



Sarcophagodes duodecima sp. nov., a new small araphid fossil diatom (Bacillariophyceae) from Lower to Middle Pleistocene sediments of Japan

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Abstract

A new fossil diatom species, *Sarcophagodes duodecima*, is described from the Lower to Middle Pleistocene Karato Formation of Himeshima Island, western Japan, based on detailed morphological observation of valves using light and scanning electron microscopes. This new species is characterized by a smaller valve length range, a wide lanceolate central area, shorter striae on the valve face, and longer striae on the mantle than other members of the genus. The new species was also found in the Lower Pleistocene Bushi Formation, central Japan, suggesting that *S. duodecima* sp. nov. was widely distributed in Japan during Early Pleistocene time. The species composition in the sample chosen as type suggests that the new fossil species occupied a brackish-water habitat. Differences in morphological features from closely related taxa are discussed.

Keywords: Brackish, Himeshima Island, new species, *Opephora sensu lato*, shallow-marine sediments

Introduction

Small araphid heteropolar (opephoroid) diatoms are frequently found in brackish, estuarine, and shallow-marine habitats, and are important components of the diatom floras in these environments (Witkowski 1994, Witkowski *et al.* 2000). Opephoroid diatoms have been often been considered to belong to *Opephora* Petit (1888) or *Fragilaria* Lyngbye (1819: 182) (Witkowski & Lange-Bertalot 1993, Sabbe & Vyverman 1995). These genera contain a number of environmental indicator species that have been used for reconstructing past environments (Vos & de Wolf 1993, Ulanova *et al.* 2009); thus, the taxonomy of small opephoroid diatoms is also important from the viewpoint of paleoenvironmental reconstruction.

The valve characteristics currently used to separate the genera of small araphid diatoms are so small that they can only be observed under a scanning electron microscope (SEM). Since the 1980s, many morphological features of *Fragilaria sensu lato* and *Opephora sensu lato* have been newly described based on SEM observations (Williams & Round 1987, Round *et al.* 1990). On the basis of these characteristics, many redefinitions of known genera and new genera have been proposed (Williams & Round 1987, Flower *et al.* 1996, Round *et al.* 1999, Morales 2001, 2002), and many small araphid taxa have been transferred to these genera. Recently, new genera have been established on the basis of molecular phylogeny as well as morphological characters (Li *et al.* 2016, 2018), and the placement of small araphid diatoms continue to be discussed (Morales *et al.* 2019). The diversity of opephoroid diatoms is also large, and they have been assigned to several genera: *Opephora*, *Stauroforma* R.J.Flower, V.J.Jones & Round (1996: 53), *Nanofrustulum* Round, Hallsteinsen & Paasche (1999: 345), *Pseudostaurosira* D.M.Williams & Round (1987: 276), *Staurosirella* D.M.Williams & Round (1987: 274), *Sarcophagodes* E.Morales (2002: 111), *Gedaniella* Chunlian Li, A.Witkowski & M.P.Ashworth (Li *et al.* 2018: 21), and *Serratifera* M.P.Ashworth, Chunlian Li & A.Witkowski (Li *et al.* 2016: 1020).

Among *Opephora sensu lato*, the taxonomic position of *Opephora mutabilis* (Grunow) Sabbe & Vyverman (1995: 241) has remained problematic for the past 30 years, since *O. mutabilis* has heteropolar valve outline, but possesses the vimines, differing from *Opephora sensu stricto*, which has no vimines (Round *et al.* 1990, Sabbe & Vyverman 1995, Morales 2002, Witkowski *et al.* 2010). Even though new progress has recently been made in the phylogeny and

taxonomy of the *O. mutabilis* and related taxa of it (Li *et al.* 2018), the generic placement of *O. mutabilis* is still a matter of debate (Morales *et al.* 2019).

Li *et al.* (2018) analyzed the molecular phylogeny of dozens of small araphid diatoms and demonstrated that *Opephora sensu stricto* and the taxa including *O. mutabilis* fell within different subclades in their phylogenetic tree. Based on those results, the genus *Gedaniella* was erected and eight taxa, including *O. mutabilis* and five newly described species, were assigned to it.

In contrast, Morales *et al.* (2019) suggested that the genus *Gedaniella* illustrated by Li *et al.* (2018) obviously contains a mixture of several morphological forms, in which at least the genera *Sarcophagodes*, *Pseudostaurosira*, and *Nanofrustulum* are included. Morales *et al.* (2019) transferred four species, including *O. mutabilis*, to the genus *Sarcophagodes* from *Gedaniella*, since they have wide and long vimines, the character defining *Sarcophagodes*. Recently, *O. mutabilis* has been regarded as an invalid name because *Sceptroneis mutabilis* Grunow in Cleve & Möller 1879, the basionym of *O. mutabilis*, is a *nomen nudum* (Morales *et al.* 2021).

In identifying fossil diatoms, the only information available for taxonomy is the valve morphology. Therefore, in this study, *O. mutabilis* and related taxa are assigned to the genus *Sarcophagodes* following the classification proposed by Morales *et al.* (2019) exclusively based on morphological information.

Accurate identification of diatoms is crucial for application of diatom fossils as paleoenvironmental indicators. Because small araphid opephoroid diatoms include marine diatoms, for example *Opephora sensu stricto*, and many freshwater species, such as *Staurosirella martyi* (Hérribaud) E.Morales & Manoylov (2006: 354) (= *Opephora martyi* Hérribaud [1902: 43], = *Martyana martyi* [Hérribaud] Round in Round, Crawford & Mann [1990: 673]), misidentification can lead to serious inaccuracies in paleoenvironmental interpretation. In addition, despite previous efforts, the diversity of living *Opephora sensu lato* is still not fully understood (Li *et al.* 2018). Therefore, when using *Opephora sensu lato* in paleoenvironmental studies, it is necessary to carefully determine whether the specimens can be identified as a previously reported taxon.

