

## RAMIPORA HOCHSTETTERI TOULA, 1875 (BRYOZOA, CYSTOPORATA), FROM THE PERMIAN OF SVALBARD

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**ABSTRACT**—This review of the goniocladiid genus *Ramipora* Toula is based on zoarial morphology. The diagnosis of *Ramipora* is emended and the type species *R. hochstetteri* Toula from the Upper Permian of Svalbard is redescribed. Anastomosing secondary branches forming a fenestrated meshwork discriminate *Ramipora* from other gonioclaidiids. Descriptions are based on new material collected from the type horizon (Kapp Starostin Formation, Akseloya) and elsewhere in the Svalbard Archipelago, and also on Toula's type specimen. *Goniocladia* Nekhoroshev and *Aetomacladia* Bretnall are herein designated junior synonyms of *Ramipora*. Some species previously assigned to *Ramipora* are transferred to *Ramiporidra*.

### INTRODUCTION

TOULA (1875) described a new cystoporate bryozoan species, *Ramipora hochstetteri*, from the Upper Permian of Akseloya ("Axel-Eiland"), Bellsund, along the western coast of Spitsbergen, Svalbard (Figure 1). Toula's material was collected by Richard von Drasche in 1873, during one of the Austrian polar expeditions (cf. Toula 1875, p. 225). Since the first description, *R. hochstetteri* has subsequently been reported from Svalbard by Etheridge (1878), Nikiforova (1936), Malecki (1968, 1977), Morozova and Kruchinina (1986), Nakrem (1988), Sakagami (1992), and Nakrem (1994). Recent field work in Svalbard has made available new and generally well-preserved material upon which the current study is based. Rock matrix surrounding bryozoans and other fossils in the Kapp Starostin Formation usually consists of silicified limestones, spiculitic shales, and cherts, with less common limestone intervals.

The bryozoans in these beds are commonly partly or completely silicified, and minute internal details are obscured. For external study, some spiculitic shales containing bryozoans with well-preserved calcareous skeletons were treated with hydrochloric acid, and latex replicas of the voids of the dissolved bryozoans yielded detailed external features suitable for high-magnification photography. Internal characters were studied using petrographic thin sections and acetate peels. Measurements of zoarial and autozooeal characters include some of those presented for fenestrates by Hageman (1991) and Snyder (1991).

Examined material was collected from Akseloya (77°44'N, 14°40'E), Bjørnøya (74°25'N, 19°E), Festningen (78°N, 13°30'E), and Mariaholmen (77°40'N, 14°30'E). Additional material from Austjøkeltinden (76°50'N, 16°40'E), collected by Terje Hellem in 1977, was made available from the collections of the Paleontological Museum, Oslo. Illustrated specimens are in the collections of the Paleontological Museum, Oslo (abbreviated PMO), and Naturhistorisches Museum, Wien (the holotype of *Ramipora hochstetteri*, museum no. 1875/XLI/40).

### SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831  
Class STENOLAEMATA Borg, 1926  
Order CYSTOPORATA Astrova, 1964  
Suborder FISTULIPORINA Astrova, 1964  
Family HEXAGONELLIDAE Crockford, 1947  
Genus RAMIPORA Toula, 1875

*Ramipora* TOULA, 1875, p. 230; ETHERIDGE, 1878, p. 625;  
SHUL'GA-NESTERENKO, 1933, p. 54; NIKIFOROVA, 1936, p. 137;

CROCKFORD, 1944, p. 192; MOROZOVA, 1960, p. 87; UTGAARD, 1983, p. 436.

*Aetomacladia* BRETNALL, 1926, p. 21; UTGAARD, 1983, p. 434.

*Goniocladia* NEKHOROSHEV, 1953, p. 166; UTGAARD, 1983, p. 434.

*Type species.*—*Ramipora hochstetteri* Toula, 1875 (by monotypy).

