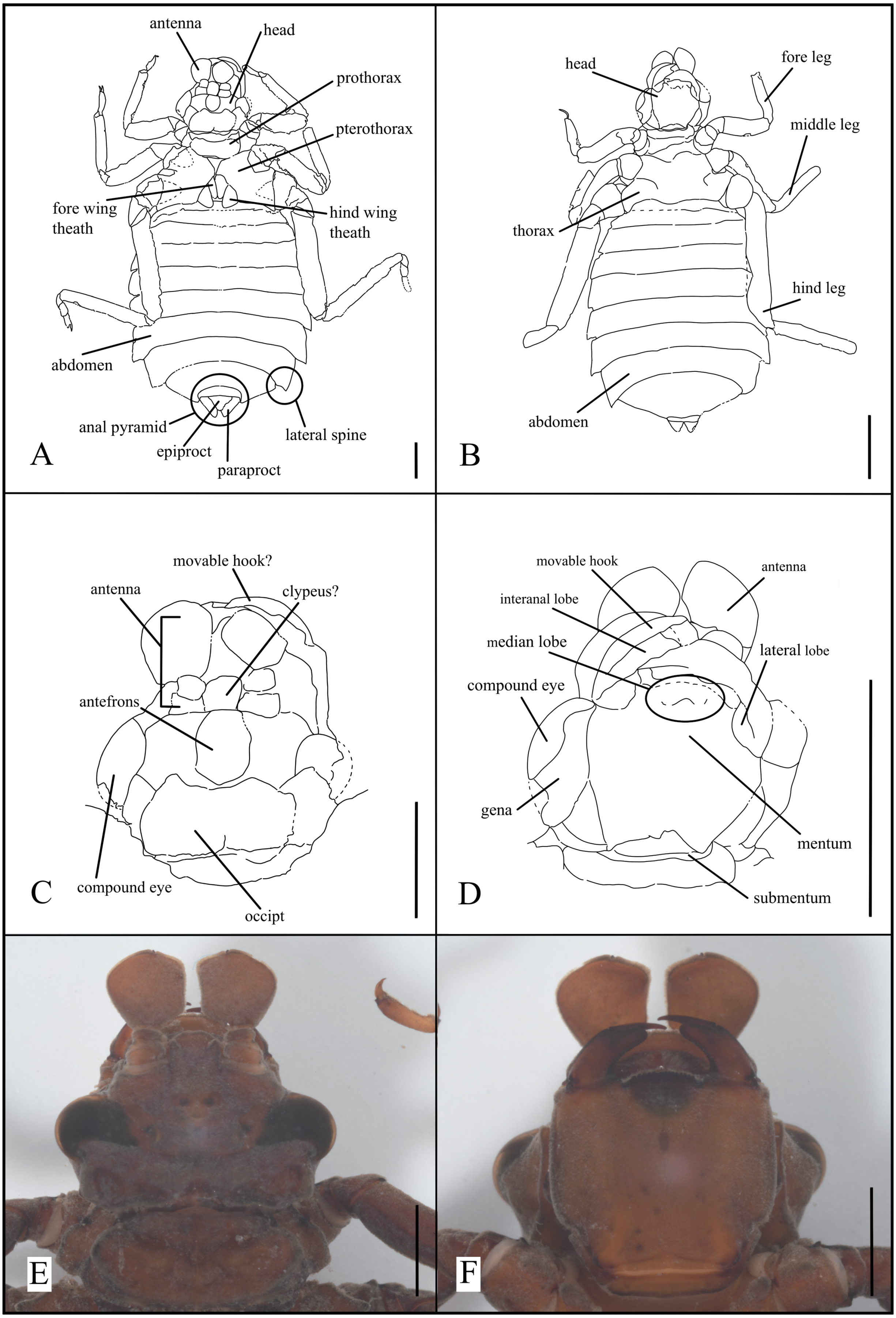

Figure 7. Interpretation of SFMA0393a and SFMA0398 with a head of extant specimen. A, SFMA0393a. B, SFMA0398. C, head of SFMA 0393a in Figure 5-C. D, head of SFMA 0398 in Figure 6-C. E, head of an extant *Sieboldius albardae* in dorsal view. F, ventral view of E. Scale bar: 2 mm.

