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LOWER DEVONIAN CRINOID *PERNEROCRINUS* FROM THE SOUTHERN KITAKAMI MOUNTAINS, N.E. JAPAN

by

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(with 4 text-figures, 2 tables and 3 plates)

Abstract

Three species of Crotalocrinitidae crinoids, *Pernerocrinus hayasakai* (Minato and Minoura), *P. perforatus* sp. nov. and *P.* sp. are described. All these species came from the lower part of the Ohno Formation (Lower Devonian) of the southern Kitakami Mountains. The first species was previously described as a tabulate coral, *Ohnopora hayasakai* gen. et sp. nov., belonging to the family Syringolitidae. Robust construction of the *Pernerocrinus* is interpreted to be especially well adapted to reef environment and its occurrence is strictly confined, at present, to the Lower Devonian.

Introduction

One of the crinoids described in this article was collected by the late Prof. M. Minato of Hokkaido Univ. in 1950, at Ohno, type locality of the Lower Devonian Ohno Formation in the southern Kitakami Mountains. At first it was taken to be as a *Thecostegites* (Minato et al., 1959), but was later described as a new tabulate coral *Ohnopora hayasakai*, belonging to the family Syringolitidae (Minato and Minoura, 1977). All the specimens available then were fragmental molds with no original calcite skeletons left. Some were interpreted as molds of fragmental colonial corallites and others as tabulae and walls replaced by silica. Two tubes, parallel to the walls and penetrating the tabulae, and tubules connecting these tubes (Minato and Minoura, 1977) are so strikingly unusaual in tabulate coral that Hill (1981, F558) expressed strong doubts for including it in the family Syringolitidae. Thus, she stated "systematic position problematical; horizontal canals in tabulae otherwise unknown in the Tabulata".

Meanwhile, several additional specimens were found in 1981 and 1982 at a few localities close to Ohno, and although all this new material also is fragmental, none being complete, preservation of some is such that the original calcite skeletons are partially undissolved with evident echinodermata microstructure. Accordingly, transfer of *Ohnopora* from Coelentrata to Echinodermata became necessary, and its close resemblance to *Pernerocrinus* was pointed out (Minato et al., 1982). Detailed examination and comparison of all the specimens reveals that they are generically identical to peculiar Crotalocrinitidae crinoid *Pernerocrinus* Bouška (1946), known from the lower Devonian of Bohemia (Bouška, 1946) and of Australia (Bates, 1972).

Detailed comparison with *Pernerocrinus* and other allied genera highlighted such morphological characteristics as more regularly arranged alternating brachia and

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heteromorphic columns in the Japanese specimens. Consequently, *Ohnopora* is now believed to be a junior synonym of *Pernerocrinus*. One specimen, included in the new material, is nearly identical to *P. hayasakai* in general morphology. Nevertheless, rather large interarticular canals, sporadically and transversely penetrating the entire depth of preserved brachial disc of this specimen, is significant to establish a new species, *Pernerocrinus perforaturs*. This paper deals with the description of these two peculiar crinoid species and an undeterminable form, *P.* sp.

Systematic description

Class Crinoidea Miller, 1821

Subclass Inadunata Wachsmuth and Springer, 1885

Order Cladida Moore and Laudon, 1943

Suborder Cyathocrinina Bather, 1899

Superfamily Gasterocomacea Roemer, 1854

Family Crotalocrinitidae Bassler, 1938

Genus *Pernerocrinus* Bouška, 1946

Type species (by original designation): *Pernerocrinus paradoxus* Bouška 1946

Diagnosis: "Large, thick walled crinoid composed of massive element. Crown heavy, low and broad. The plates of cup and column are extremely elongate in transverse direction. Arms constructed similarly as in crotalocrinitid but without meshes. The brachials are in firm contact laterally both within the rays and between adjacent rays. The tegmen consists of a large number of small, thick plates which are unequal in shape and size. Column short, broad, joined inconspicuously to the cup. Root heavy with long branching appendages" (Bouška, 1950)

Some of the supplementary statements given by Bates (1972) are as follows: tube-like column with very wide lumen; arms fused into a solid subhorizontal disc pierced by large axial canals and bearing on its upper surface adoral grooves; no anal plate.

Subhorizontal and thick discoid crown is quite characteristic for this peculiar crinoid. Even fragmental molds of disc, frequently found in the Ohno Formation, are at least generically identifiable by "appearance of *Favosites* structure" as mentioned by Bouška (1950).

Discussion: The taxonomic relationships between *Pernerocrinus* and such other Crotalocrinitidae genera as *Crotalocrinites, Enallocrinus* and *Syndetocrinus* has been sufficiently discussed by Bouška (1950) and by Bates (1972). But whereas the present writer fully agrees with their suggestions, it is to be noted that interarticular canals found in *P. perforatus* superficially recall the net-work structure of the arms of *Crotalocrinites*, although the function or the morphological details of these canals are still unknown.

Included species:

Pernerocrinus paradoxus Bouška, 1946, Koneprusy, Central Bohemia; Lower Devonian.

Parapernerocrinus sibiricus Yakovlev, 1949, Northern Ural, USSR; Coblenzian.

Pernerocrinus discus Bates, 1972, Lilydale Ls., Victoria, Australia; Siegenian-Emsian.

Pernerocrinus hayasakai (Minato and Minoura), 1977, Ohno Formation; Lower Devonian
Pernerocrinus perforatus Minoura, 1987, Ohno Formation; Lower Devonian

Pernerocrinus hayasakai (Minato and Minoura)

(Pl. 1, figs. 1-3; Pl. 3, fig. 1; Text-figs. 1, a-c; 3, a; 4, a-d)

1959 *Thecostegites* sp., Minato et al, p. 75 (listed only)
1977 *Ohnopora hayasaki* Minato and Minoura, p.560, pl. 3, figs. 1,2.
1979 *Ohnopora hayasakai*, Minato et al., p.62, pl. 8, figs. 1-4, pl. 9.
1982 *Ohnopora* sp., Minato et al. p.773, pl. 1, fig. 1; non figs. 2-4.

Material: Partial inner mold (UHR 30190-3 = Holotype of *O. hayasakai*); Outer mold of partial disc (UHR 30189 = Paratype of *O. hayasakai*); Partial disc (UHR 30669); Outer mold of partial disc and column (UHR 30668); Outer mold of partial disc (UHR 30672).