Our current understanding of the taxonomy, biostratigraphy, and paleobiogeography of diatoms in shallow-marine to brackish environments during the Pleistocene Epoch continues to be poor. In Japan, the biostratigraphy of *Lanceina rectilatus* Naya (2010: 113), a Pleistocene fossil species of Rhabdioneidaceae (Naya 2010, 2019), and the stratigraphic distribution of the genus *Thalassiosira* Cleve (1873: 6) during the last million years (Naya 2012) have been reported from the Kanto Plain, central Japan. But little is known about the past distribution of small araphid diatoms (including opephoroid taxa) in Pleistocene shallow-marine environments.

In this manuscript, we describe a new species of *Sarcophagodes* identified from lowest Lower to lowest Middle Pleistocene sediments of Japan. This discovery provides new insights into the diversity and paleobiogeography of *Sarcophagodes*.

Materials and methods

Diatom fossil samples were collected from the outcrop of the Lower to Middle Pleistocene Karato Formation (Kasama & Fuzita 1955, Itoh *et al.* 1997) in Himeshima Island, Oita Prefecture, western Japan (33° 43' 30.0" N, 131° 40' 20.1" E, Figs 1, 2). The geologic column in Fig. 2 is presented in this study for the first time. The Karato Formation consists of several depositional cycles intercalated with shallow-marine and fluvial deposits (Mizuno 2018). The Karato 2 tephra layer (Mizuno 2018) is intercalated within the sediments immediately above the shallow-marine bed investigated in this study (Fig. 2), and is correlated with the Imakuma II tephra (Yoshikawa 1984) of the Plio-Pleistocene Osaka Group. The Imakuma II tephra occurs within a non-marine deposit immediately above the Ma4 marine clay bed of the Osaka Group (Yoshikawa *et al.* 2000). The Matuyama-Brunhes geomagnetic reversal boundary has been identified in the Ma4 marine clay bed (Biswas *et al.* 1999). Based on the stratigraphic relationship between the tephra and the marine beds of the Osaka Group, the shallow-marine deposits investigated in this study can be correlated with the Ma4 marine clay bed of the Osaka Group, and the deposition period of this marine bed can be constrained to Marine Isotope Stage 19 (0.761–0.790 Ma, Lisiecki & Raymo 2005).

Additional diatom fossil samples were collected from the outcrop of the M1 and M2 marine beds (Naya & Mizuno 2020) in the Lower Pleistocene Bushi Formation in Iruma City, Saitama Prefecture, central Japan (M1: 35° 50' 15.9" N, 139° 20' 44.0" E, M2: 35° 50' 21.2" N, 139° 20' 53.8" E, Fig. 1). The M1 and M2 marine beds are the lowest and second-lowest of the eight shallow-marine beds (marine beds M1 to M8) recognized in the Bushi Formation. The depositional ages of beds M1 and M2 are estimated to be ca. 2.5–2.4 Ma (earliest Pleistocene), based on tephrostratigraphy (Naya & Mizuno 2020).

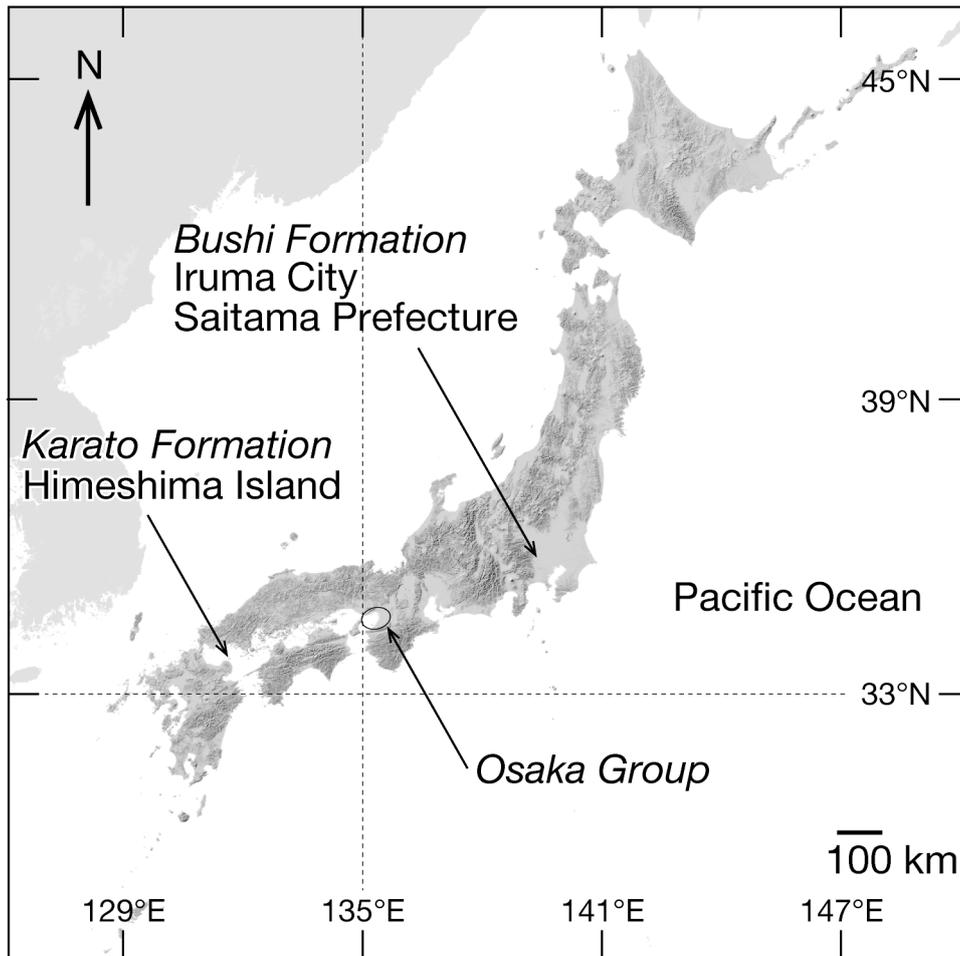


FIGURE 1. Location of the Karato Formation in Himeshima Island, Oita Prefecture, western Japan (the type locality of *Sarcophagodes duodecima* sp. nov), the Bushi Formation in Saitama Prefecture, central Japan, and the Osaka Group in the Kinki district, central Japan.

