1, 2-1, 3). A small attachment scar also occurs on the adapical side of the first lateral saddle in one of the two figured specimens (Figure 1-4). Many similar small oval and crescentic scars are present in the interspaces between pseudosutures (Figures 1-2, 1-3). All these attachment scars were originally expressed as shallow depressions or pores on the inside surface of the shell wall. There are no traces of organic remains (cameral membranes and/or gels) around the oval and crescentic scars.

Comparison and discussion

Preservation of muscle attachment scars is extremely rare in the Goniatitina and has only been documented in *Goniatites* and *Muensteroceras* (Crick, 1898; Jordan, 1968). The muscle scars of the two genera described by these authors differ from the unpaired ventral attachment scars of *Goniatites multiliratus* described herein and are both represented by dorsal paired attachment scars that occur on the anterolateral side of the steinkerns of the body chambers. In their shape and mid-ventral position within each chamber, the unpaired ventral attachment scars of *G. multiliratus* are comparable to those known from various Mesozoic ammonites (Crick, 1898; Jordan, 1968; Sarikadze *et al.*, 1990; see also Doguzhaeva and Mutvei, 1996, table 1 for a complete list of genera with this kind of attachment scar), members of the Orthocerida (Ristedt, 1971; Figure 4-1a, b) and Aulacocerida (Figure 4-3), and *Spirula* (Figure 4-4a, b). In extant *Nautilus*, the attachment site for the paired retractor muscles is located in the posterior region of the body chamber, where it is demarcated by the conspicuous ridge of the myoadhesive epithelial zone. Mutvei and Doguzhaeva (1997) demonstrated that the myoadhesive epithelium secretes a thick prismatic myostracal layer, consisting of bundles of vertically oriented acicular crystallites, at the attachment site to which the muscle is firmly attached. In *Spirula*, the myoadhesive epithelial zone is situated near the shell aperture (mz, Figure 4-4a). The myostracal layer at its muscle attachment site likewise consists of bundles of crystallites (Figure 4-4b). Bundles of crystallites are also observed on the unpaired ventral muscle scar in the aulacocerid specimen from Arkansas (Figure 4-3). Although the prismatic myostracal layer is not preserved in the two goniatite specimens examined here, the small, round depressions on the mid-ventral scars were presumably sites for attachment of bundles of crystallites secreted by the myoadhesive epithelium, as in *Nautilus*, *Spirula* and the Aulacocerida.

The unpaired mid-ventral muscle scars of *Goniatites multiliratus* (Figures 1, 2) are remarkably similar in their overall shape to unpaired dorsal attachment scars known from some Mesozoic Ceratitina (e.g. *Amphipopanoceras*, Lehmann, 1990, fig. 4.38) and Ammonitina (e.g. *Quenstedtoceras* and *Kosmoceras*, Bandel, 1982, pl. 13, figs. 3-5; *Euhoplites*, Landman and Bandel, 1985, fig. 31). In close-up, many small mounds of crystallites are developed on the inner surface of the dorsal scars in these genera (Figure 4-2).

Our observations strongly suggest that in *Goniatites multiliratus*, the unpaired ventral muscle was attached to the shell wall at the base of the body chamber for some time before formation of the next chamber. A similar condition is postulated for the unpaired dorsal muscle in some Mesozoic ammonites. In contrast, the round, oval, or irregularly shaped smaller pits observed on the ventral and lateral sides of each chamber (m, Figures 1-1, 1-2, 1-4) appear to indicate a weaker and less permanent attachment of muscular or ligamental tissue to the shell wall. These latter scars were presumably formed during the slow and stepwise forward movement of the body during growth.

As our data indicate, there are still many questions regarding the attachment of the soft body to the shell. A variety of models have been proposed to explain septal morphogenesis and the forward movement of the body (e.g., Checa and Garcia-Ruiz, 1996), but most of them lack comparative anatomical background. Are all the pseudosutures we observed related to pseudosepta and/or to the presence of so-called cameral gel? Are the small oval and crescentic scars between pseudosutures present in other ammonoids? How do all these different kinds of attachment scars fit in with the tie point model of septal formation (e.g. Seilacher, 1988) and with the more recent model of the "Cartesian Diver" (Seilacher and LaBarbera, 1995)? Future studies of well-preserved material and comparison with the anatomy of extant cephalopods may yield solutions to these problems.

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Ophiura sarsii sarsii (Echinodermata, Ophiuroidea) from the Late Pliocene Hachioji Formation in Niigata Prefecture, Central Japan

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Abstract. Specimens of the Recent species *Ophiura sarsii sarsii* Lütken, collected from the Late Pliocene Hachioji Formation in Kashiwazaki City, Niigata Prefecture, central Japan, represent the first record of this species from the Pliocene, although this species has been found from the Middle-Late Miocene. The fossil specimens have been compared and contrasted with related species using morphometric characteristics of the disk, basal arm portions and radial shields.