*Species included.*—*Ramipora ambrosioides* (Bretnall, 1926), *R. kashstanica* (Nekhoroshev, 1953), *R. parallela* (Nekhoroshev, 1956), and *R. hochstetteri* Toula, 1875. Unnamed species mentioned by Sakagami and Sugimura (1979), Madsen and Håkansson (1989), and Sakagami (1990) also belong in this genus.

*Emended diagnosis.*—Zoarium reticulate with bifoliate branches. Primary branches straight and weakly curved. Vertical mesotheca forming weak keel on rounded noncelluliferous reverse side and more pronounced keel on celluliferous obverse side. Primary branches with opposing outgrowths of secondary and tertiary branches diverge distolaterally, commonly in pairs. Secondary and tertiary branches carrying autozooea merge to form frond with large polygonal fenestrules. Two or more rows of autozooea, separated by obverse keel on each side of mesotheca. Autozooeal apertures open on obverse side of colony, subcircular with weakly developed lunaria, separated by stereom. Autozooeal tubes curved and partially isolated at mesotheca, long and straight in exozone. Diaphragms not observed. Blisterlike vesicles in endozone, less common in exozone. Massive laminated stereom with stylets piercing through most of exozone.

*Remarks.*—*Ramipora* is distinguished from similar goniocladiid genera by the fenestrated zoarium built by anastomosing secondary branches (Figure 2). In *Ramiporella* Shul'ga-Nesterenko, 1933, lateral branches are offset, arising alternately from either side of the primary branch. *Ramiporalia* Shul'ga-Nesterenko, 1933, is characterized by a bifurcating growth pattern. *Ramiporidra* Nikiforova, 1938, has secondary branches arising in opposite pairs from the primary branch, but not forming anastomoses or a reticulate meshwork. *Ramiporidra* was first mentioned and separated from *Ramipora* by Nikiforova (1936, p. 137) in order to discriminate species originally described as *Ramipora* by Shul'ga-Nesterenko (1933). *Ramiporina* Shul'ga-Nesterenko, 1933, is regarded as a junior synonym of the hexagonelliid *Volgia* Stuckenberg, 1905, with autozooea opening on both obverse and reverse side of zoarium (Utgaard, 1983). *Ramipora* is distinguished from *Goniocladia* Etheridge, 1876, in having dendroid fenestrated zoarium, whereas *Goniocladia* has a reticulate meshwork without differentiated primary and

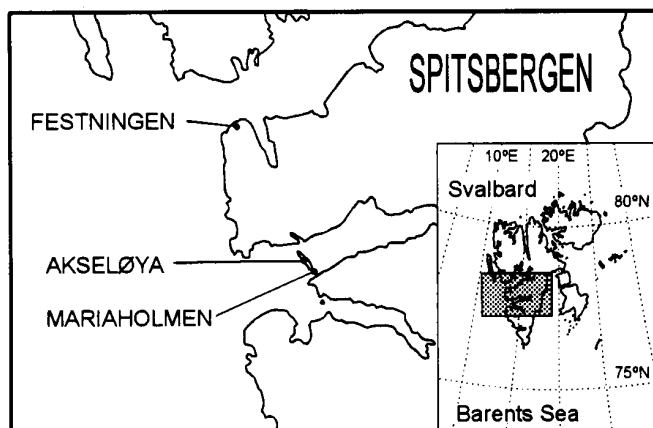


FIGURE 1—Map of Spitsbergen and Akseloya collecting localities, and their location (shaded) in inset map of Svalbard in the Barents Sea.

secondary branches. *Ramipora ambigua* Sakagami, 1961, from the Lower Permian of Japan, was described and illustrated as being without anastomosing secondary branches or fenestrules, and is herein transferred to *Ramiporidra* based on the branching geometry. *Ramipora* sp. from the *Pseudostaffella antiqua* Zone (Carboniferous, Early Bashkirian) of Japan was mentioned by Sakagami and Sugimura (1979) and Sakagami (1990), but no description or illustration indicates anastomosing secondary branches or the presence of fenestrules to identify placement in the genus *Ramipora*.