4. Systematic Paleontology

Class **Insecta** Linnaeus 1758
Order **Odonata** Fabricius 1793
Suborder **Anisoptera** Selys 1840
Superfamily **Gomphoidae** Rambur 1842
Family **Gomphidae** Rambur 1842
Genus ***Sieboldius*** Selys 1854

Sieboldius albardae Selys 1886[30)]
Japanese name: Ko-oni-yanma
(Figures 5, 6, 7, 8)

Referred specimens. SFMA0391 (a, b), SFMA0392 (a, b), SFMA0393 (a, b), SFMA0395 (a, b), SFMA0396, SFMA0397, SFMA0398, SFMA0399 (a, b), SFMA0702, SFMA0703.

Description. SFMA0391, 0392, 0393, 0395, and 0399 are preserved as parts and counterparts (Figures 5, 8). In SFMA0391, 0392, 0393, 0395, and 0398, the body from the head to the abdomen is preserve; the dorsal view is observed entirely in SFMA0393 (Figures 5-A, 7-A), and the ventral view is preserved well in SFMA0398 (Figures 6-A, 7-B). SFMA0396, 0397, and 0702 shows thorax and abdomen. SFMA0399 and SFMA0703 include only poorly preserved abdomens but the structure of anal pyramid is clearly shown. The detailed structure of head is unclear, and the whole leg is rarely observed in most specimens (Figure 8).

The head is small for the body (Figures 5-A, 6-A) and possesses the antenna which is composed of three large segments (Figures 5-C, 7-C). Third segment of the antenna is the shape of large pentagonal fan (Figures 5-C, 7-C). In addition, the head has a labium composed of square mentum, probable submentum, rounded interanal lobe, and sharp movable hook (Figures 6-C, 7-D). A pair of compound eyes is covered with probable occipital lobe (Figure 7-C).

TW is smaller than AW (Figure 5-A, Table 2). The pterothorax is remarkably large and broad compared to the prothorax possessing elliptic outline (Figure 5-D). The shape of pterothorax is trapezoid having the long side in posterior margin (Figure 5-D). The small wing sheathes are preserved in dorsal view of these specimens, moreover, this wing sheath shows that is grows straightly backward (Figures 5-D, 8-H). All femora and tibiae are thick, and the end of hind femur reaches to about 7th abdomen segment (Figure 5-E).

The abdomen is very broad; the AW is about three times as large as the HW (Figure 5-E, Table 2). The outline of abdomen expands from 1st segment to 6th segment and contracts for later segments, especially, that of 9th segment contract strongly, so 10th segment is included in 9th segment (Figure 5-F). There are lateral spines in 3rd to 8th segments (Figure 5-E). The anal pyramid whose width is broader than length is small for the abdomen size (Figures 5-F, 6-D). The epiproct is isosceles triangle whose apex is sharp, and the length of base is a little long (Figure 5-F). The base possesses a pair of circles. The triangle paraproct is larger than the epiproct.

Remarks. The specimens described in this paper have the antenna in which 3rd segment is very broad and the flat mentum, and these features agree with all gomphid species. Gomphidae species have flat and short body compared to other families of Odonata, but our specimens have extremely flat body and large abdomen (Figures 5-B, 6-B), so they are identified as larvae of *Sieboldius*. Genus *Sieboldius* includes eight species in the world[31)], and only *S. albardae* inhabits in Japan. The abdomen of *S. japonicus*, which inhabits in the Malay Peninsula, gradually increases in width from 1st segment to the posterior margin of 8th segment, thence suddenly narrowed to the anal pyramid. As a result, the abdomen outline of this species is closer to trapezoid rather than oval[32)]. Therefore, the abdomen of fossil specimens does not agree with that of *S. japonicus*. Moreover, *Hagenius brevistylus*, which inhabits in Southeastern United States, are also similar to these specimens, but this species differs from our specimens in that the lateral spine of 7th and 8th abdomen segments sticks out backward and the hind femur is almost as long as the hind femur[33)]. Although we cannot compare these specimens with all species of *Sieboldius* larva because of the lack of sufficient dat, all features of our specimens described in this section correspond with those of *S. albardae*; therefore, we identify them as *S. albardae*.