Key words : Hachioji Formation, Late Pliocene, *Ophiura sarsii sarsii*, Ophiuroidea

Introduction

Ophiura sarsii sarsii is an extant, circumpolar species in the Northern Hemisphere, occurring in high-density populations in the upper bathyal zone surrounding northern Japan (Fujita and Ohta, 1989). Fossil ophiuroids assigned to *Ophiura s. sarsii* have been found in the Pleistocene from off northern Norway (Jensen and Thomsen, 1987), from southern Norway (Bjørlykke, 1898), from the Middle Pleistocene Ichijuku Formation (Kazusa Group) in Chiba Prefecture (Ishida and Inoue, 1993, 1995), from the Plio-Pleistocene Hijikata Formation in Shizuoka Prefecture (Ishida *et al*., 1996), from the Late Miocene Ogawa Formation in Nagano Prefecture (Ishida, Kurita *et al*., 1997 ; Ishida *et al*., 1998), from the Late Miocene Hongo Formation in Yamagata Prefecture (Ishida, Tokairin *et al*., 1997), and from the Middle-Late Miocene Wakkanai Formation in Hokkaido (Ishida and Fujita, 1998).

We have recently discovered fossil ophiuroids in the Late Pliocene Hachioji Formation, Kashiwazaki City (Ishida, Kurita *et al*., 1997), which proved to be assignable to *Ophiura s. sarsii*, based on a detailed morphological analysis. This paper describes *Ophiura s. sarsii* from the Pliocene in detail and discusses the comparison of the fossils with related species, which are important for its identification.

Locality and age

Thirty-five individuals were collected from a cliff outcrop of the Hachikoku Oil Field, about two kilometers southeast of Nagatori Station on the Japan Railways Shin-etsu Line in the district of Kashiwazaki City, Niigata Prefecture in May 1995 (Figure 1). The Pliocene and Pleistocene in this area comprise, in ascending order, the Hododaira Formation, the Hachikokusan Formation, the Suganuma Formation, the Hachioji Formation and the Uonuma Formation (Yasui *et al*., 1983 ; Kobayashi *et al*., 1989). The strata in this cliff are

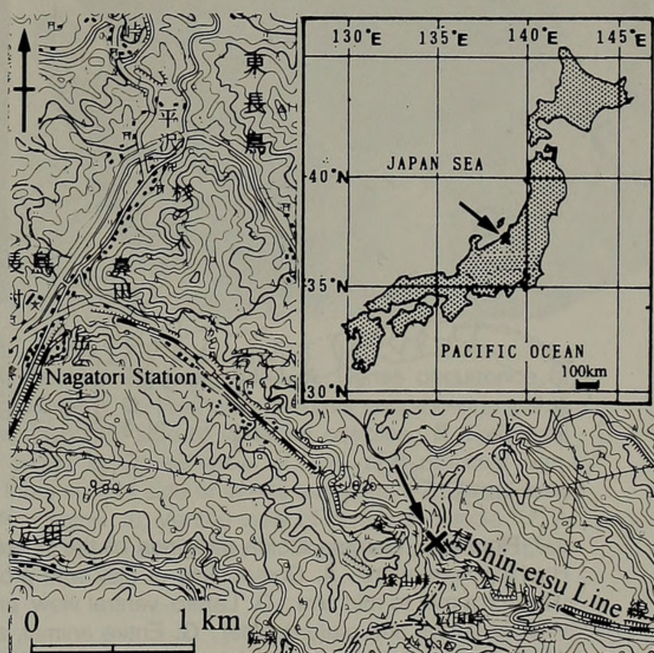

Figure 1. Sampling locality in the Hachikoku Oil Field. Part of the "Kashiwazaki" 1 : 50,000 topographic map by the Geographical Survey Institute. × : Sampling locality.

composed of massive sandy siltstone assigned to the middle part of the Hachioji Formation (Yasui *et al.*, 1983 ; Kobayashi *et al.*, 1989).

The age of the Hachioji Formation is inferred to be Late Pliocene from the following studies. The formation was correlated with the Pliocene Nishiyama Formation of the standard succession in the Niigata area on the basis of tephra-stratigraphy and foraminiferal biostratigraphical data (Kobayashi *et al.*, 1989). From an analysis of the stratigraphic sequence of the Niigata sedimentary basin, the Hachioji Formation falls into the Late Pliocene (Arato, 1997). The Hachioji Formation was correlated lithologically with the Asojima Formation in the Yoneyama area (Kobayashi *et al.*, 1989). Fission track ages of 3.24 and 2.91 Ma have been obtained for the Asojima Formation (Unpublished data of Muramatsu, in Kobayashi *et al.*, 1989).

Fossil specimens of *Ophiura s. sarsii* have been described from the Middle Pleistocene, the Plio-Pleistocene boundary and the Late Miocene (Ishida and Inoue, 1993 ; Ishida *et al.*, 1996, 1998), and also from the Middle-Late Miocene (Ishida and Fujita, 1998), but this is the first report of the species from the Pliocene.