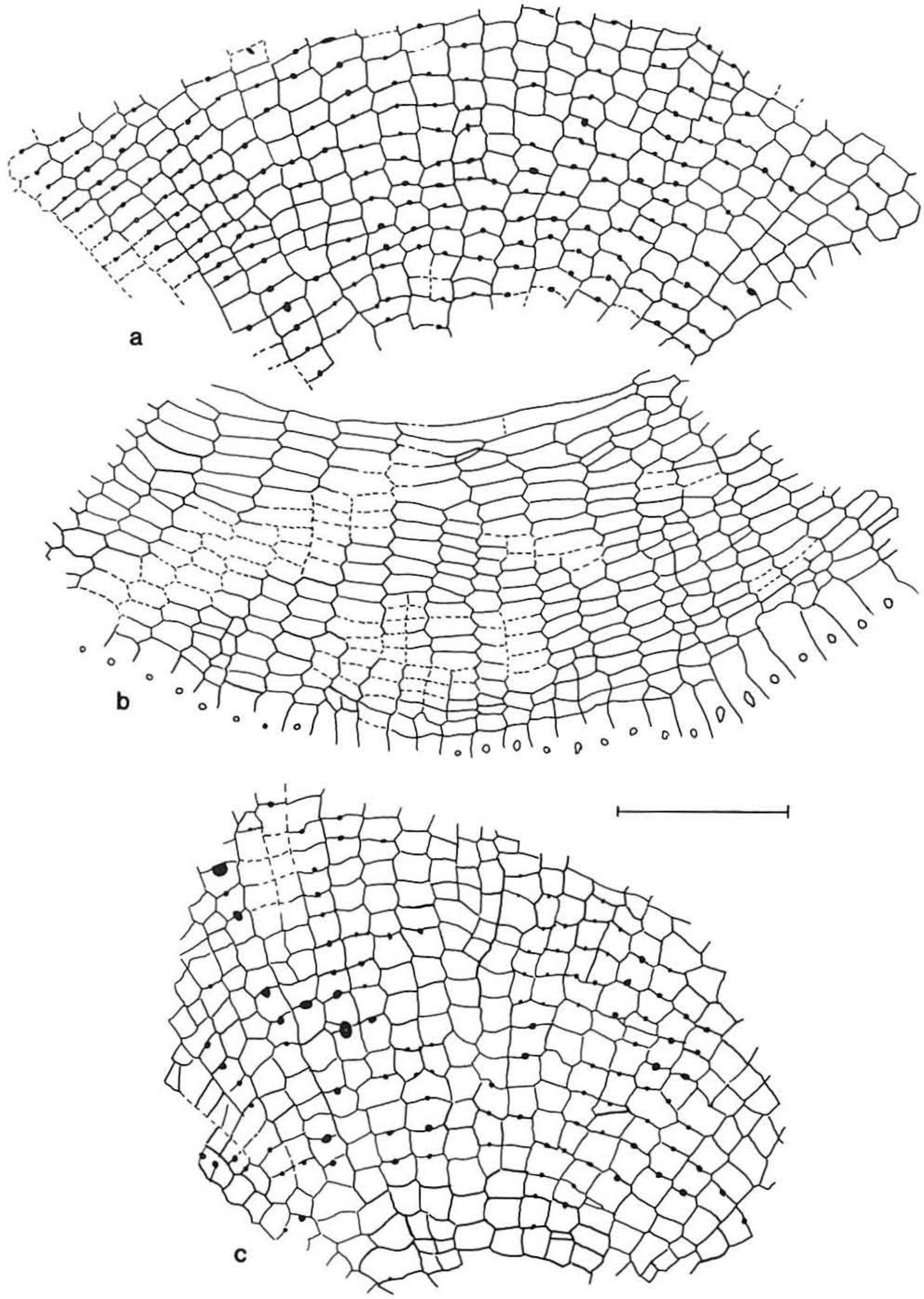
Locality and horizon: No less than 20 fragmental specimens are known from Oh1 and Oh2 Members designated by S. Haga (1978, M.S.: in Minato et al., 1979) of the Ohno Formation. Specimens herein described and figured are collected from the following localities, all in Ohfunato City, Iwate Pref.; UHR 30189 and UHR 30190: Ohno, Hikoroichi, coll. by M. Minato; UHR 30668 and UHR 30672: Nameriishi*, Hikoroichi, coll. by S. Haga; UHR 30669: Eastern Ridge at Ohfunezawa, Okusakamotozawa, Hikoroichi, coll. by H. Yokoyama.

Description: Column is estimated to be circular and its outside diameter attains 45 mm, slightly tapers distally to about 35 m, large lumen occupies more than 80 percent of the outside diameter of the column (Text-fig. 4, d). Internal surface of the lumen appears to be heteromorphic, at least partially, formed of lower (0.8–1.0 mm), and higher (1.8–2.0 mm) columnals. These two types of columnals, longitudinally alternate with each other, and have vertical seams, which in the former are 1 mm and in the latter 2–4 mm apart (pl. 2, figs. 1a,b; Text-fig. 3, a). Details of the other part of the column and presence of root are unknown due to poor or no preservation.

Plate arrangement of the crown except that of brachials is not observable. Uniserial brachia, bifurcate isotomously at repeated intervals of every 5–10 brachials, are in firm contact with each other, laterally fused into a solid subhorizontal disc (Text-fig. 1, a-c). Brachials are extremely deep, more than 10 times deeper than the height, pierced by axial canals at about two-third depth from the adoral surface where deep U-shaped adoral grooves are present. Brachial articulation is syzygial. Between successive brachials exist a central and two lateral canals vertically connecting the adoral groove and the axial canal (pl. 1, figs. 2,3b). Laterally fused arms are alternately arranged, giving most brachials flattened hexagonal shape both in dorsal and ventral outlines (Text-fig. 1). Width of the brachial is 1.5–2.1 mm, height is 1.2–1.7 mm.

Comparison: This species is slightly larger than *P. discus* and having more regularly alternating brachia, if not entrirely so. Heteromorphic column of the present form, though observed only in a rather ill preserved specimen, is entirely unknown in other species. *P. sibiricus* and *P. perforatus* are of nearly the same size as this species.

* Practically same locality to Ohno.



Text-fig. 1 Brachial plate arrangement of *Pernerocrinus hayasakai* (Minato and Minoura) (scale-bar is 10 mm).
a: Ventral surface drawn from the photo shown as plate 1, fig. 1a. b: Dorsal surface from plate 1, fig. 1b. c: Ventral side from Plate 1, fig. 3a.

However, lateral canals are absent in the former species and interarticular canals are present in the latter form. *P. paradoxus* is extremely large in size in comparison with all other species, and has characteristic rolled-up free arms.

Pernerocrinus perforatus sp. nov.

(Pl. 2, figs. 1-3; Text-figs. 2, a-b; 3, b-c; 4, e)

1982 *Ohnopora* sp., Minato et al. p.773, pl. 1, figs 2-4; non fig. 1.

Derivation of the specific name: Interarticular canals appear as if they are perforating the disc.

Material: The material (Holotype, UHR 30671), consists of slightly deformed partial column and disc, was originally found in a hand specimen (pl. 2, figs. 2a,b).

Locality and horizon: Only one specimen here described is known from the lower part of the Ohno Formation at Ohfunezawa, Okusakamotozawa, Hikoroichi, Ohfunato City, Iwate Pref., coll. by H. Yokoyama.