After examining the external features and the growth patterns in the holotype of *Goniocladia* Nekhoroshev, 1953, we regard this genus as a junior synonym of *Ramipora*. Subsequently, the illustrated *Goniocladia* sp. in Madsen and Håkansson (1989) is regarded as *Ramipora* sp. in the present study. It should be noted that Morozova (1960) incorrectly quoted *Goniocladia parallela* Nekhoroshev, 1956, as type species for *Goniocladia*, and also that internal characters in *Goniocladia* have not been described. *Aetomacladia ambrosioides* Bretnall, 1926 (Lower Permian of Eastern Australia and Western Australia), was subsequently transferred to *Ramipora* by Crockford (1944) and Wass (1968) but retained as a valid genus by Utgaard (1983). This genus was originally described as having a dendroid, non-fenestrated zoarium; however, new material from Western Australia (Engel and Ross, 1993, Pl. 13 fig. 20) has revealed fenestrate zoaria resembling those of *Ramipora*. We propose that *Aetomacladia* be regarded as a junior synonym of *Ramipora*. *Acanthocladia acuticostata* Bassler, 1929, from the Permian of Timor was "considered to be possibly identical to *Aetomacladia ambrosioides*" by Wass (1968, p. 22), and was subsequently transferred to *Ramipora*. *Ramipora* (*Ramiporella*) *flexuosa* Crockford, 1947, may belong to *Ramipora*, not *Ramiporella*, because of anastomosis in secondary branches possibly forming reticulate meshwork (Crockford, 1947, text-fig. 21).

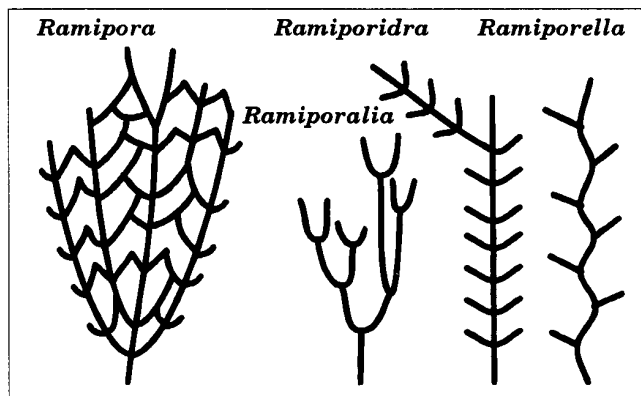


FIGURE 2—Colony geometry in *Ramipora*, *Ramiporalia*, *Ramiporidra*, and *Ramiporella*.

Internal characters of the genera *Goniocladia* and *Aetomacladia* have received little study, and they cannot be identified in random or transverse sections of colony fragments.

Records of *Ramipora* in the Ordovician of Wales, and in the Devonian of southern England, are considered to represent *Pinatopora*, see below.

**Stratigraphical range.**—*Ramipora* has been recorded from the Lower Carboniferous of Kazakhstan and Altai (Nekhoroshev, 1953); Lower Permian of Eastern and Western Australia (e.g. Crockford, 1944, and Wass, 1968); Lower Permian of the Pamirs (Reed, 1925); ?Upper Permian of Tibet (Metz, 1946), Timor (Bassler, 1929), Greenland (Madsen and Håkansson, 1989), Svalbard and Novaya Zemlya (Morozova and Kruchinina, 1986). Unverified records have been published from the Middle Carboniferous (Bashkirian) of Japan (Sakagami and Sugimura, 1979, and Sakagami, 1990), and ?Carboniferous of eastern Australia (Crockford, 1947).

#### RAMIPORA HOCHSTETTERI Toulou, 1875

Figures 3, 4

*Ramipora hochstetteri*, TOULOU, 1875, p. 230, Pl. X, figs. 1a, b [note that the original figures are mirror images of the actual specimen]; ETHERIDGE, 1878, p. 627; NIKIFOROVA, 1936, p. 127, 138, Pl. 2, figs. 7–10, text-figs. 1, 2; METZ, 1946, p. 184, Pl. 21, figs. 1–7; UTGAARD, 1983, p. 436, fig. 215/3a–c; NAKREM, 1988, p. 113; SAKAGAMI, 1992, Pl. 1, fig. 1.