Systematic description

Family Ophiuridae Lyman, 1865
Subfamily Ophiurinae Lyman, 1865
Genus ***Ophiura*** Lamarck, 1816

Ophiura sarsii sarsii Lütken, 1855

Figures 2, 3

Ophiura sarsii Lütken, 1855, p. 101 ; Clark, 1911, p. 37 ; Matsumoto, 1917, p. 272, fig. 74 ; Mortensen, 1927, p. 238, figs. 128-1, 2 ; Berry, 1934, p. 98, pls. 5, 6 ; D'yakonov, 1954, p. 98, fig. 35 ; Irimura, 1990, p. 98 ; Ishida and Inoue, 1993, p. 104, pls. 1-3 ; Ishida *et al.*, 1996, p. 67-69, fig. 3 ; Ishida *et al.*,

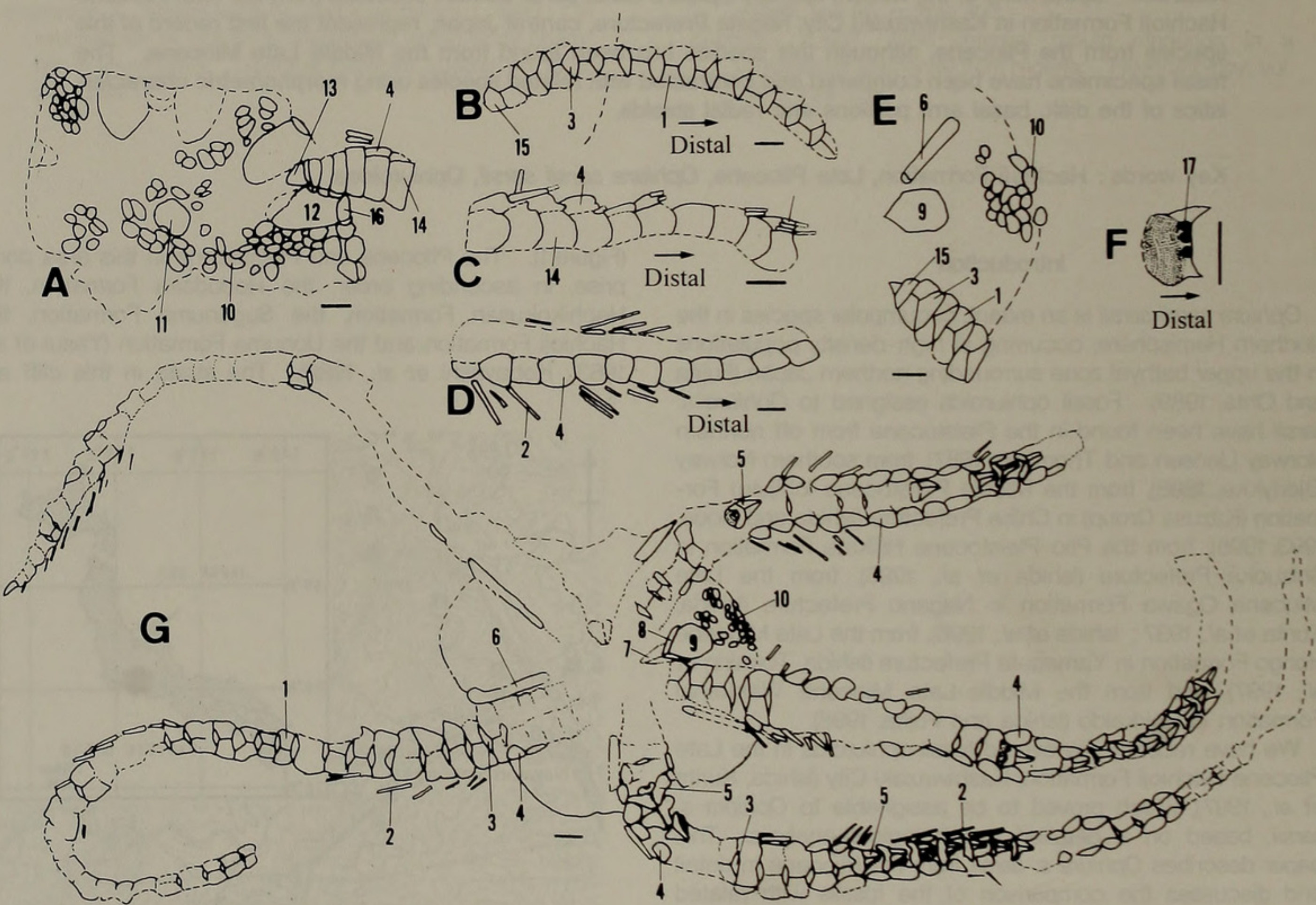

Figure 2. Camera lucida drawings of the figured specimens of *Ophiura sarsii sarsii* Lütken, 1855 from the Hachioji Formation. **A.** Dorsal view of disk and proximal arm ; **B.** Ventral view, proximal to mid arm ; **C.** Dorsal view, proximal to mid arm ; **D.** Latero-ventral view, proximal to mid arm ; **E.** Partial ventral view of disk ; **F.** Lateral view of lateral arm plate (inside) ; **G.** Entire animal, showing ventral side (vertebral ossicles showing dorsal side). Abbreviation : 1, Lateral arm plate (ventral view) ; 2, Arm spine ; 3, Ventral arm plate ; 4, Lateral arm plate (lateral side) ; 5, Vertebral ossicle (dorsal side) ; 6, A part of genital plate ; 7, Oral plate ; 8, Adoral plate ; 9, Oral shield ; 10, Disk scale ; 11, Primary scale ; 12, Radial shield ; 13, First dorsal arm plate ; 14, Dorsal arm plate ; 15, First ventral arm plate ; 16, Arm comb plate ; 17, Socket of arm spine. Scale bars equal 1 mm.