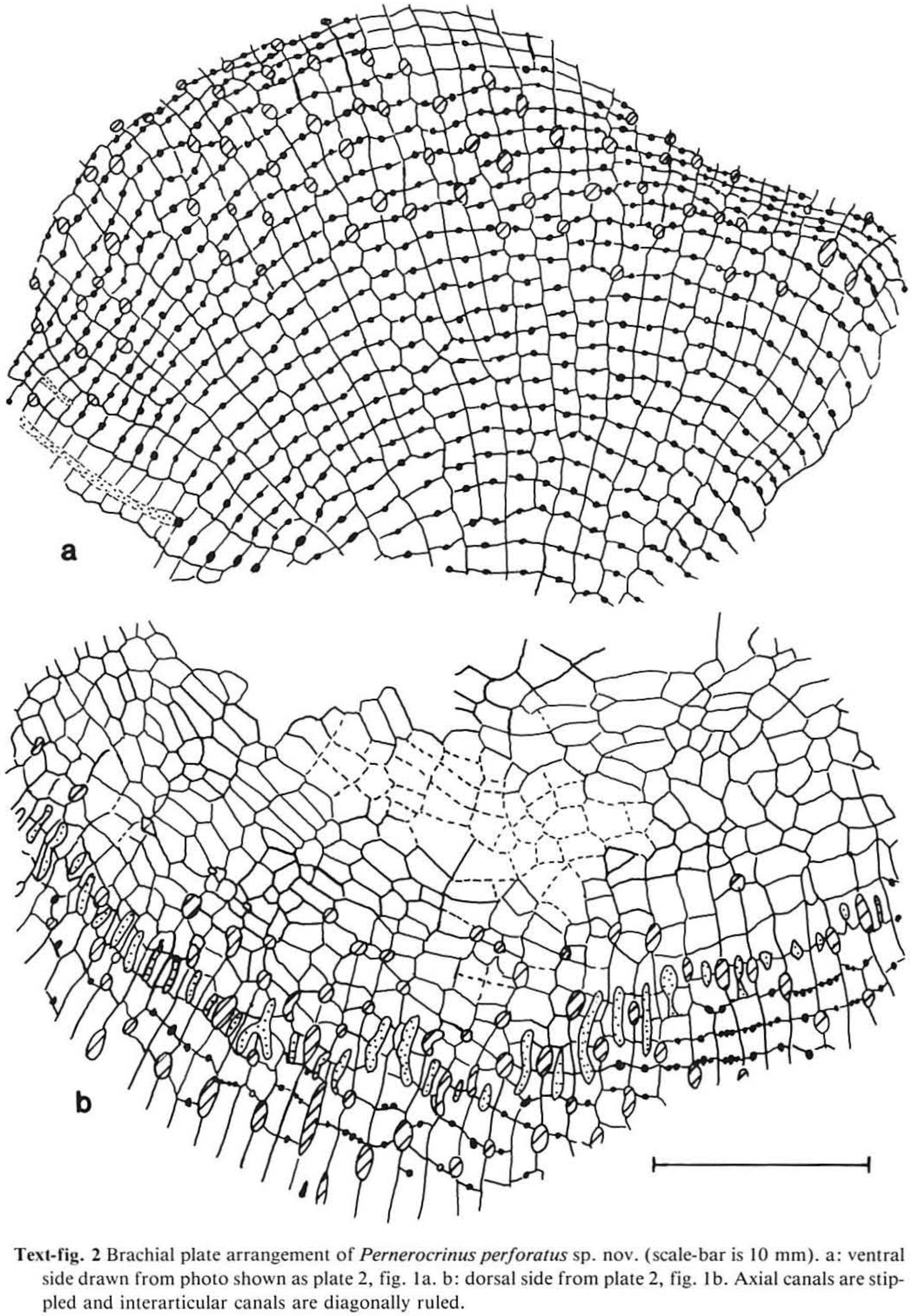
Specific diagnosis: Pernerocrinus with interarticular canals.

Description: Although its preservation is the best of all the Japanese material of *Pernerocrinus*, both adoral and aboral surfaces are lacking probably due to the abrasion before being entrapped in the sediment. Further, no more than half a millimeter of the specimen was ground before removing surficial matrix. Column is also slightly ground down, thus no more than a millimeter is lost except lower several millimeters of the column, where a few millimeters are ground to attempt observing the columnal outer surface (pl. 2, figs. 2a,b).

Although less than half a disc is preserved, its diamter is estimated to be no less than 65 mm and reconstructed to be 100–110 mm. Maximum depth of the preserved brachial is 14 mm. Width attains 1.5 and 1.8 mm on preserved dorsal and ventral sides, respectively. Height is no more than 1.5 mm. Arm branching is isotomous and its alternate arrangement (Text-fig. 2, a,b) is not so significant as that of *P. hayasakai*. And brachial plate arrangement at proximal dorsal side seems rather irregular, therefore, brachials at this portion may be vertically twisted. Plate arrangement at calyx is unknown.

No adoral groove is preserved. Axial canals, oval in ventrodorsal cross section and 0.5–0.6 × 0.8 mm in size penetrate the brachials. Between each brachial, a central canal, less than half a millimeter diameter, and two lateral canals, smaller than the former are present, though not always they are visible in lateral view (pl. 2, fig. 1b).

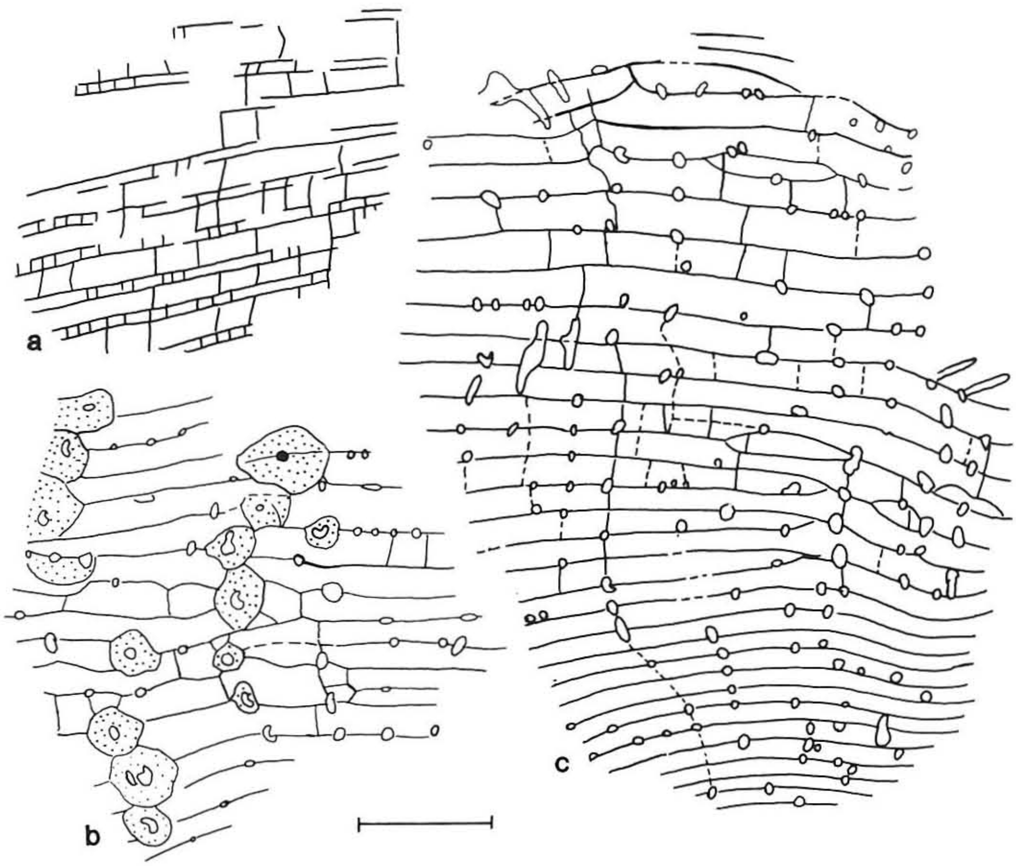
Two to five rather thick interarticular canals, 0.5–1.0 mm in diameter, exist between each brachia (pl. 2, figs. 1a,b; Text-fig. 2, a,b). None is seen in proximal 10–12 brachials, but they appear at preserved 13–15th brachial, and further distally in intervals of every 3–5 brachials. They penetrate entire depth of preserved brachial disc, e.g. below the level of axial canals aborally. Although detail of these interarticular canals are unknown, they are not gonioporoid exospires. Since their distribution is too irregular and sporadic, and they seem much larger than ordinary exospires. Although morphologically they are quite different with each other, superficially these canals



Text-fig. 2 Brachial plate arrangement of *Pernerocrinus perforatus* sp. nov. (scale-bar is 10 mm). a: ventral side drawn from photo shown as plate 2, fig. 1a. b: dorsal side from plate 2, fig. 1b. Axial canals are stippled and interarticular canals are diagonally ruled.

rather recall net-work structure of *Crotalocrinites*, whose arms are believed to be more or less flexible.