?*Ramipora* cf. *hochstetteri* Toulou. NAKREM, 1988, p. 114; NAKREM, 1994, pl. 2, figs. F, H.

*Ramipora* cf. *hochstetteri* Toulou. REED, 1925, p. 107, Pl. 10, fig. 9, 9a.

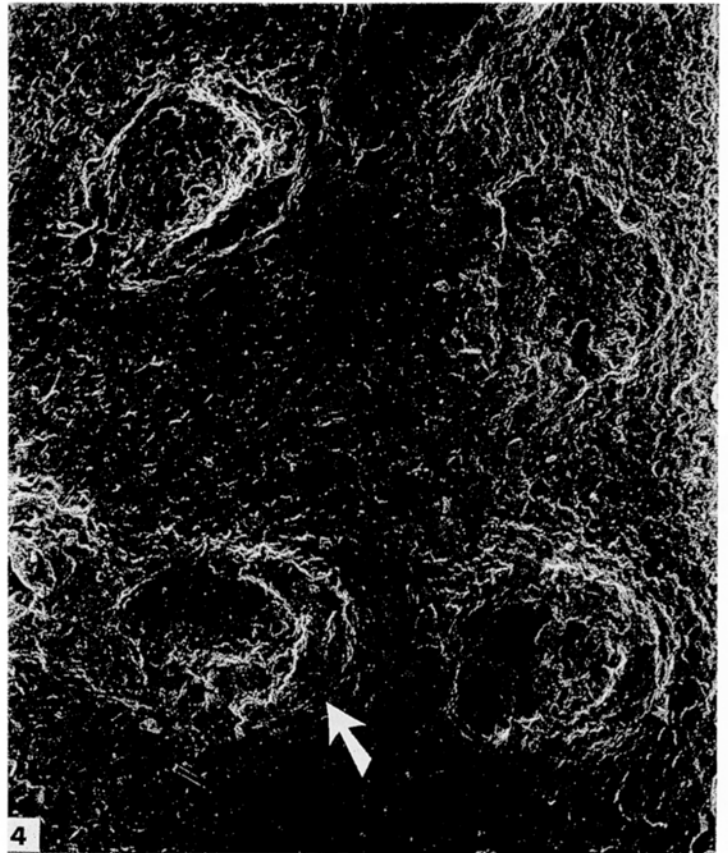
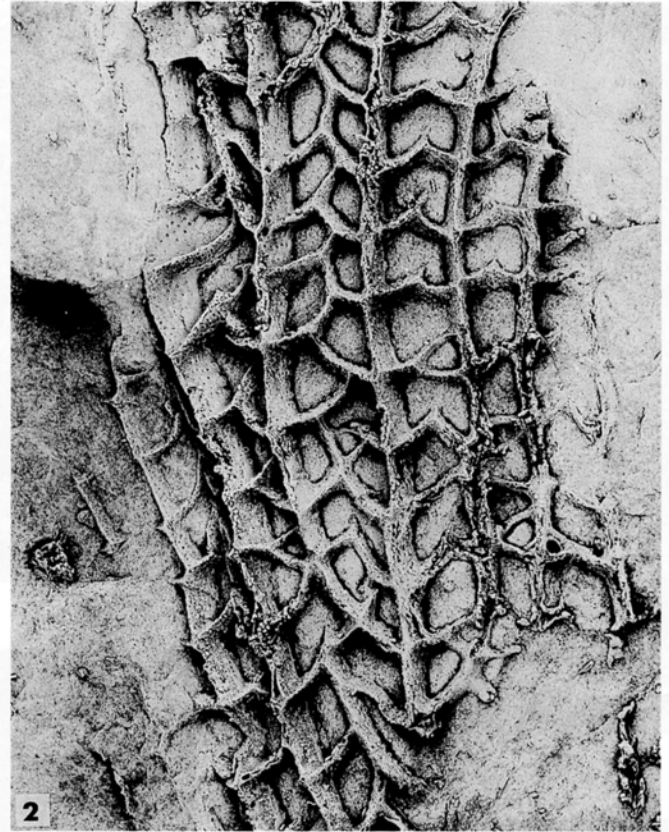
*Ramipora lepida* MOROZOVA in Morozova and Kruchinina, 1986, p. 41, Pl. 8, fig. 1a–c.