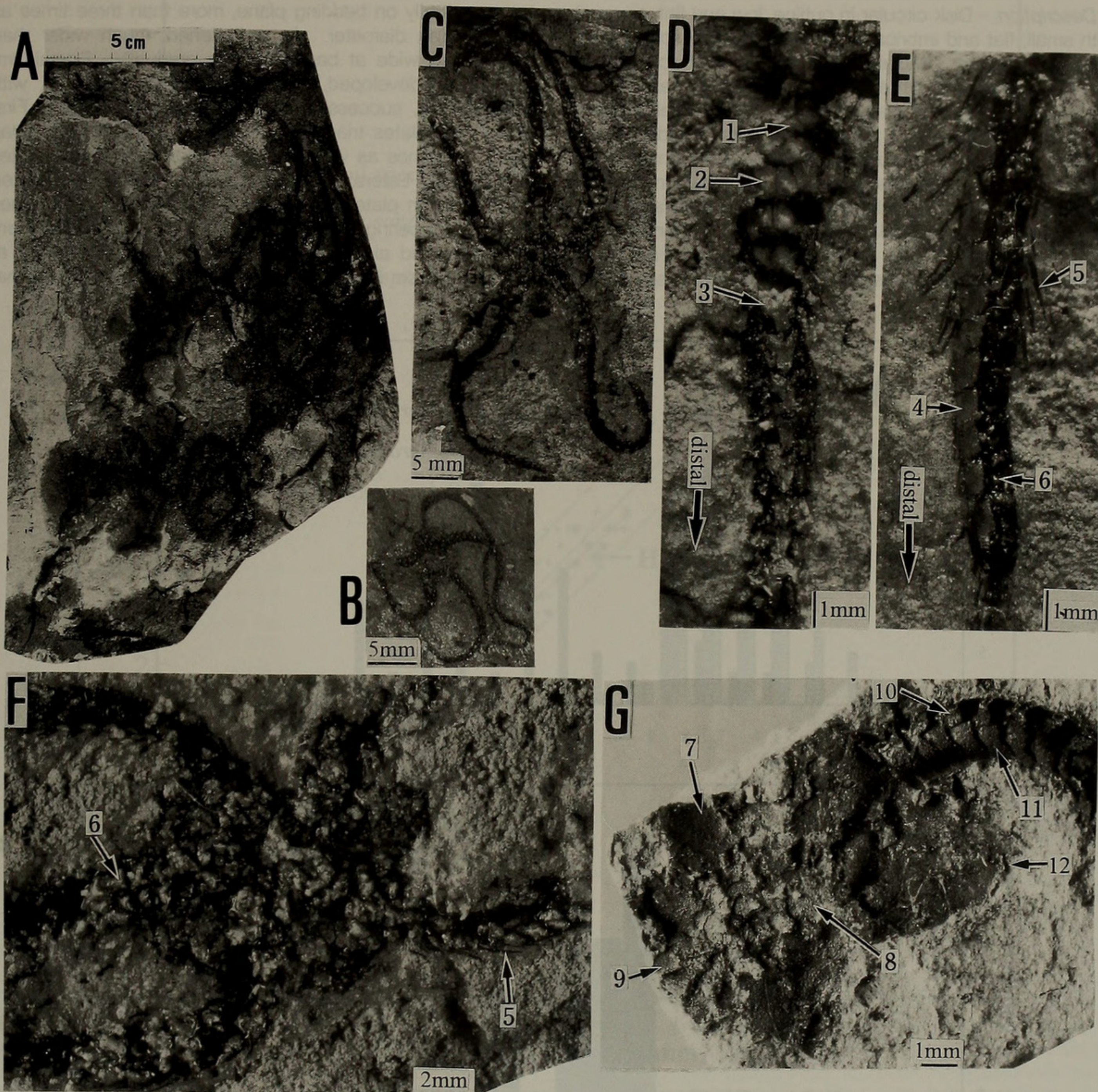

Figure 3. Fossil *Ophiura sarsii sarsii* Lütken, 1855 from the Hachioji Formation. **A.** Dense occurrence of fossils ; **B.** Small individuals ; **C.** Dorsal view of a complete specimen ; **D.** Free arm, proximal part showing inside of ventral arm plates and lateral arm plates, distal part showing dorsal side of vertebral ossicles ; **E.** Free arm, latero-ventral view ; **F.** Ventral view of disk and proximal arms ; **G.** Dorsal view of disk and proximal arm. Morphological explanation : 1, Inside of ventral arm plate ; 2, Inner ventral side of lateral arm plate ; 3, Dorsal view of vertebral ossicle ; 4, Lateral side of lateral arm plate ; 5, Arm spine ; 6, Ventral view of vertebral ossicle ; 7, A part of radial shield ; 8, Central plate ; 9, Scale ; 10, Lateral side of lateral arm plate ; 11, Dorsal arm plate ; 12, Disk margin.

1998, p. 10-12, figs. 3, 4.

Materials.—Thirty-five specimens from the Hachioji Formation, three of which are illustrated here, are housed at the Municipal Nagaoka Science Museum, Niigata Prefecture (Gf8-10).

Measurements.—Measurements are based on 31 specimens ; disk diameter ranges from 6.0-14.1 mm ; mean, 9.7 mm ; median, 9.9 mm.

Description.—Disk circular in outline, low and flat, covered with small, flat and imbricated scales. Primary scales fairly large and circular. Radial shields oval, about twice as long as wide, separated from each other and about half as long as disk radius. Comb plates elliptical. Oral shields about one third of disk radius, pentagonal with rounded distal borders, with a pointed corner proximally and slightly longer than wide. Adoral plates slender, rectangular, in contact with each other at adoral margin. Oral plates fairly long, rectangular with a pointed corner proximally, in contact with each other at adoral side. Genital plates slender and long. First 4 or 5 arm segments insert laterally into disk. Arms bent gradually on bedding plane, more than three times as long as disk diameter. Arms flattened, much wider than high, rather wide at base, tapering gradually. Dorsal arm plates well developed, rectangular, wider than long, with median keel, successive plates broadly in contact. First dorsal arm plates triangular. Ventral arm plates triangular, about 2–3 times as wide as long. First ventral arm plates trapezoidal. Lateral arm plates well developed, separated by dorsal arm plates, but in contact ventrally. Arm spines long and tapering, about twice as long as arm segment proximally and almost equal to length of arm segment at mid-arm, three in number, adpressed or often somewhat