5. Discussion

Based on the 10 larval fossils of *Sieboldius albardae* from Shiobara described here, we discuss on the

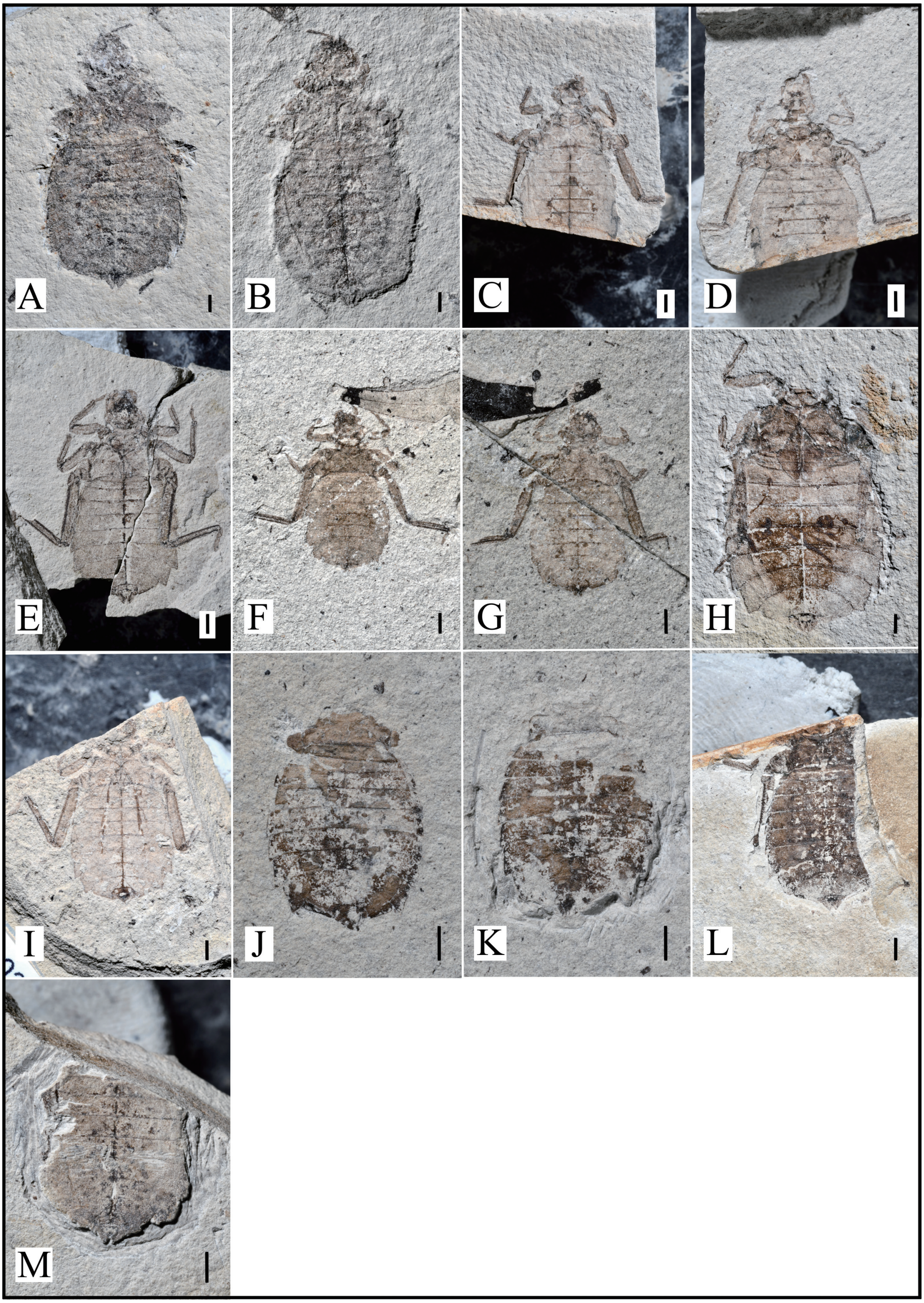

Figure 8. Fossil specimens of *Sieboldius albardae* from the Shiobara Group. A, SFMA0391a. B, SFMA0391b. C, SFMA0392a, D, SFMA0392b. E, SFMA0393b. F, SFMA0395a, G, SFMA0395b. H, SFMA0396. I, SFMA0397. J, SFMA0399a, K, SFMA0399b. L, SFMA0702. M, SFMA0703. Scale bar: 2 mm.

Table 2. Measurements of fossil specimens. See Table = 1 for anatomical abbreviations and definitions of the measured sections.