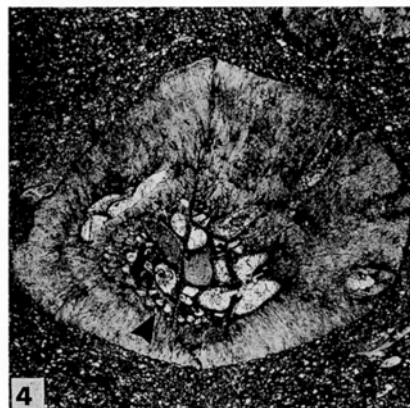
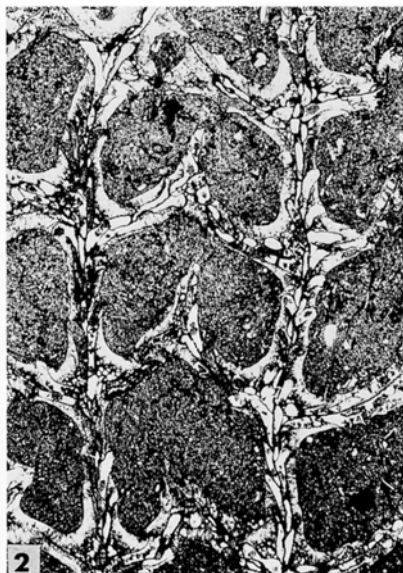
*Ramipora fragilis* MOROZOVA in Morozova and Kruchinina, 1986, p. 42, Pl. 8, figs. 2a, b, 3.

?*Polypora* sp. cf. *russiensis* Shul'ga-Nesterenko. MAŁECKI, 1968, p. 22, Pl. 7, figs. 3, 4, 7–9.

*Septopora phyllata* MAŁECKI, 1977, p. 85, Pl. 7, fig. 2, text-fig. 2.

FIGURE 3—*Ramipora hochstetteri* Toulou, external features. 1, Toulou's holotype, Akseloya, unknown high stratigraphical position in the Kapp Starostin Formation,  $\times 3$ , Naturhistorisches Museum, Wien 1875/XLI/40; 2, zoarium showing branching geometry, Mariaholmen, 208.0 m above the base of the Kapp Starostin Formation,  $\times 2$ , latex cast, PMO 138.107; 3, detail of zoarium showing branches with up to six rows of apertures (left branch), Mariaholmen, 208.0 m above the base of the Kapp Starostin Formation,  $\times 6$ , latex cast, PMO 138.107; 4, autozoecial apertures with lunarium (arrow), branch orientation as in Figure 2.3, Mariaholmen, 208.0 m above the base of the Kapp Starostin Formation,  $\times 100$ , latex cast, PMO 138.107, SE micrograph.