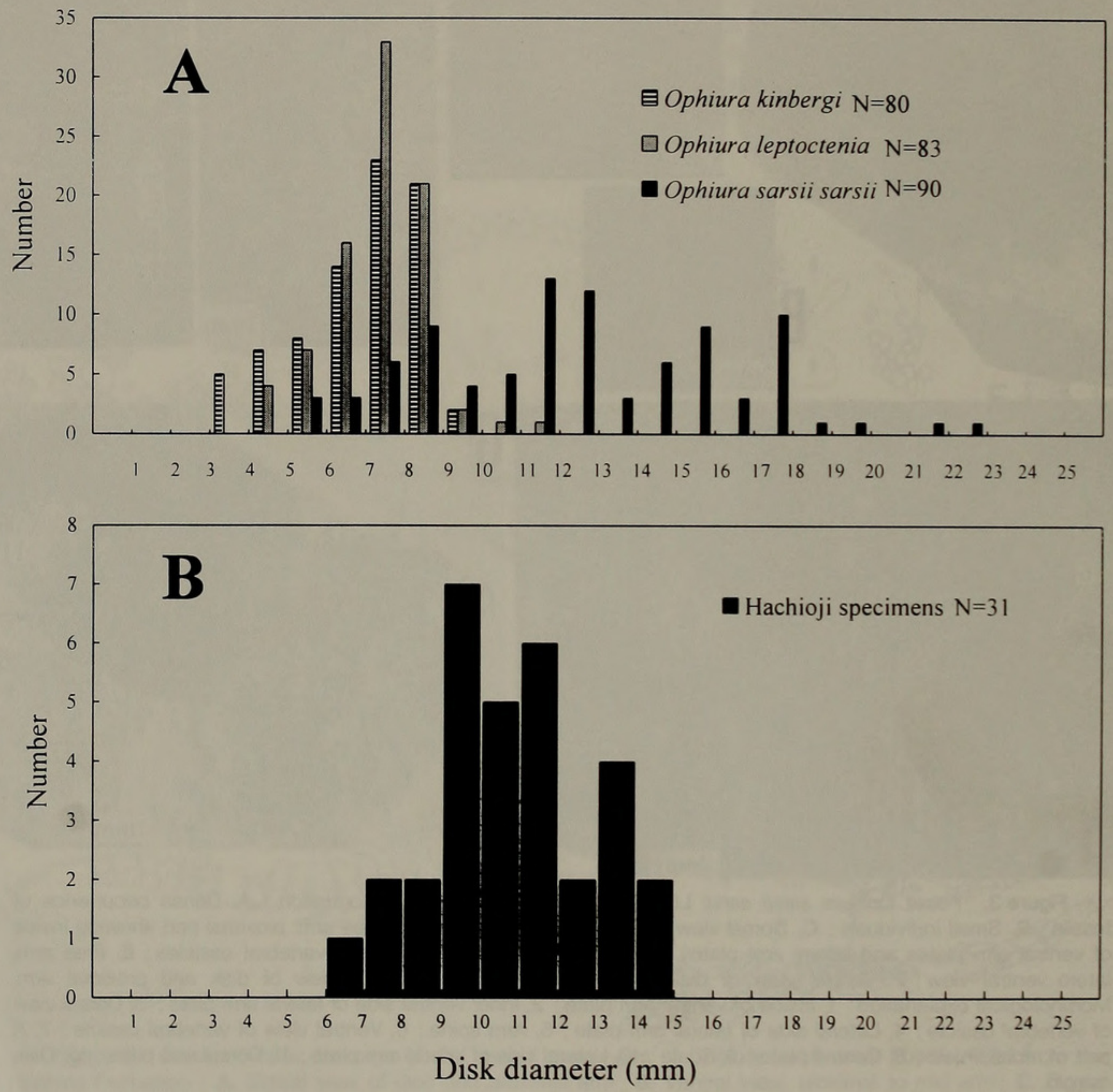

Figure 4. Size frequency distribution of Recent *Ophiura sarsii sarsii*, *Ophiura leptoctenia*, *Ophiura kinbergi* (**A**) and fossil *Ophiura sarsii sarsii* from the Hachioji Formation (**B**). Data for these Recent specimens are from the specimens stored at the National Science Museum, Tokyo (*Ophiura s. sarsii*, NSMT-E 1608, Wakasa Bay, Fukui Prefecture, 270 m depth ; 1414, Toyama Bay, Toyama Prefecture, ca. 200 m depth ; *Ophiura leptoctenia*, NSMT-E 1987, Off Otsuchi, Iwate Prefecture, 1,038–1,055 m depth ; *Ophiura kinbergi*, NSMT-E 0670, Amakusa Isls., Kumamoto Prefecture, ca. 30 m depth).