For detailed valve observation, sediment samples were cleaned in 30% H₂O₂ solution on a hot plate at 120 °C for approximately 30 min, and rinsed several times in 0.1 % sodium diphosphate anhydrous with distilled water added in various concentrations to remove clay particles. Cleaned slurries were diluted and dried on cover slips and mounted in Styrax (SIGMA-ALDRICH Inc, St. Louis, MO, USA, refractive index = 1.59) or Mountmedia (FUJIFILM Wako Pure Chemical Corporation, Osaka, Japan, refractive index = ca.1.7) for light microscopy (LM) observations. A Nikon ECLIPSE E80i microscope equipped with Plan Apo VC 100× objective lens, 1.40 N.A., and Nikon DS-Fi1 digital camera were used for this purpose.

For scanning electron microscopy (SEM) observations, a cleaned slurry was filtered and dried on a MF 0.45-µm membrane filter or an ISOPORE 0.4-µm polycarbonate membrane filter, and the filter was mounted on a brass stub and coated with gold-palladium using a HITACHI E-1020 ion sputter for 150 seconds at 10–15 mA. The stub was analysed using a JEOL JSM-6390LV electron microscope at 5–10 kV and 10 mm working distance.

For diatom valve enumeration, smear slides were prepared following the method described in Naya (2019). Smear slides were mounted in NOA 61 ultraviolet curing resin (Norland Products Inc., Cranbury, NJ, USA, refractive index = 1.56). The relative abundances of each taxon were determined by counting under LM at 1000× magnification, and counting at least 200 valves (Fig. 2).

All LM and SEM pictures were mounted using Adobe Photoshop 2021(Adobe Inc., San Jose, CA, USA). Morphological terminology follows Williams & Round (1987), Round *et al.* (1990) and Cox (2012).

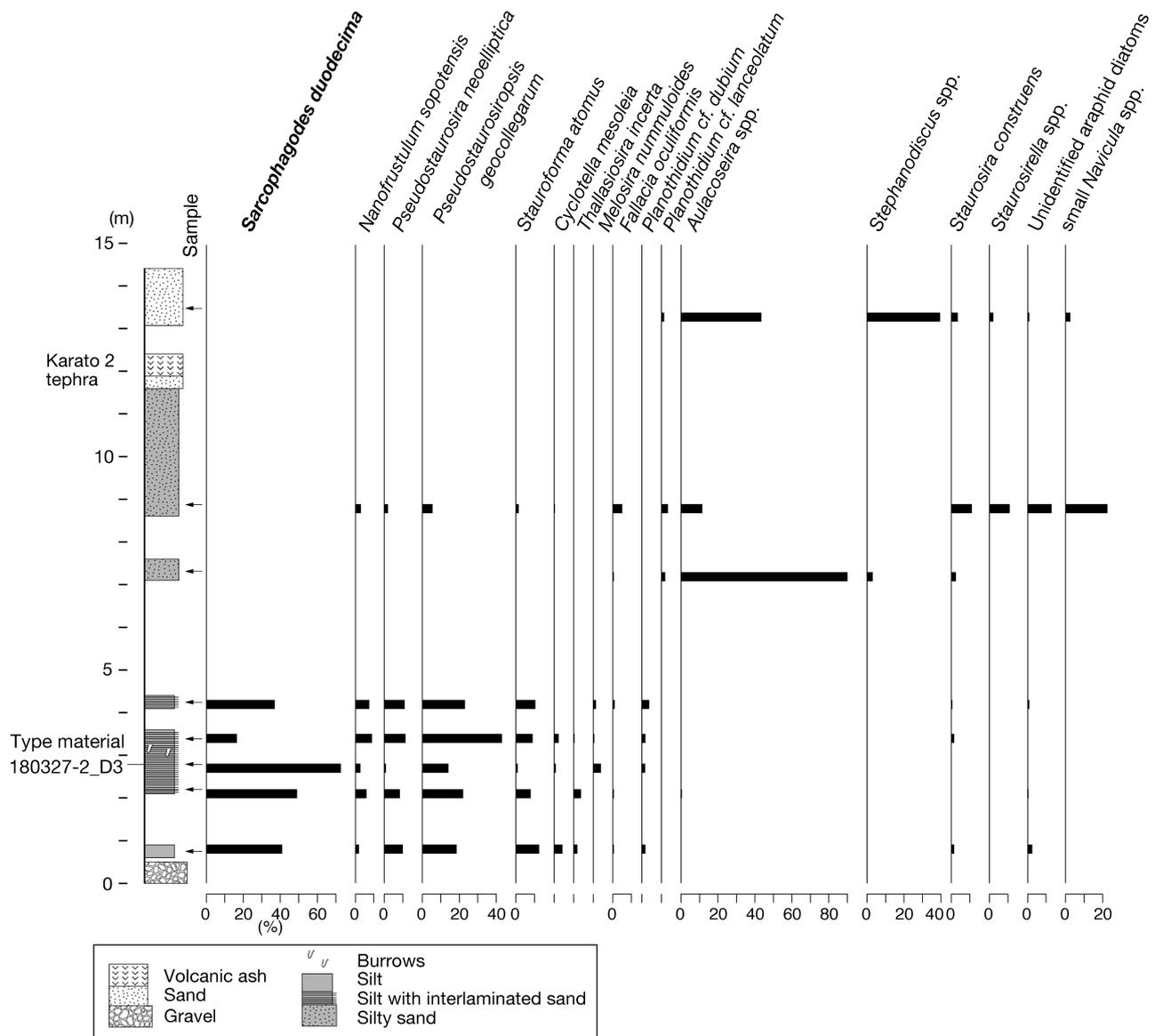
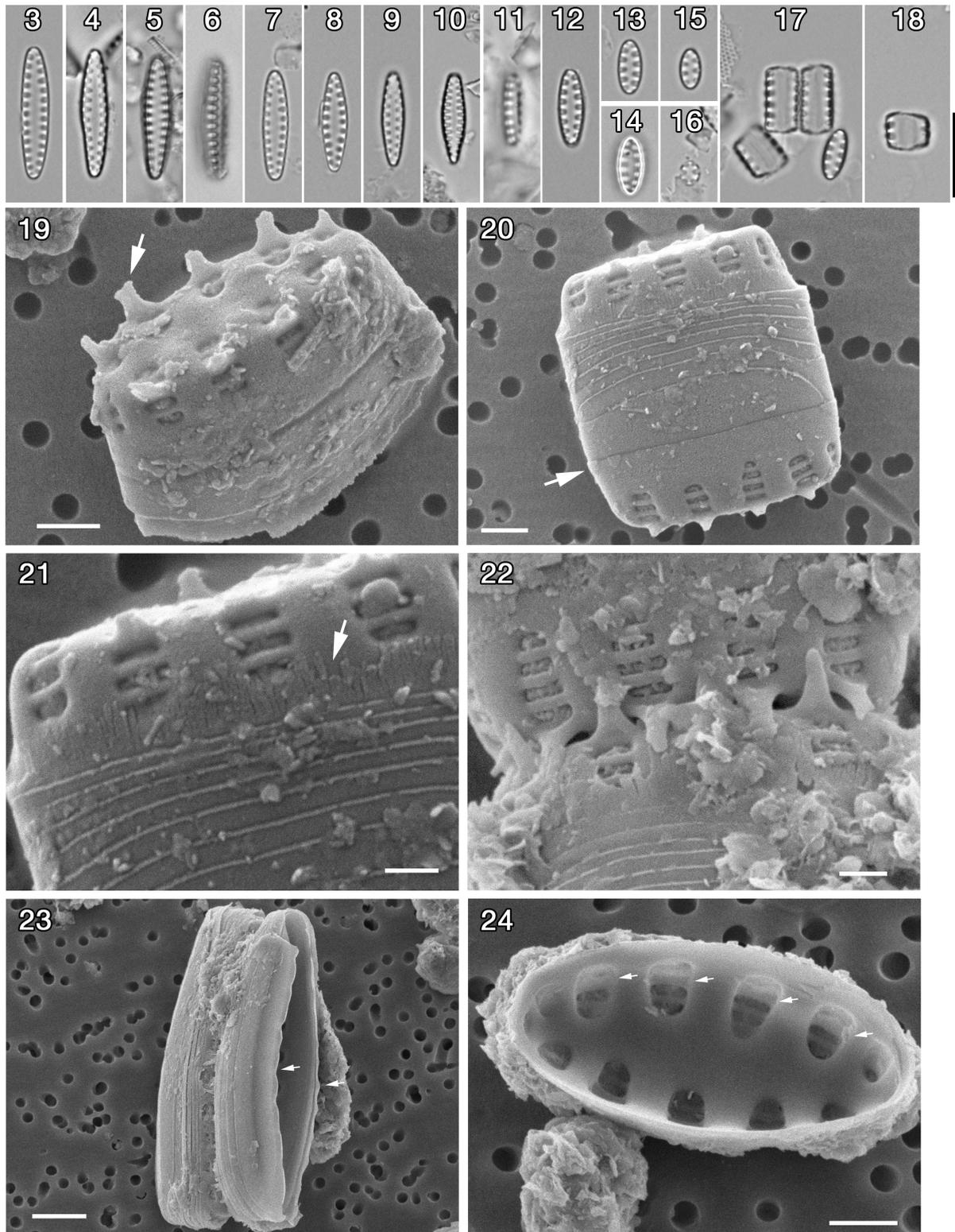