Column is estimated to be circular and slightly tapers distally (Text-fig. 4, e). External diameter at proximal portion and length preserved are about 40 and 50 mm, respectively. Diameter of the lumen at proximal portion is 23 mm and slightly tapers distally to 20 mm. Height of proximal columnals is 2.5 mm, gradually decreases to 1.1 mm at distal edge (pl.2, figs. 3a,b, Text-fig. 3, c). Thickness of the columnal wall is about 4–5 mm but its external surface is not exactly known, since outer surface of the coulumn is full of numerous facets for the reception of roots. These are round, hexagonal or octagonal in shape, 3–6 mm in diameter, and centers are pierced by central canals, of oval or kidney-bean shape (pl. 2, figs. 2a,b, Text-fig. 3, b). These central canals internally appear, on the facets of every or every other columnal, as if aligned along longitudinal rows 6–8 mm apart (Text-fig. 3, c). At least several proximal col-



Text-fig. 3 Sketch showing the plate arrangement of column. (scale-bar is ca. 10 mm) a: internal surface of the lumen of *Pernerocrinus hayasakai* (Minato and Minoura) drawn from photo shown as plate 3, fig. 1a. b: Weathered external surface of column of *Pernerocrinus perforatus* sp. nov. from plate 2, fig. 3b. c: internal surface of the lumen of *Pernerocrinus perforatus* sp. nov. from plate 2, figs 3a, b.

umnals seem to have longitudinal or sinuous seams in random interval. Thus internally ground surface of the lumen appears as if layers of bricks with many vertically aligned black spots between the layers (Text-fig. 3, b,c). No distinct root is preserved, but numerous roots are apparently suggested by numerous facets, and they probably attach even at proximal column.

Comparison: Size and shape of this species closely resemble those of *P. hayasakai*. Interarticular canals sporadically develop at relatively distal part of the brachial disc constituting most significant character of the present species, entirely unknown in any other species.

Pernerocrinus sp.

(Pl. 3, figs. 2a-c; Text-fig. 4f)

Material: Partial outer mold of a disc with tegmen and branching roots (UHR 30670)
Locality and horizon: Oh1 Member of the Ohno Formation at Nameriishi, Ohmorizawa, Hikoroichi, Ohfunato City, Iwate Pref. coll. by S. Haga.
Description: Brachial disc preserved is no more than one fourth of an individual, and its total height is 92 mm. Accordingly, it is reconstructed to be 240 mm in original diameter. Brachials appear, though very few can be observed, as flattened hexagonal in outline, by which alternate arrangement of brachia is suggested (pl. 3, fig. 2b). Depth of brachial reaches at least 20 mm, height and width are 1.8 mm and 2.2–2.4 mm, respectively. This extremely deep brachial is pierced by an axial canal, at 2/3 to 3/4 depth from the adoral surface, where deep U-shaped adoral groove presents. Width of the axial canal, judged from its mold, is 1.1–1.5 mm in diameter, and that of the groove is 1/2 to 1/3 of that of the brachial. The former is wider and the latter is slightly narrower than those of the other species. Extremely thin, less than 0.4 mm wide and 0.8–1.0 mm high, slit-like structures vertical to the both sides of the groove probably are mold of the facets for covering plates (pl. 3, fig. 2c).

Central canals, connecting the groove and the axial canal, are present between successive brachials. Although several molds of wall-like structures are apparent along the central canals, and they are suggestive of lateral canals, no obvious one is recognizable. Isotomous bifurcation of brachia occurs less frequently than in the other species. It means that interval of the bifurcation seems longer in this species than in the other species.

Several tegminal plates barely visible are small, 1.5–1.8 mm in diameter, irregular, and appear pentagonal, hexagonal, or octagonal in shape (pl. 3, fig. 2a). Beneath the proximal tegmen opening of adoral grooves and axial canals are seen. Then, thickness of the tegmen is estimated to be 5–6 mm. The lateral extent of the tegmen, which is estimated to be slightly domed centrally, is not exactly known. Nevertheless it may reach more than half the preserved disc (pl. 3, fig. 2a).

Three fragmental roots, of which two are apparently branching, are preserved directly on the dorsal side of the disc, circular, in cross section, 7–8 mm wide and at maximum 25 mm long, slightly tapers distally (pl. 3, fig. 2b). These roots are composed of ossicles, about 2 mm high, and are pierced by 2–2.5 mm wide axial canals. No column is preserved.

Discussion

All the material available in this study is not only more or less deformed and fragmental, but is also mostly poorly preserved outer or silicified inner mold. At best half a disc and partial column of an individual are obtained. Although no less than 20 fragmental specimens, identifiable as *Pernerocrinus* by its characteristic shape of the mold are known from various localities, only a few are preserved well enough to be determined specifically with some reliability.

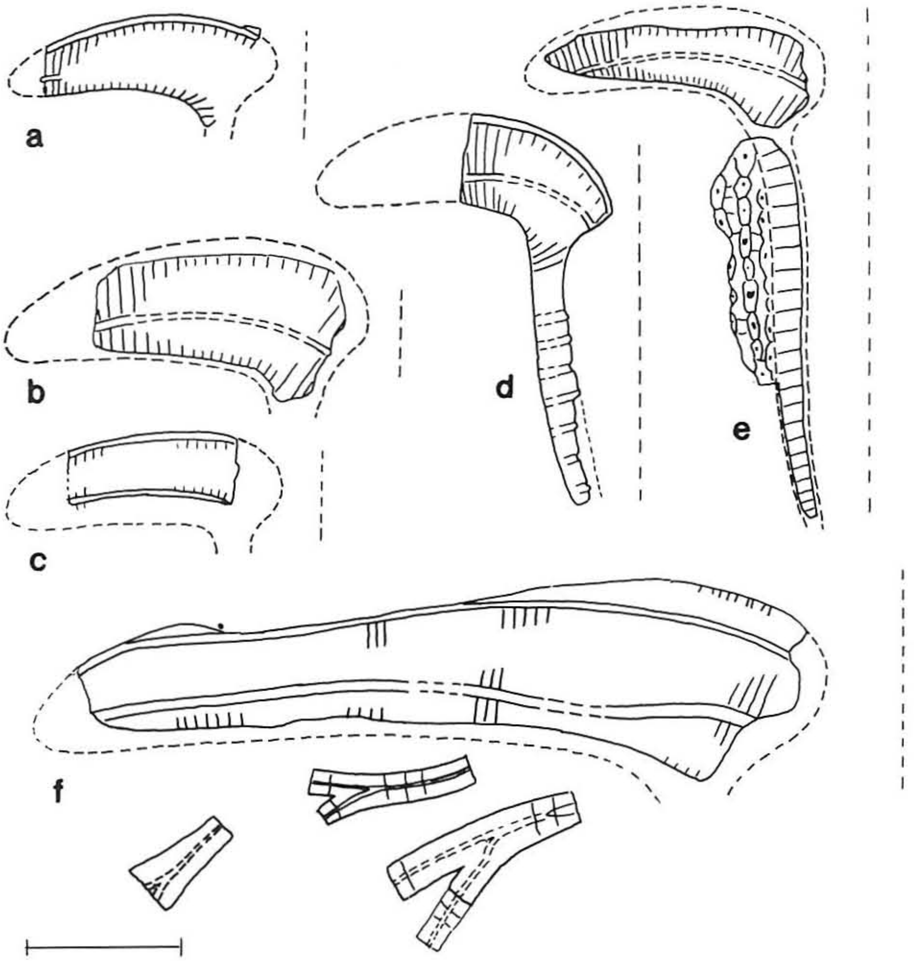
Reconstructed vertical profile, with some amount of interpretation and extrapolation (Text-fig. 4), would reveal that both *P. hayasakai* and *P. perforatus* are nearly identical in outer shape and size. Disc diameter in these two species is estimated to be 130–110 mm and 122 mm, respectively. And column diameter of *P. hayasakai* is 45 mm (UHR 30668), while that of *P. perforatus* is 40 mm (UHR 30671). Measurable thickness of columnal wall is 4 mm in the former species and 5 mm in the latter species. Variation in outer shape is rather apparent in the former species as steep (UHR 30668) and gentle (UHR 30189) curvature of the proximal ventral profile.