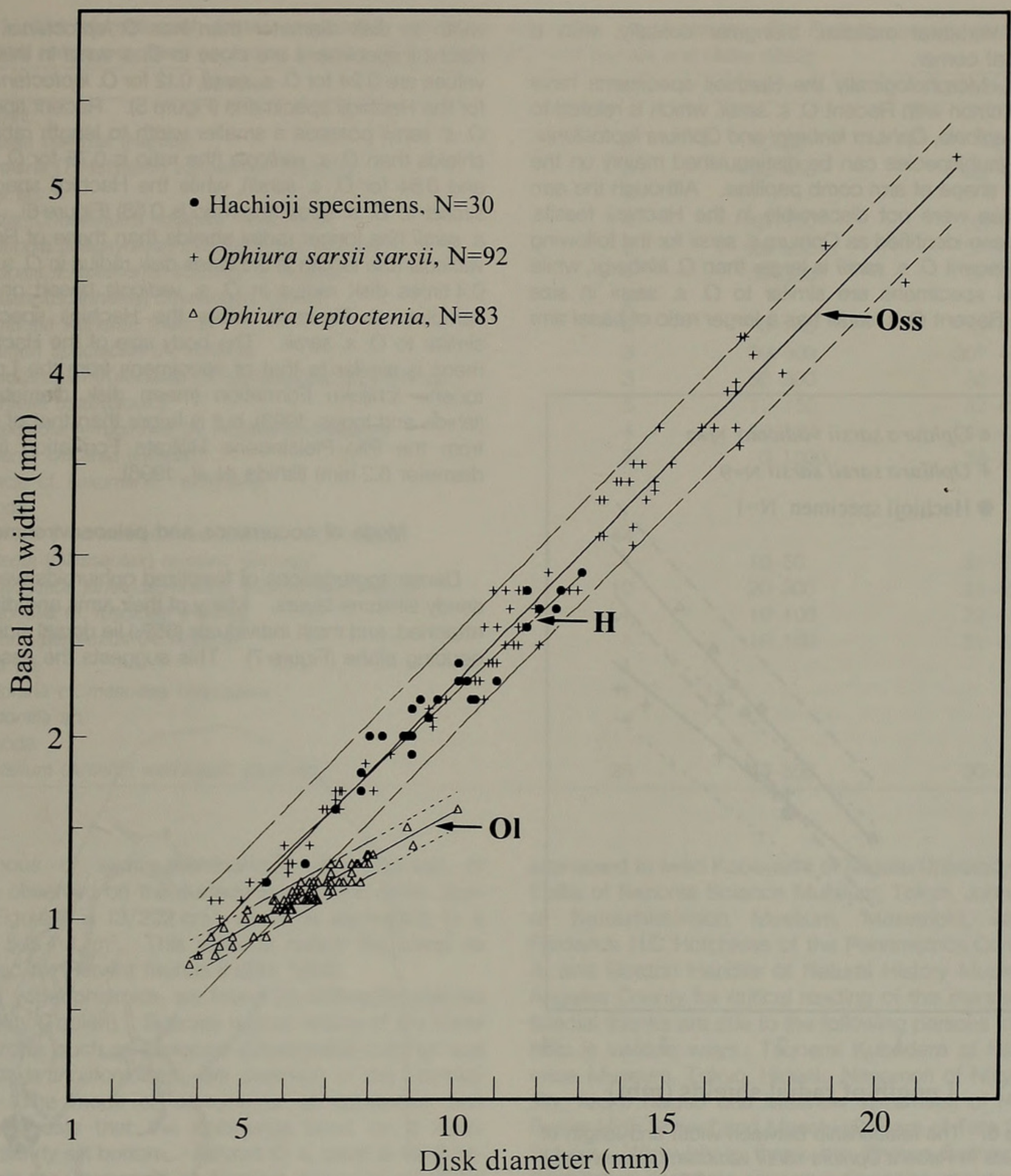

Figure 5. The relationship between disk diameter and basal arm width of Recent *Ophiura sarsii sarsii*, *Ophiura leptoctenia* and fossil *Ophiura sarsii sarsii* from the Hachioji Formation. Solid lines show linear regression and broken lines show 95% confidence limits. Each regression line is statistically significant {$r=0.99$, $p<0.05$ for living *O. s. sarsii* (Oss), $r=0.95$, $p<0.05$ for *O. leptoctenia* (Ol) and $r=0.97$, $p<0.05$ for fossil specimens of *O. s. sarsii* from the Hachioji Formation (H)}. There is a statistically significant difference on intercept ($p<0.05$) and regression coefficient ($p<0.05$) between the two regression lines (Oss, Ol). The fossil specimens safely fall into the confidence interval of Recent *O. s. sarsii*, but not into that of *O. leptoctenia*. Data for Recent *O. s. sarsii* and *O. leptoctenia* are from specimens stored at the National Science Museum, Tokyo (*O. s. sarsii* NSMT-E 0568, Wakasa Bay, 275 m depth; 1414, 1608, 1609, Wakasa Bay, 240 m depth; *O. leptoctenia* NSMT-E 1987).

detached. Vertebral ossicles, triangular dorsally, with a pointed distal corner.

Remarks.—Morphologically the Hachioji specimens have much in common with Recent *O. s. sarsii*, which is related to *Ophiura s. vadicola*, *Ophiura kinbergi* and *Ophiura leptoctenia*. These four (sub)species can be distinguished mainly on the basis of the shape of arm comb