FIGURE 2. Geologic column of the type locality of *Sarcophagodes duodecima* sp. nov. in the Karato Formation, and the diatom stratigraphy of the section.

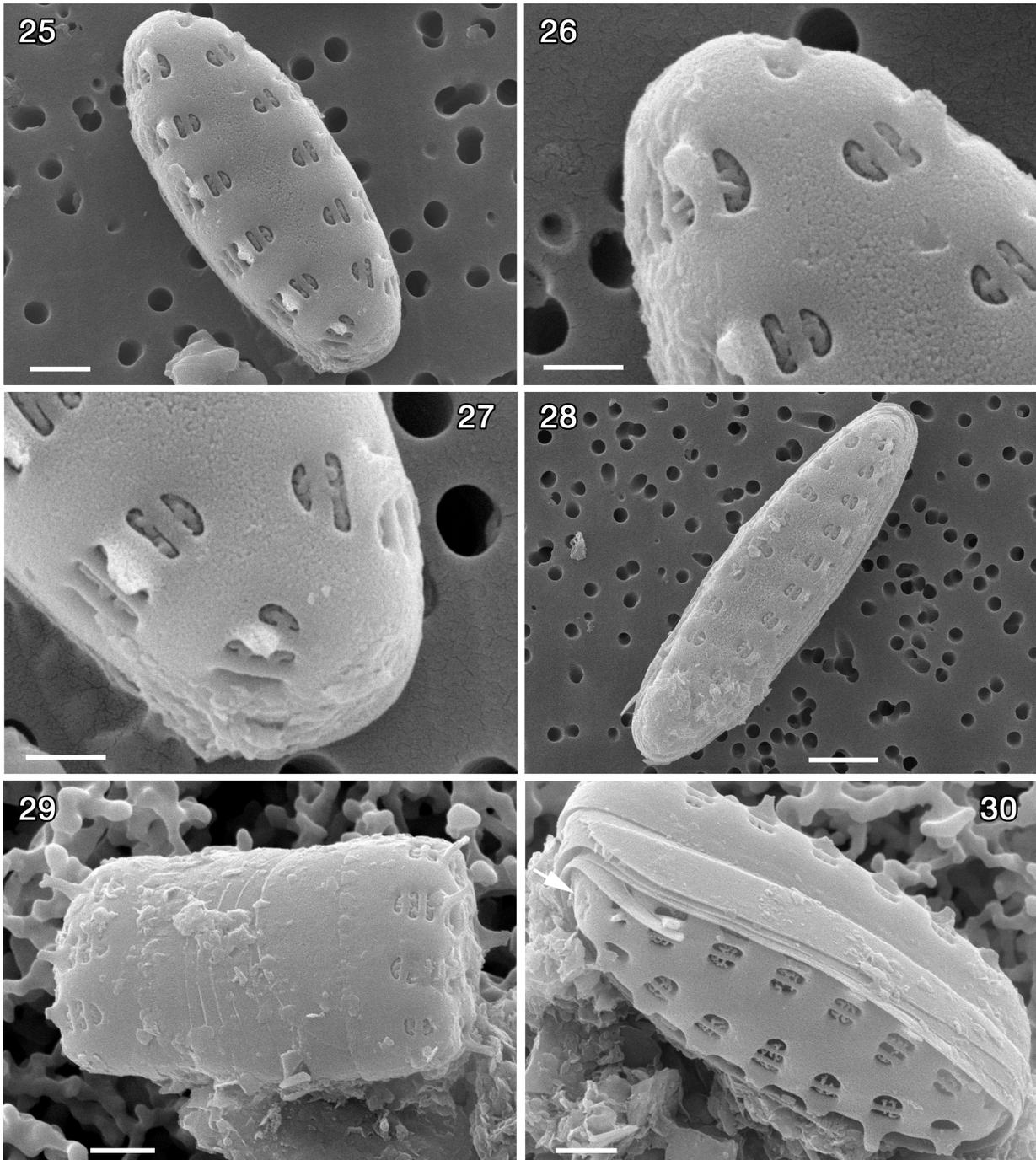
Results

Sarcophagodes duodecima Naya sp. nov. (LM: Figs 3–18, SEM: Figs 19–35)

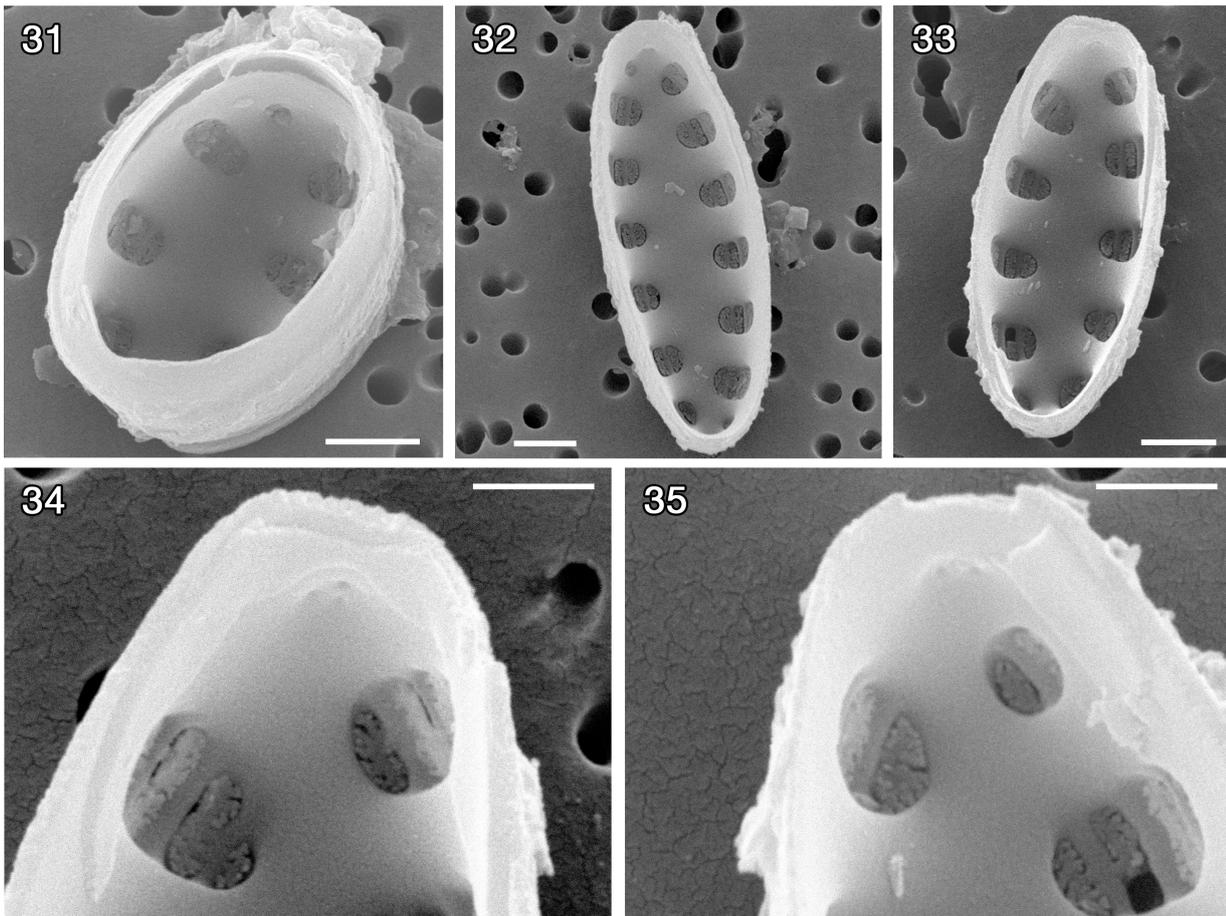
Description:—In LM, frustule rectangular in girdle view with round corners (Figs 17, 18), attached at valve face by interlocking spines (Fig. 17). The larger valves are heteropolar clavate (Figs 4, 5, 7, 9, 10) or isopolar elliptic (Figs 3, 6, 8) and the smaller valves isopolar elliptic (Figs 11–16). Sternum widely lanceolate (Figs 12, 19). Striae alternate and robust (Fig. 12). Length 3–16 μm , width 2.5–3 μm , and striae density 8–10 in 10 μm . In SEM, striae uniseriate, composed of up to three areolae on the valve face and two to four on the mantle (Figs 19–22, 25–30). Areolae apically reniform at the ends of each stria, otherwise rectangular with rounded corners (Figs 20, 25–27, 29), occluded by one or multiple profusely branched volae with stalk-like rod extending from vimines (Figs 21, 26, 27, 30, 35). Marginal spines solid, spatulate (Fig. 19) or conical (Fig. 22), interrupting the striae on the thickened vimen at valve face-mantle junction (Figs 19, 25–30). Apical pore field present at both poles, consisting of multiple round pores present at both poles (Figs 30, 34, 35). Cingulum formed of up to eight wide open copulae (Figs 20, 29, 30). Valvocopula wider than other copulae. Edge of pars interior of valvocopula undulate (Fig. 23). Fringed structure observed at the end of copula (Fig. 21). Mantle plaques present (Figs 20, 29). No rimoportulae.