Size and shape variations found in *P. hayasakai* and *P. perforatus* are much less significant than those in *P. discus* described by Bates (1972). Column diameter of *P. discus* ranges from 18 to 40 mm. Thickness of the columnal wall ranges from 1.7 to 3.8 mm. Disc is basically subhorizontal on a vertical column, but an umbrella-like convex one, irregularly sloping away from the central tegmen, and a shallow bowl-shaped concave one, are mentioned for the Australian form (Bates, 1972, p. 333).

Size of skeleton in various species of *Pernerocrinus* is indeed quite variable. Actually column diameter in various forms of the genus ranges from 18 to 100 mm or more, of which the largest one has been suggested as one of the widest fossil crinoidal column (Ubaghs 1978, T63). Nevertheless, no detailed size comparison has been made yet for the genus. Based on descriptions and measurements on illustrations, various sizes of most specimens described and figured are tabulated (Table 1) to delineate different specific characters of *Pernerocrinus*. Included are those of allied genus *Parapernerocrinus* Yakovlev 1949, which is a junior synonym of *Pernerocrinus*, as mentioned elsewhere.

Since plate size is so variable even in a specimen, as axillary is sometimes nearly two times wider than that of brachial, it is, calculated in such a manner that several plates are measured together at a time. This procedure is repeated on as many portions of a specimen as possible and then averaged.

Even disc diameter has not been described, it is easily measuable on the illustrations if distal edge of the disc is preserved. Unfortunately, all *Pernerocrinus* described and illustrated are fragmental and none is complete. Accordingly, it is not directly measurable on the illustrations. Disc diameters in Table 1, therefore, are estimated



Text-fig. 4 Reconstructed vertical cross section of the Japanese *Pernerocrinus*. Broken lines are estimated portion and probable center of each specimen. (scale-bar is 20 mm) a: *P. hayasakai* based on Paratype UHR 30189. b: *P. hayasakai* based on UHR 30669. c: *P. hayasakai* based on UHR 30672. d: *P. hayasakai* based on UHR 30668. e: *P. perforatus* based on Holotype UHR 30671. f: *P.* sp. based on UHR 30670.

after such a rather lengthy discussion as follows:

P. paradoxus is reconstructed to have rolled-up free arms all around its distal edge (Bouška, 1950, Text-fig. 4), though no specimen with free arms directly attached to the disc is known but based on separately found fragmental rolled arms. This fact may suggest that the fragmentation is most susceptible at or close to the distal edge of the disc, if flexible arms are present. On the Australian specimens no such free arms are suggested, because distal edge of some specimens is rounded and no fragment of rolled-up portion of arms is found (Bates 1972, p.333). Although distal parts of all the Japanese specimens are missing due to fragmentation and presence or absence of free arm is unknown, no fragment suggesting rolled portion of the arms is found.

In an arm of an Australian specimen which its distal edge seems rounded (pl. 58, fig. 9), 22 brachials, at maximum, are counted. Bifurcation in this arm is four. In the Japanese specimens, 24 brachials with 4 bifurcations at maximum are preserved in an arm of UHR 30671 (Text-fig. 2, a).

Table 1 Size of specimens of *Pernerocrinus* in mm, except width of adoral groove and axial canal which are indicated by ratio to width of brachial. Depth of adoral groove also is ratio to width of adoral groove. Disc diameters in parentheses are calculated values by the following equations, as discussed in the text:
$D = 28 \times h \times 2 + C.W.$ (Japanese specimens)
$D = 25 \times h \times 2 + C.W.$ (Australian specimens)
where h is height of a brachial; C.W. is column diameter.
v. and d. at top of the column denote measurements on ventral and dorsal surfaces, respectively.
* Value originally described but differs from the measurement on illustrations.

Specimens			Brachials					Column (als)			Lumen	Disc	Adoral groove		Canal
			height	n	width	n	depth	width	height	thickness	diameter	diameter	width	depth	width
Minoura, 1987	*P. hayasakai*	UHR30668	v. 1.51	25	2.06	9	15.4	45-35	2, 1	4-3	32-26	68 + (130)	2/3	1	1/2
		UHR30669	v. 1.67 d. 1.66	95 23	1.75 1.43	70 32	15 +					80 +	2/3		2/3
		UHR30189	v. 1.41 d. 1.18	35 25	2.04 2.06	31 29	13	30			20?	71 + (109)	2/3	1	2/3
		UHR30672					8.5 +					50 +	1/2	1	1/2
	P. per.	UHR30671	v. 1.36 d. 1.47	67 45	1.49 1.77	65 38	14 +	40-25	2.5-1.1	5-4	23-20	65 + (122)			1/2
	P. sp.	UHR30670	v. d. 1.84	 12	2.17 2.37	12 6	20					190 +	1/3	1.5	2/3
Bouška, 1950	*P. paradoxus*	pl.3, fig.1	d. 2.97	7	5.29	10	36	100	1.83	15	70	300	3/4		1/2
		pl.3, fig.2	v. 3.74 d. 2.84	5 6			32	60	3.23	10	31 *70	95 +	3/4		1/3
		pl.4, fig.1	d. 2.30	34	2.65	21	15.6	100				250	3/4		
	P. sp.	pl.4, fig.4						125	2.25	17.5	90				
Bates, 1972	*P. discus*	P 26707	d. 1.26	33	1.24	36	9.6	27		3	21	58 + (90)	1/3	1.5	1/3
		P 26699	v. 1.69	84	2.41	37						56 +	1/2		
		P 26696	v. d.		1.71 1.40	15 3	7.9-4.4		1			44 +			1/2
		P 26695	v. 1.82	32	2.22	20						72 +	1/3		
		P 26691	v. 0.94 d. 0.98	15 12			8.5-5	20				42 + (67)			
		P 28037	v. 1.63	34	1.96	35						42 +	1/3		
		P 26701	d. 1.64	15	2.24	12		29		3.5	22	47 + (111)			
		P 26693						23		2.5	18		1/3	1	1/3
		Text-fig.4	v. 1.13	14			7.7	25	1.2	4.6		44 + (82)			
	P. sp.	P 26722	v. 1.39	10	2.10	9	20 +	100		*5	90	260	1/3		2/3
Yakovlev, 1949	*P. sibiricus*	pl.1, fig.5	d. 1.53	50	2.22	43			1.7						
		pl.1, fig.7			3.3	11	20								
		pl.2, fig.1	2.9	4	3.26	16	18								
		pl.1, fig.6						30	1.4	3	24				
		pl.2, fig.2						22	1.2	6.5	9?				