papillae. Although the arm comb papillae were not discernible in the Hachioji fossils, they have been identified as *Ophiura s. sarsii* for the following reasons. Recent *O. s. sarsii* is larger than *O. kinbergi*, while the Hachioji specimens are similar to *O. s. sarsii* in size (Figure 4). Recent *O. s. sarsii* has a larger ratio of basal arm width to disk diameter than has *O. leptoctenia*, while the Hachioji specimens are close to *O. s. sarsii* in this ratio : the values are 0.24 for *O. s. sarsii*, 0.12 for *O. leptoctenia* and 0.22 for the Hachioji specimens (Figure 5). Recent specimens of *O. s. sarsii* possess a smaller width to length ratio for radial shields than *O. s. vadicola* (the ratio is 0.75 for *O. s. vadicola* and 0.54 for *O. s. sarsii*), while the Hachioji specimens are similar to *O. s. sarsii* (the ratio is 0.58) (Figure 6). Recent *O. s. sarsii* has longer radial shields than those of Recent *O. s. vadicola* (the length is 0.5 times disk radius in *O. s. sarsii*, and 0.4 times disk radius in *O. s. vadicola* based on the same samples as Figure 6), while the Hachioji specimens are similar to *O. s. sarsii*. The body size of the Hachioji specimens is similar to that of specimens from the Lower Pleistocene Ichijuku Formation (mean disk diameter 9.6 mm) (Ishida and Inoue, 1993), but is larger than that of specimens from the Plio-Pleistocene Hijikata Formation (mean disk diameter 8.2 mm) (Ishida *et al*., 1996).