FIGURES 3–24. *Sarcophagodes duodecima* sp. nov. from the type locality. 3–18. LM images. Figs 3, 4, 7–9, 11–18 sample 180327-2 D3 (type material, Fig. 12 corresponds to the holotype); Figs 5, 6, 10, sample 13HMO3. 19–24. SEM images, sample 180327-2 D3 (type material). 19. An entire valve showing valve outline, valve face, spatulate marginal spines at the valve face–mantle junction (indicated by arrow), mantle, and parts of the girdle band. 20. Girdle view showing mantle areolae, open copulae, and mantle plaques (indicated by arrow). 21. Close-up of external valve of Fig. 20 showing fringed structure (indicated by arrow) observed at the end of copula. 22. Close-up of girdle view showing conical marginal spines. 23. Entire girdle view showing valvocopula. Undulate edge of the pars interior (indicated by arrows). 24. Internal view showing large internal openings of striae, with thickened vimines at the valve-face mantle junction (indicated by arrows) observed as distinct bars crossing the middle of the stria. Scale bars = 10 μ m (Figs 3–18), 0.5 μ m (Figs 21, 22), 1 μ m (Figs 19, 20, 24), 2 μ m (Fig. 23).



FIGURES 25–30. SEM external views of *Sarcophagodes duodecima* sp. nov. from the type locality. Figs 25–28, sample 180327-2 D2; Figs 29, 30, sample 13HMO1. 25. Valve outline and widely lanceolate axial area. 26, 27. Close-up of the specimen in Fig. 25 showing each apex, apically reniform areolae at the ends of striae, rectangular areolae with rounded corners at the midway of the striae, and profusely branched volae extending from vimines. 28. Larger valve. 29. Girdle view showing mantle areolae, marginal spines at the valve face–mantle junction, mantle plaques, and open copulae. 30. Oblique view showing the apical pore field at the foot pole composed of multiple round pores (indicated by arrow). Scale bars = 0.5 μ m (Figs 26, 27), 1 μ m (Figs 25, 29, 30), 2 μ m (Fig. 28).



FIGURES 31–35. SEM internal views of *Sarcophagodes duodecima* sp. nov. from the type locality, sample 180327-2 D2. 31–33. Valves of different sizes and large internal openings of striae are visible. Note that rimoportulae are not present. 34, 35. Close-up of both apices of the specimen illustrated in Fig. 33, showing the apical pore fields composed of small round pores, uniseriate row of areolae, and volae. Scale bars = 0.5 μm (Figs 34, 35), 1 μm (Figs 31–33).

Type:—JAPAN. Higashiomi, Oita Prefecture: Himeshima village, from siliceous silt of the Lower to Middle Pleistocene Karato Formation, sample 180327–2 D3, 33°43'30.0" N, 131°40'20.1" E, *T. Naya and Y. Horiuchi 27 March 2018* (holotype: slide MPC-44141=Fig. 12, Micropaleontology Collection, National Museum of Nature and Science, Tsukuba, Japan, England Finder M35/0)

Etymology:—Duodecim, Latin = twelfth, after a myth of Himeshima Island, where the type locality is situated. According to the Kojiki, the oldest extant chronicle in Japan (Kurano 1963), Himeshima Island was the twelfth island in the Japanese archipelago to be created.

Observation:—The isopolar valves are observed in the entire size range of the species, whereas the heteropolar valves are recognized in only approximately half of the larger valves (>10 μm). However, due to the small proportion of the larger valves, few heteropolar valves occurred in the analyzed samples (Figs 4, 5, 7, 9, 10, 23, 30). Vimines are thickened at the valve-face mantle junction (Figs 26–27). Each thickened vimen can be observed as a distinct bar crossing the middle of the stria in internal view under SEM (Figs 24, 32, 33); the vimines are also visible vaguely under LM (Figs 5, 6, 11). A reduced apical pore field is observed at both poles, consisting of multiple round pores. In most specimens, the apical pore field could not be observed in external view, and could be seen only at the foot pole of the heteropolar valve (Fig. 30). Mantle plaques are arranged along the external rim of the mantle (Figs. 20, 29).

Distribution and geologic age:—Thus far, *S. duodecima* has been found at two localities in Japan. The type locality of the species is in the Karato Formation on Himeshima Island, western Japan. The age of these sediments is inferred to be ca. 0.78 Ma. The other locality is in the Lower Pleistocene Bushi Formation in Iruma City, Saitama Prefecture, central Japan (Fig. 1). *S. duodecima* occurs in the M1 and M2 marine beds in the Bushi Formation (Figs 36–45); the age of these beds is estimated to be 2.5–2.4 Ma (Naya and Mizuno 2020).