Rigid construction of completely fused brachial disc of this genus *Pernerocrinus* may allow an assumption that abrasion by current action is more or less limited and possibly occur concentrically. Actually, fragmental specimens of not only some of the Australian but also the Japanese forms retain somehow circular lateral outline at preserved distal edges, which suggests that the above assumption is not too absurd, if not very precise. Then the above maximum number of brachial plates preserved in both the Australian as well as the Japanese specimens can be considered to denote not very far from the distal edge of the disc. This means less than 25 brachials, with some allowance, may limit the distal edge of arms of the Australian specimens. In the same way, less than 28 plates are considered to characterize the Japanese specimens. Once distal edge of the disc is defined as above, disc diameter can be calculated simply, by multiplying the average height of brachial plate, number of plates and two, added to the column diameter. Although this estimation is based on quite an arbitral assumption applied to the Australian and the Japanese specimens only, profiles of the Japanese material thus obtained show similarity to both Bohemian and Australian species. This would suggest certain amount of reliability for the procedure of the reconstruction.

As above measured and estimated, size of the skeleton is extremely variable as apparent in Table 1. Also plate size is quite variable even within a species. Nevertheless, two groups can be easily discriminated by size of disc and column. One is larger, having column and/or disc diameters more than 90 mm and 200 mm, respectively. The other is smaller less than 45 mm and 130 mm. The larger group includes such species as *P. paradoxus* and *P.* spp. of Bates and of this study. The smaller group includes *P. discus, P. hayasakai* and *P. perforatus*.

Although size difference seems to be gradual and no critical limit is apparent, *P. hayasakai* and *P. perforatus* are considered to be slightly larger than *P. discus*, even thecal plates of these three species seem in a same size range as a whole. Since, column and disc of *P. hayasakai* and *P. perforatus* can be in a same size range, but are slightly larger than those of *P. discus*. Besides, brachials are much deeper in the former two species with 13–15 mm, than those of the latter which measures 7–10 mm. Accordingly, although not so apparent in appearance, *P. discus* is judged to be smaller than the former two species.

Parapernerocrinus sibiricus Yakovlev 1949 is apparently in the same size-range of the smaller species, in column diameter, wall thickness and plate size, though some wide brachials are figured (Yakovlev, 1949, pl. 1, figs. 7,8; pl. 2, fig. 1), and exact disc diameter is unknown. On this point, together with very slight morphological distinction, the author quite agrees with Bates (1972, p.333) to include this species in the genus *Pernerocrinus*.

Although the larger species can be grouped as having extremely large disc, which ranges from 200 to 300 mm or more, thecal plates of these species are extremely variable in size. Those of *P. paradoxus* are quite large, nearly twice as large as those of the smaller species in every dimension. Those of *P.* spp. of Bates and of this study, are approximately same size-range to those of the other smaller species (Table 1). Significance of this relatively small plates of these two species is not well understood but will be later discussed briefly.

As above mentioned, even great size variability is characteristic in the genus *Pernerocrinus*, all species can be arranged in such an order from small to large, as *P. discus, P. hayasakai, P. perforatus, P. sibiricus, P.* sp. of this study, *P.* sp of Bates and *P. paradoxus*.

Distinction between the smallest *P. discus* and the largest *P. paradoxus* by size is a matter of evidence. Size difference of the smaller four species is so gradual and sometimes overlaps that no significant limit is appreciable. Nevertheless, presence or absence of certain skeletal elements is so significant that specific distinction among these four species is readily made.

Lateral canals develop in *P. discus, P. hayasakai* and *P. perforatus*. Interarticular canals are restricted in *P. perforatus*. Heteromorphic column is known only in *P. hayasakai*. Further differences are as follows: Adjacent arms of *P. hayasakai* and *P. sibiricus* are mostly alternate with each other thus brachials are mostly hexagonal shape both in ventral and dorsal outlines. Cup plates of *P. sibiricus* and columnal plates of *P. perforatus* are, at least partially, sinuous in outline. Adoral grooves of *P. sibiricus* is described as isosceles triangle shape in cross-section while those of other species are U-shaped. Key to discriminate the species of the genus *Pernerocrinus* is briefly tabulated in Table 2.

Among the larger three species, *P. paradoxus, P.* spp. of Bates and of this study, the first species is quite distinct in having rolled-up free arms, extremely large skeletal plates consisting the disc, and axial canals penetrate at relatively close to the dorsal surface. Distinction between the latter two species is more or less vague in many aspects. Disc diameter and size of the skeletal plates are nearly compatible between these two species (Table 1). Axial canals are relatively larger than those of the other species. Root system of the Australian specimen is directly attached to cup and disc, without intervening stem, while fragmental roots are preserved directly on the dorsal side of the disc, even column is unknown, in the Japanese specimen. Furthermore, lateral canals are apparently not developed in the Australian form, while those of the Japanese form

Table 2 Key to species of *Pernerocrinus*

species	size	arm alternation	lateral canal	interarticular canal	movable arm	root
P. paradoxus	large	slightly	no	no	present	many
P. discus	small	partly	present	no	no	many
P. sibiricus	medium	mostly	no	no	unknown	unknown
P. hayasakai	medium	mostly	present	no	unknown	unknown
P. perforatus	medium	mostly	present	present	unknown	many
P. sp., Bates	large	partly	no	no	unknown	many
P. sp., Minoura	large	mostly	unknown	no	unknown	many?

are unknown. Although these similarities are suggestive that these two specimens are specifically identical, no confirmation is presently possible. Since both materials are fragmental and detailed comparison is impossible. More material is needed to solve the above problem.

Environmental and geologic implication

Reefal habitat of *Pernerocrinus* is well established both on the Bohemian and the Australian species. Extremely wide stem with complex root system and compactness of the brachial disc of the genus are interpreted for this genus to be highly adapted to reef environment (Bouška, 1949, p.21). Some Australian specimens which are fragmental and embedded in matrix further provide evidences of rolling and abrasion by turbulent current in the reef (Bates, 1872, p.329). In this manner, both the Bohemian and the Japanese specimens also are apparently fragmental and embedded in matrix. Actually, all the Japanese specimens are fragmental and found in hand specimens in which numerous fragmental crinoids and corals are scattered, though very few of them are identifiable. It is quite reasonable to consider, therefore, that the Japanese species also are reef dweller and rolled and abraded before incorporated in sediments.

Although no reefal or biohermal structure has been precisely investigated in the Ohno Formation, of which pyroclastic sediments prevailed, lenticular and patched limestones commonly develop in this formation and have been believed as representing small reefs or reef debris. In this way, although not abundant, common occurrence of *Pernerocrinus* from various localities of the Ohno Formation is quite a definite evidence of reef environment.

Although *P. paradoxus* and *P. discus* are reported to be from Lower to Middle Devonian by Bates (1972, p.326), the horizon of the former species is described as "Lower Devonian, Barrande's étage —F-f2—" (Bouška, 1950, p.11) which is correlatable to Siegenian. For *P. discus* is described, "the material comes from the lower Devonian Lilydale Limestone, probably upper Siegenian or lower Emsian in age" (Bates, 1972, p.326). Also, the horizon of *P. sibiricus* is "Coblenzian" (Yakovlev, 1949, p.19). Accordingly it is evident that the genus *Pernerocrinus* is restricted to the Lower Devonian. This geologic range of the genus is very well in accordance with the Ohno Formation from which the Japanese specimens are found.