	BL	TOL	HL	HW	ATL	TL	TW	HWL	FL	AL	AW	EL	PL	APW
SFMA0391	25.98	25.98	4.20	4.77	N/A	7.19	8.70	3.15	N/A	15.88	13.74	1.19	1.73	2.40
SFMA0392	16.45	16.45	3.05	3.08	N/A	4.14	5.86	1.10	5.87	9.42	9.69	N/A	N/A	N/A
SFMA0393	19.12	20.04	3.32	3.90	1.88	4.24	6.51	1.24	6.24	12.07	10.25	0.87	1.38	2.12
SFMA0395	13.65	13.65	2.87	2.65	N/A	2.60	4.95	N/A	4.14	8.55	7.26	N/A	N/A	N/A
SFMA0396	N/A	24.50	N/A	N/A	N/A	6.76	7.77	4.21	8.66	17.61	15.78	N/A	0.94	1.71
SFMA0367	N/A	17.45	N/A	N/A	N/A	4.59	5.98	1.21	5.81	11.37	9.74	N/A	N/A	2.17
SFMA0398	11.33	11.82	2.03	2.26	N/A	1.83	3.17	N/A	3.53	7.20	5.63	N/A	0.42	1.00
SFMA0399	N/A	11.79	N/A	N/A	N/A	N/A	N/A	N/A	N/A	10.39	8.51	N/A	N/A	N/A
SFMA0702	N/A	15.48	N/A	N/A	N/A	N/A	5.59	1.01	N/A	11.78	N/A	0.86	0.78	1.96
SFMA0703	N/A	11.63	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

paleoenvironment of the Paleo-Shiobara Lake.

5．1 Larval ontogenetic stages

The wing sheath can be observed from middle instar of Odonata larva[28], and that of common final instar larva reaches 3rd or 4th abdomen segment[27]. In addition, it is known that the larval instar relates to the body size[34]. So, based on the AW, HWL, AL (Table 2) and the appearance of the fossils, we estimated the number of larval instars on the fossils. Following previous publications[34, 35], we express the final larval instar as F-0 (=Final) and the penultimate larval instar as F-1 (=F minus 1), after that, the same expression follows (Table 3). The specimens include larval instars from F-1 to F-4, and five specimens out of ten represent F-3 instar (Figures 5, 6, 8). In addition, we estimated the instar of SFMA0395 and SFMA0398 as F-5 because their BL is a little smaller than that of SFMA0392 (Figure 8, Table 2). The final instar (F-0) larva of *S. albardae* from the Miyajima Formation had already been reported in a previous study [8], and it is known that the middle instar larva of this species is about 10.2 mm[26]; this size corresponds to F-4 or F-5. Therefore, every instar from middle to final larva of *S. albardae* has been described from the Miyajima Formation.

Table 3. Estimated larval instar preserved in fossil specimens.

	instar
SFMA0391	F-2
SFMA0392	F-4
SFMA0393	F-3
SFMA0395	F-5?
SFMA0396	F-1
SFMA0397	F-3
SFMA0398	F-5?
SFMA0399	F-3
SFMA0702	F-3
SFMA0703	F-3

All Odonata fossil larvae of *S. albardae* and *Macromia amphigena amphigena* reported from the Shiobara Group[8] are over middle instars, that is, larvae in early stages have not been reported in this group yet. But early-stage larvae should be more abundant than those at final instar, and it is strange that the formers are missing in the records.

This result might reflect the difference of cuticle thickness between instar stages of Odonata larva. All insects molt to grow up through the larval stages, and an Odonata larvae usually molts 10 times[28]. The body size varies considerably between early and final stages, and the large insect might have more sclerotized cuticle to support their large body. Therefore, Odonata larvae over middle instar might have had a better chance to be preserved as fossils due to harder sclerotization than that in early stage.

5．2 Paleoenvironment of the Paleo-Shiobara Lake

Aquatic insects such as larvae of Odonata and Ephemeroptera are usually restricted to their habitats and used as bioindicators[36]. In this section, we attempt to assess the paleoenvironment of the Paleo-Shiobara Lake using its fossil aquatic insects.

The Miyajima Formation has yielded various aquatic insects: Ephemeroptera[8, 37], Odonata[4, 8, 13], Plecoptera[8], Coleoptera[8, 23, 38], and Trichoptera[8]. The paleoenvironment of the Paleo-Shiobara Lake have been discussed in a number of previous works. For instance, based on the analysis of 22 specimens of Ephemeroptera, Nishimoto et al.[37] suggested the presence of gentle river flow(s) into the Paleo-Shiobara Lake, and Hayashi et al.[38] reported the occurrence(s) of certain taxa of Pshephenidae whose habitats includes running water.