TABLE 1. Morphological features of *Sarcophagodes duodecima* sp. nov. and related species.

taxon	reference	valve shape	length (µm)	width (µm)	striae in 10 µm	axial area	valvae type	number of areolae in stria on valve face	number of subdivided areolae in stria on mantle	spine	thicker cross bar (vimen) at the valve face mantle junction	apical pore field	mantle plaque	Modern environmental distribution
<i>Sarcophagodes duodecima</i>	this study	elliptic to clavate	3–16	2.5–3.0	8–10	widely lanceolate	profusely branched volae	1–3 (often 2)	2–4	present	present	present at both apices	present	—
<i>Sarcophagodes mutabilis</i>	Sundbäck (1987), Sabbe & Vyverman (1995), Li <i>et al.</i> (2018), Morales <i>et al.</i> (2019)	ovate to clavate	3.7–27	2.5–6.0	8–16	very narrow	multiple branched volae	2–5	2–4	present (club-shaped)	present	present at both apices, reduced at the head pole	present	marine to brackish
<i>Sarcophagodes alfred-wegeneri</i>	Li <i>et al.</i> (2018)	lanceolate to clavate	18.5–22.0	2.0–3.5	9–10	narrow-linear	branched volae	1–3	1–3	absent	present	present at both apices	not observed	brackish ??
<i>Sarcophagodes arenaria</i>	Li <i>et al.</i> (2018)	clavate	5.0–23.0	2.0–3.0	12–15	narrow-linear	branched volae	2–4	3	absent	absent	present at both apices	not observed	brackish
<i>Sarcophagodes delicatula</i>	Morales (2002)	clavate	13–16	2–3	14–16	broadly lanceolate	dichotomously branching volae	1–3	1	rudimentary spine	present	present at both apices	absent	freshwater
<i>Sarcophagodes boltonii</i>	Li <i>et al.</i> (2018)	clavate, elliptical, oval	(2.5)*–19.5 (2.0)*–5.0	14–16	14–16	narrow-linear	branched volae	4–7	2–4	present	present	present at both apices	present	marine
<i>Sarcophagodes poulinii</i>	Witkowski <i>et al.</i> (2010)	clavate	24–45	6–10	5.5–6.5	distinct	branched volae**	1–7**	2–4**	present	present	present at both apices	not observed	marine
<i>Opophora horstiana</i>	Witkowski (1994)	clavate	5–8	1.5–2.0	15–18	distinct	branched volae**	2 ?	2 ?	present	present	present at both apices	not observed	brackish to marine
<i>Staurosirella guenter-grassii</i>	Witkowski & Lange-Bertalot (1993)	elliptical to clavate	4.5–7	2–3	9–12	disinct	branched volae	difficult to distinguish between valve face and mantle	difficult to distinguish between valve face and mantle	absent	absent	present at both apices	not observed	brackish to marine

* Morales *et al.* (2019) transferred only the larger form of *Gedaniella boltonii* presented by Li *et al.* (2018) to the genus *Sarcophagodes*.

** Counted or observed by the authors from published illustrations.

Discussion

Comparison with related taxa

The species described here could be assigned to *Opephora sensu lato* on the basis of its heteropolar valve outline in the larger valves. However, having wide and long vimines, the presence of a spine on the stria, and the profusely branched volae that develop from the vimen are clearly different from the characteristics of *Opephora sensu stricto* proposed by Round *et al.* (1990). Among the well-known species of *Opephora sensu lato*, these morphological characteristics are very similar to those of *O. mutabilis* (Sundbäck 1987 [as *O. olsenii*], Sabbe & Vyverman 1995), which is currently named *Sarcophagodes mutabilis* E.Morales (Morales *et al.* 2019: 280, *nom. inval.*). In particular, wide and long vimines are typical feature distinguishing the genus *Sarcophagodes* (Morales *et al.* 2019), and the new species evidently belongs *Sarcophagodes*.

Sarcophagodes duodecima can be clearly distinguished from the six species that Morales *et al.* (2019) placed in the genus *Sarcophagodes* (Table 1). Under LM, *S. duodecima* is characterized by a smaller length range (5–16 µm) than other *Sarcophagodes* species, and by having a lanceolate, slightly wider axial area. *Sarcophagodes delicatula* E.Morales (2002: 111), the generitype of the genus, is very similar to *S. duodecima* in having the smaller length range, wide lanceolate axial area and short striae on the valve face, which bear two areolae, but can be distinguished from *S. duodecima* in the finer striae density, possessing rudimentary spines, having only one areola on the shorter striae on the mantle, and absence of the mantle plaques.

Under SEM, *Sarcophagodes arenaria* (Chunlian Li, A.Witkowski & S.Sato) E.Morales, C.E.Wetzel & Ector (Morales *et al.* 2019: 280) and *S. alfred-wegeneri* (Chunlian Li, S.Sato & A.Witkowski) E.Morales, Novais & M.Morais in Morales *et al.* (2019: 280) can be distinguished from *S. duodecima* by the absence of a marginal spine. *Sarcophagodes mutabilis* and *S. boltonii* (Chunlian Li, Krawczyk, Dabek & A.Witkowski) C.E.Wetzel, E.Morales & Ector (Morales *et al.* 2019: 280) are similar to *S. duodecima* in having spines on the vimines and having mantle plaques, but can be distinguished from *S. duodecima* by their narrow axial area and their longer striae on the valve face, which are divided into up to 5–7 areolae.

Sarcophagodes duodecima is also similar to *Staurosirella guenter-grassii* (A.Witkowski & Lange-Bertalot) E.Morales, C.E.Wetzel & Ector (Morales *et al.* 2019: 281) and *Opephora horstiana* A.Witkowski (1994: 173) in having a shorter (<10 µm) valve length. *O. horstiana* differs from *S. duodecima* in having a higher striae density. *S. guenter-grassii* can be distinguished from *S. duodecima* by SEM observation by means of its lack of spines, but it may be difficult to distinguish the two species under LM because both taxa overlap in valve outline and range of striae density.