Conformably overlying the Silurian Kawauchi Formation, the Ohno Formation is

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Explanation of Plate 1

scale-bars are 10 mm, a: axial canal, ad: adoral groove, c: central canal, 1: lateral canal.

Figs. 1-3 *Pernerocrinus hayasakai* (Minato and Minoura)

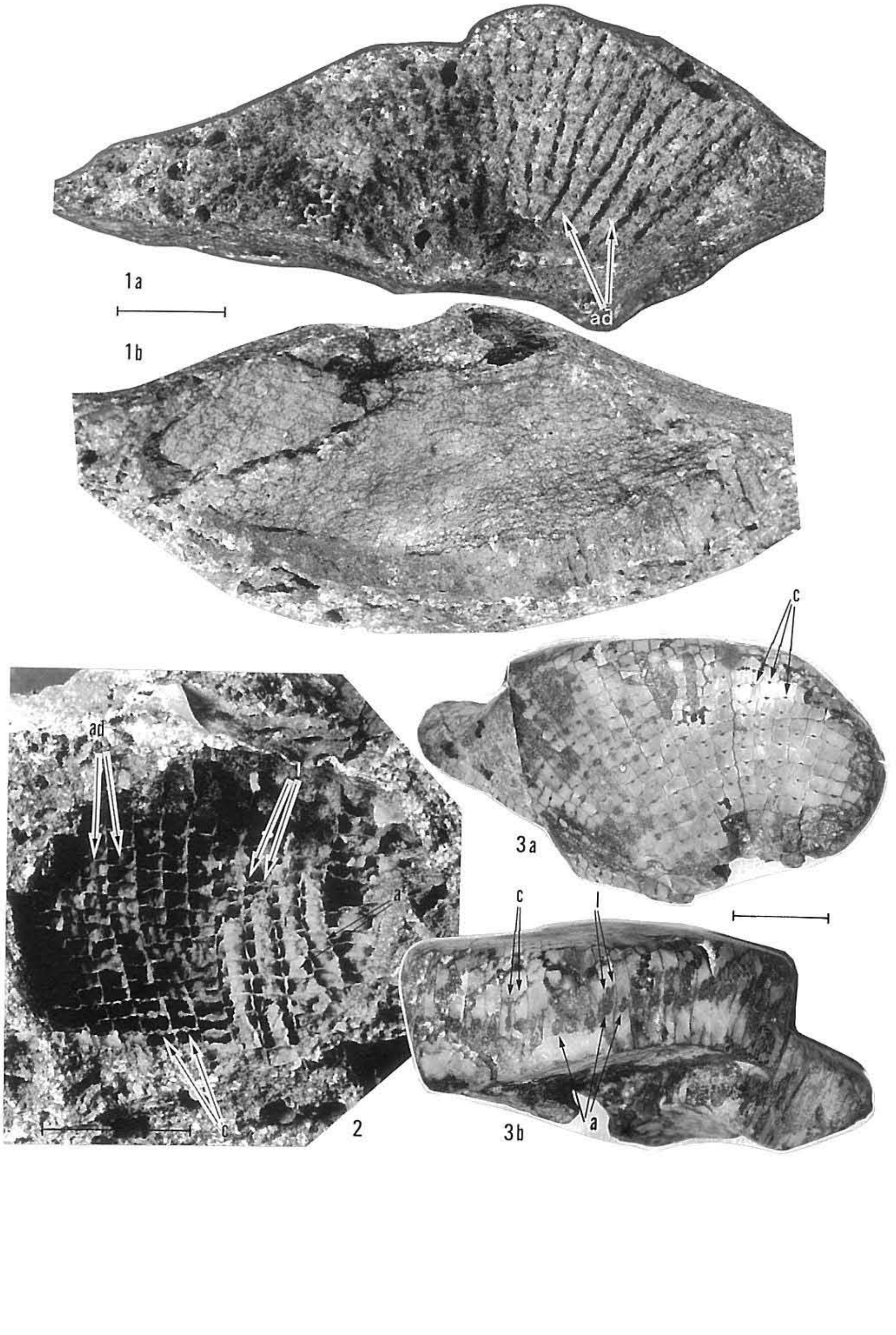
Fig. 1a: Outer mold of partial disc showing ventral surface. Paratype UHR 30189.

Fig. 1b: Same as above specimen showing dorsal surface.

Fig. 2: Silicified internal mold of partial disc viewed from dorsal side. Holotype UHR 30190-3.

Fig. 3a: Partial brachial disc viewed from ventral side. Central canals are not always distinct. UHR 30669.

Fig. 3b: Same as above specimen viewed from the distal side.


1a
ad
1b
c
ad
l
a
3a
c
l
a
c
2
3b

mainly composed of tuffs, and is subdivided into three members, Oh1, Oh2, and Oh3, in ascending order (Haga, 1978 M.S.: in Minato et al.,1979). Although occurrence of megafossils is rather scarce, and none has been described, the following corals are known from the lower two members, Oh1 and Oh2, of the Ohno Formation:
Acanthophyllum? sp., *Xystriphyllum interlineatum* (Quenstedt), cf. *Pseudamplexus obesus* (Počta), *Pseudochonophyllum*? sp., *Australophyllum cyathophylloides* (Etheridge), *Spongophyllum halysitoides* (Etheridge), *Stringophyllum*? sp., *Thamnopora* sp., *Favosites* cf. *pseudosocialis* Dubatolov, and *Squameofavosites* sp. This fauna is closely related to "Coblenzian" corals of Europe and Australia and, as a whole, denotes the Lower Devonian. Although the uppermost Oh3 member is barren of megafossils the entire Ohno Formation is interpreted to be deposits ranging from Gedinnian to Emsian, since in addition to the above Lower Devonian fauna, Oh3 member is conformably overlain by Nakazato Formation which yields "Eifelian" to Givetian fauna (Kato and Minato, 1979; Kato et al 1980).

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Explanation of Plate 2

scale-bars are 10 mm, a: axial canal, c: central canal, i: interarticular canal, l: lateral canal.

Figs 1-3 *Pernerocrinus perforatus* sp. nov. Holotype UHR 30671

Fig. 1a; Partial disc viewed from ventral side. Central and interarticular canals are distinct, while lateral canals are not visible.