We reviewed the habitats and number of specimens of the aquatic insects previously reported from the Miyajima Formation, and checked the number of specimens reported for each species[4, 8, 13, 23, 36, 38](Table 4). It was found that

Table 4. The habitats and number of aquatic insects reported from the Miyajima Formation. Preferred habitats are based on Kawai and Tanida[29].

taxon	developmental stage	number of specimens	reference	habitat
Ephemeroptera				
Baetis sp. A	larva	30	Aiba 2015	most river
Baetis sp. B	larva	1	Aiba 2015	most river
Ecdyonurus cf. *yoshidae*	larva	2	Aiba 2015	river, shore of lake or dam
Procloeon sp.	larva	9	Nishimoto et al.2020	river
cf. *Procloeon* sp.	larva	6	Nishimoto et al.2020	river
Heptageniidae gen. et sp. indet.	larva	4	Nishimoto et al.2020	
Ephemeroptera fam., gen. et sp. indet.	larva	4	Nishimoto et al.2020	
Odonata				
Sieboldius albardae	larva	14	Aiba 2015, this study	river, lake
Macromia amphigena amphigena	larva and adult	4	Aiba 2015, Asahina 1959	river, lake, pond
Gomphidae gen. et sp. indet.	adult	1	Aiba et al. 2019	
Plecoptera				
Plecoptera fam. gen. et sp. indet. A	adult	1	Aiba 2015	most river
Plecoptera fam. gen. et sp. indet. B	larva	1	Aiba 2015	most river
Plecoptera fam. gen. et sp. indet. C	larva	1	Aiba 2015	most river
Coleoptera				
Ectopria opaca	larva	2	Hayashi et al. 2020	river, spring
Malacopsephenoides japonicus	pupa	1	Hayashi et al. 2020	river
Psepheninae gen. et sp. indet.	larva	1	Hayashi and Aiba 2016	
Trichoptera				
Nemotaulius admorsus	adult	1	Aiba 2015	pond
Trichoptera fam. gen. et sp. indet.	larva	1	Aiba 2015	

Ephemeroptera, which inhabit mostly in river, represent the largest number of individuals in the studied collection from the Paleo-Shiobara Lake, and Odonata follows. Most aquatic insects reported from this formation inhabit lotic environments today. Meanwhile, an adult of the trichopteran species *Nemotaulius admorsus* is the only specimen of a taxon which lives only in still water. Living individuals of *Sieboldius albardae* described in this study occasionally inhabit in a large lake such as Biwa Lake and Akan Lake[27] in Japan with river(s) flowing in/out. These data on the habitats and quantity of reported taxa of aquatic insects suggest that there would have been river(s) connected to the Paleo-Shiobara Lake, and this view supports Nishimoto et al.[37].

S. albardae inhabit under the root of an emersed plant and dead leaves or in a space between gravel with gentle flows[26, 27]. Many fossil leaves of various land plants and emersed plant remains occur in the Miyajima Formation[1, 8]. *S. albardae* living in the Paleo-Shiobara Lake would have inhabited in or under the piled dead leaves or the root of emersed plants in gentle flows as living individuals do today.

6. Conclusion

In this study, 10 insect fossils from the Middle Pleistocene Shiobara Group in Nasushiobara City, Tochigi Prefecture, Japan are described. These specimens are identified as the larvae of *Sieboldius albardae*, and every stage of instars from middle to final larvae of *S. albardae* have been described. We imply the possibility that the preservation in the Shiobara Group represents the difference of cuticle strength between instar stages. Most aquatic insects obtained from the Miyajima Formation inhabit lotic environment today. So, the result in this study supports Nishimoto et al.[37] who suggested the presence of gentle river flow(s) into the Paleo-Shiobara Lake, based on the habitat preference of the fossils of Ephemeroptera from the same deposits.

7. Acknowledgment

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栃木県那須塩原市から産出したヤゴ化石

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要　旨

栃木県那須塩原市にある中期更新統の塩原層群から産出した昆虫化石（ヤゴ）10標本を記載し，中齢から亜終齢までのコオニヤンマ*Sieboldius albardae*と同定した。塩原では中齢から終齢までのヤゴのみが産出していることから，ある程度成長し体の強度が増加したものだけが化石として産出する可能性が考えられる。また，これまで塩原層群から産出した多様な水生昆虫の現在の生息環境から，古塩原湖と接続した川の存在が示唆される。

キーワード：昆虫化石，トンボ目，更新世，古環境，齢

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