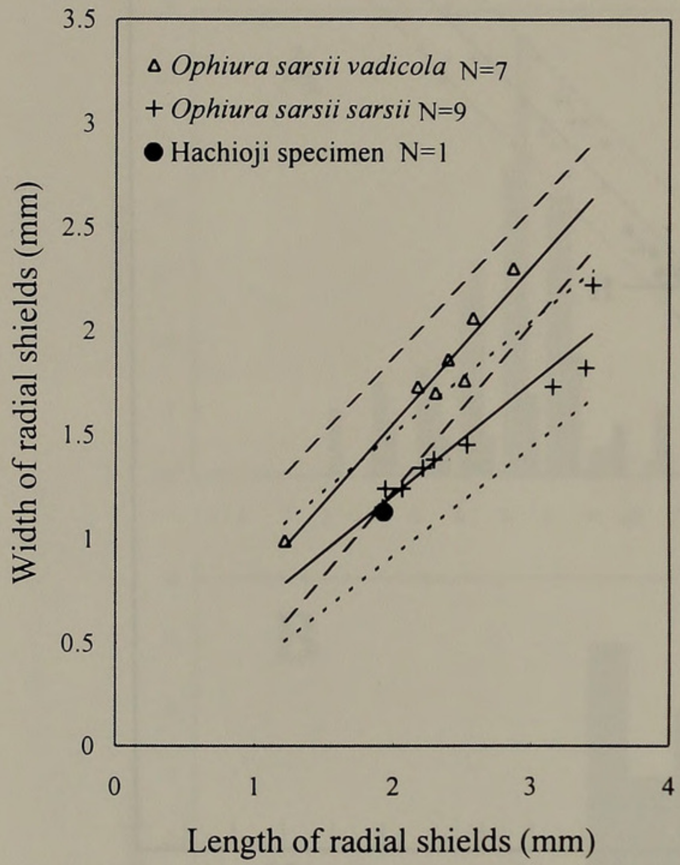

Figure 6. The relationship between width and length of radial shields in Recent *Ophiura sarsii vadicola*, *Ophiura sarsii sarsii* and a fossil specimen from the Hachioji Formation. The value at each point for *O. s. vadicola* and *O. s. sarsii* indicates the mean value measured from five radial shields in the specimen. The value for the fossil specimen indicates the mean value measured from three radial shields in the specimen. Solid lines show linear regression and broken lines show 95% confidence limits. Each regression line is statistically significant ($r=0.97$, $p<0.05$ for living *O. s. vadicola*, $r=0.95$, $p<0.05$ for *O. s. sarsii*). There is a statistically significant difference on intercept ($p<0.05$) and regression coefficient ($p<0.05$) between the two regression lines. The fossil specimen safely falls into the confidence interval of Recent *O. s. sarsii*, but not into that of *O. s. vadicola*. Data for Recent specimens of *O. s. vadicola* and *O. s. sarsii* are from the specimens stored at the National Science Museum, Tokyo (*O. s. vadicola* NSMT-E1821, *O. s. sarsii* NSMT-E1609, 0568).

Mode of occurrence and paleoenvironment

Dense aggregations of fossilized ophiuroids were found in sandy siltstone layers. Many of their arms and disks are still attached, and most individuals (85%) lie dorsal side up on the bedding plane (Figure 7). This suggests the assemblage is

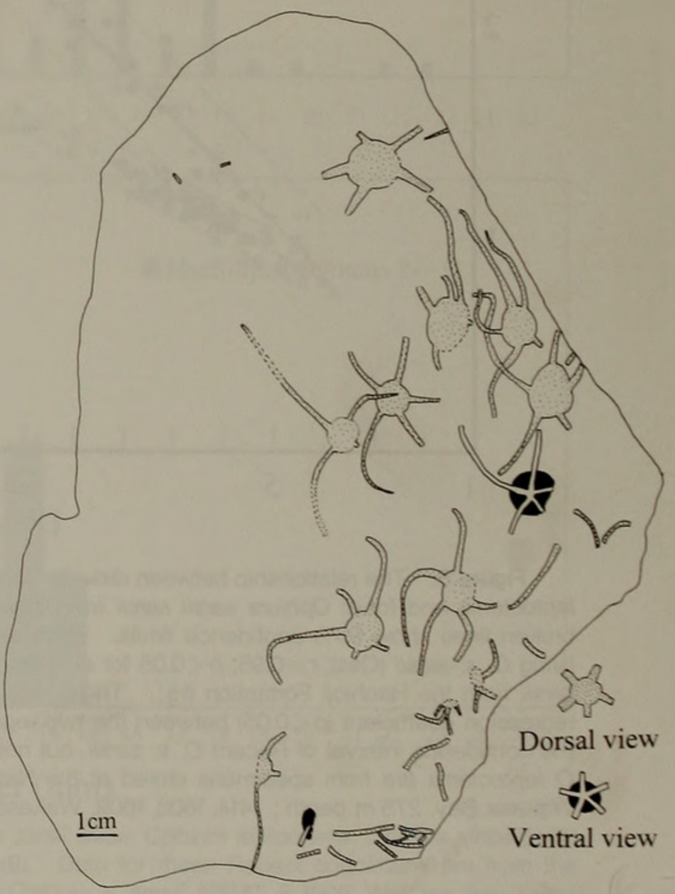

Figure 7. Sketch illustrating the dense occurrence of fossil *Ophiura sarsii sarsii* in sandy siltstone matrix from the Hachioji Formation.