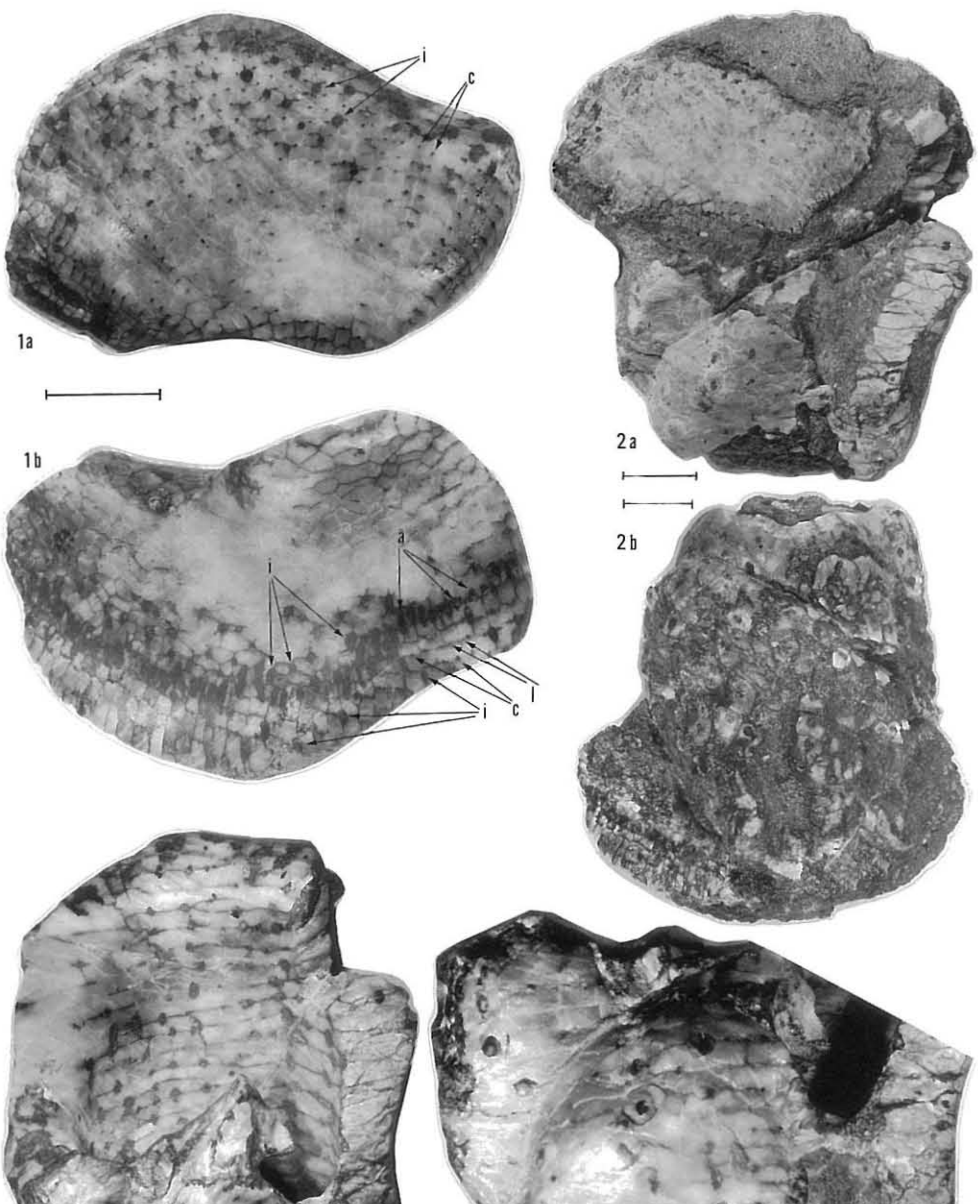
Fig. 1b; Same as above specimen viewed from dorsal side. Axial and interarticular canals are tangentially cut, while lateral canals are only sporadically visible.

Fig. 2a; Partial disc and column showing specimen before cut into two pieces.

Fig. 2b: Opposite side of 2a showing numerous facets for roots.

Fig. 3a: Partial column obliquely viewed showing internal surface of the lumen and weathered external surface. Oval black dots are axial canals of roots.

Fig. 3b: Distal edge of the internal surface of the lumen showing much lower columnals than the proximal ones.


i
c
1a
1b
a
i
l
c
i
2a
2b
3a
3b

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Explanation of Plate 3

scale-bars are 10 mm, r: root, s: slit-like structure.

Fig. 1: *Pernerocrinus hayasakai* (Minato and Minoura) UHR 30668.

Fig. 1a: Internal surface of outer mold of partial column which apparently is heteromorphic.

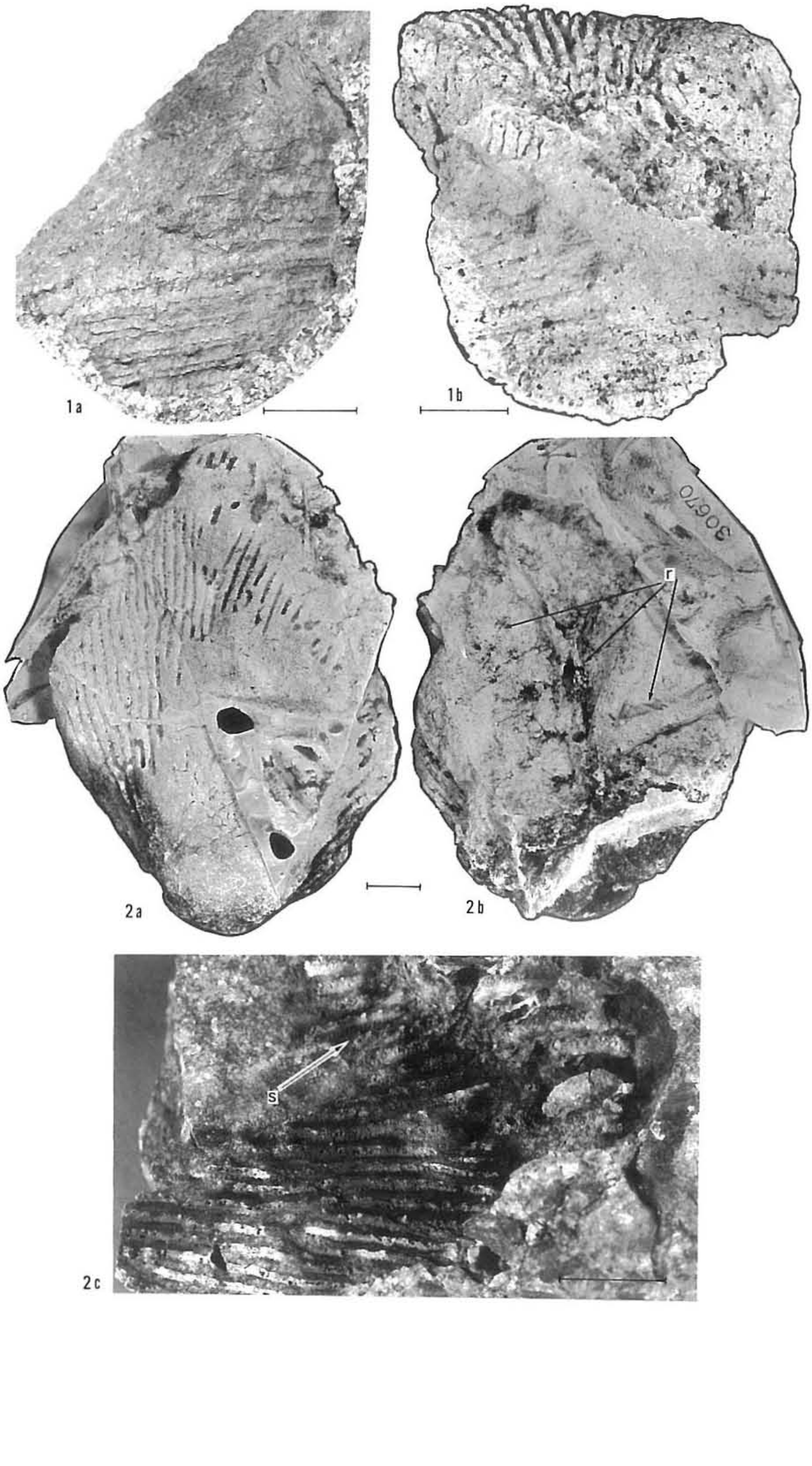
Fig. 1b: Artificial cast of the above mold showing nearly same portion and proximal disc.

Fig. 2: *Pernerocrinus* sp. UHR 30670.

Fig. 2a: Artificial cast after outer mold of partial disc showing ventral side.

Fig. 2b: As above showing dorsal side. Fragmental roots are faintly visible.

Fig. 2c: Oblique view of the outer mold showing mold of adoral grooves and slit-like structure.


1a
1b
30670
r
2a
2b
s
2c