Probable habitat of *S. duodecima*

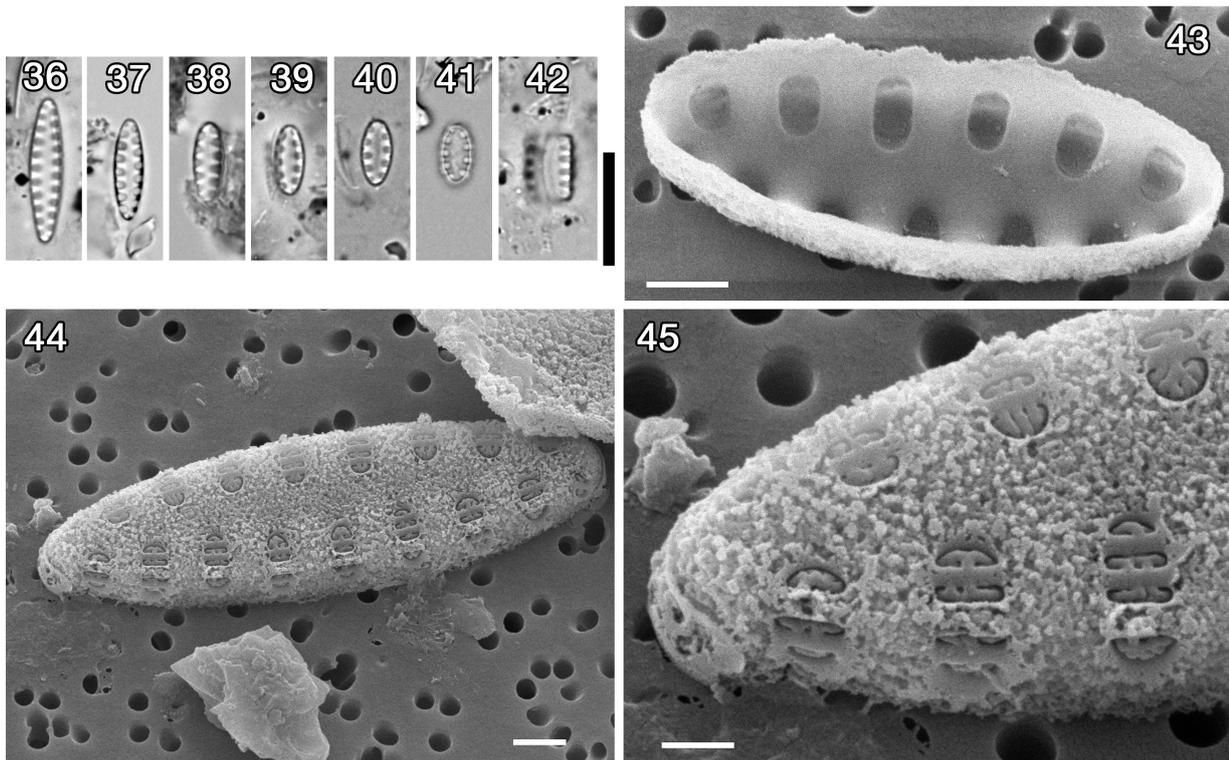
Sarcophagodes duodecima is abundant at its type locality in the Karato Formation, forming up to 70 % of the total diatom assemblage. Other taxa in the assemblage (Fig. 2) include *Nanofrustulum sopotensis* (A.Witkowski & Lange-Bertalot) E.Morales, C.E.Wetzel & Ector in Morales *et al.* (2019: 275), *Pseudostaurosira neoelliptica* (A.Witkowski) E.Morales (2002: 105), *Pseudostaurosiroopsis geocollegarum* (A.Witkowski) E.Morales (2002: 104), and *Stauroforma atomus* (Hustedt) D.Talgatti, C.E. Wetzel, E.Morales & L.C.Torgan (Talgatti *et al.* 2014: 45). These species mainly occur in brackish water (Witkowski & Lange-Bertalot 1993, Witkowski 1994).

Sarcophagodes duodecima is also found in the M1 and M2 marine beds of the Bushi Formation, but at a low abundance of less than 5% of the total diatom assemblage (Naya & Mizuno 2020: counted as part of *Opephora* spp.). The dominant diatoms in the M1 and M2 marine beds are brackish-water and marine taxa such as *Pseudopodosira kosugii* Y.Tanimura & H.Sato (1997: 358) (ca. 50 %), *Diploneis smithii* (Brébisson) Cleve (1894: 96) (10 %–15 %), and *Tryblionella granulata* (Grunow) D.G.Mann (Round *et al.* 1990: 678) (10 %–20 %; Naya & Mizuno 2020).

As the predominant species associated with *S. duodecima* are brackish-water taxa, the habitat of *S. duodecima* is inferred to be brackish-water environments such as salt marshes and estuaries. The fact that all *Sarcophagodes* species except for *S. delicatula* inhabit brackish to marine environments is consistent with this conclusion.

This study is the first report of a small araphid opephoroid diatoms within the genus *Sarcophagodes* from Lower and Middle Pleistocene strata, and may be also the first report of the genus *Sarcophagodes*, as such, from Asia. The present results indicate that this group of diatoms was widely distributed in Japan, at least during Early Pleistocene time. This group of diatoms has probably been confused with other small araphid diatoms, such as *Pseudostaurosira*, short-striated *Staurosirella*, *Staurosira*, and *Opephora*, in previous studies, because of their small valve size and difficulty of identification under LM. Further investigations should be carried out to reveal the biogeographical distribution

and determine the stratigraphic range of *S. duodecima* and related taxa in brackish-water environments in Asia and worldwide.



FIGURES 36–45. *Sarcophagodes duodecima* sp. nov. from the Lower Pleistocene Bushi Formation. Figs 36–42. LM images; Figs 43–45. SEM images. 43. Internal view showing valve outline, with large openings of striae. 44. External view showing valve outline, uniseriate row of areolae. 45. Close-up of Fig. 44 showing apical part of the valve, areolae occluded by branched volae with stalk-like rod extending from vimes. Scale bars = 10 μm (Figs 36–42), 0.5 μm (Fig. 45), 1 μm (Figs 43, 44).

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