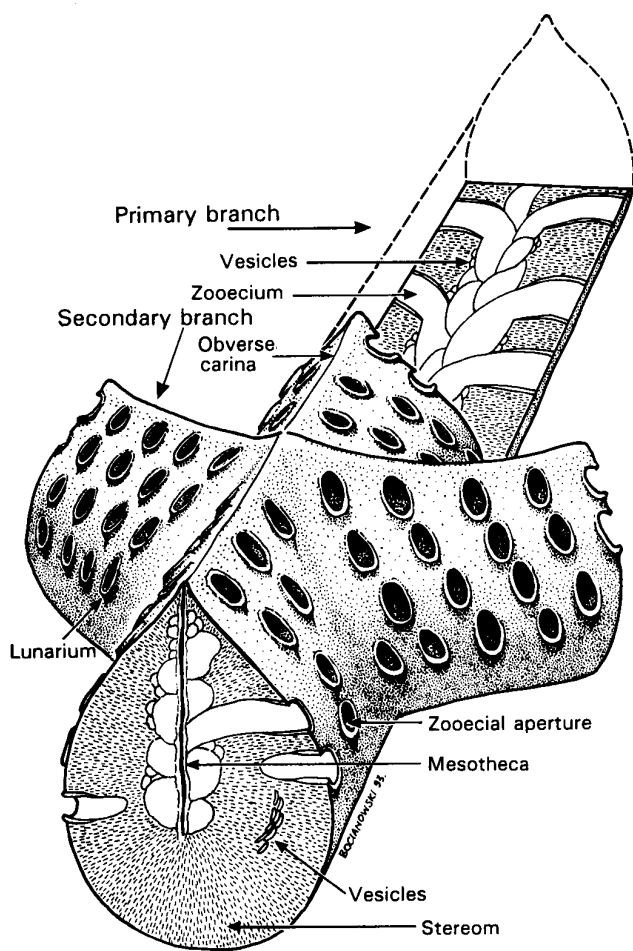


FIGURE 5—Idealized three-dimensional drawing of *Ramipora hochstetteri* Toula showing relationship between external and internal structures. Branch width about 1.5 mm.

**Emended diagnosis.**—*Ramipora* with robust primary branches near colony origin connected by secondary branches forming zoarium with polygonal fenestrules of varying dimensions. Branches are oval to tear-drop shaped in cross section, rounded on reverse side and carrying a keel on obverse side. Distal portions of colonies with branches commonly thinner and narrower than proximal parts. Secondary branches originate at relatively regular intervals, branching off at about 51° from primary branch. Secondary branches from adjacent (neighboring) primary branches anastomose, forming irregular polygonal fenestrules,

### Branch dimensions

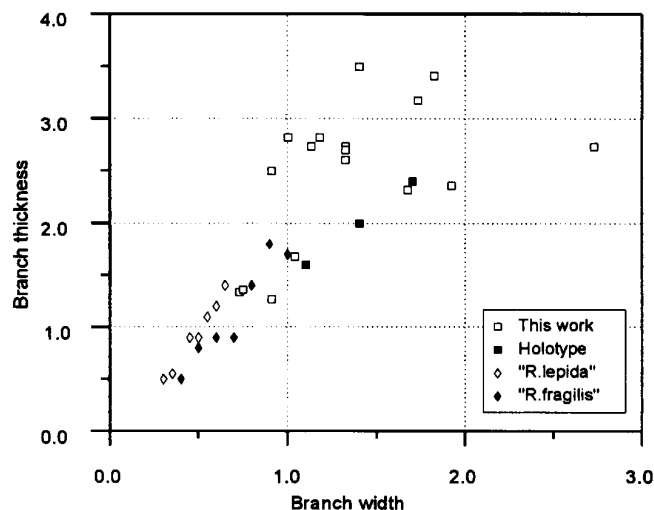


FIGURE 6—Branch thickness and width in *Ramipora hochstetteri* Toula.

and sometimes give rise to tertiary branches. All branches carry autozoecia, up to five or six rows on primary branches; lower number on secondary branches. Regularly spaced autozoecial apertures carry indistinct lunaria, as well as an elevated rim above colony surface. Autozoecial tubes originate from near median mesotheca; slightly curved proximally, elongated and straight distally, abruptly bent when meeting colony surface at almost right angles. Space between autozoecial tubes filled with blisterlike vesicular tissue in endozone; laminated massive stereom separates tubes in exozone.

**Description.**—Zoarium characterized by large polygonal fenestrules and relatively robust bilaterally compressed branches. Primary branches widest and thickest near zoarium origin with decreasing dimensions distolaterally. Maximum branch width 2.73 mm, average width 1.35 mm, range in holotype 1.1–1.7 mm. Maximum branch thickness (obverse–reverse direction) 3.50 mm, average 2.47 mm, range in holotype 1.6–2.5 mm. Secondary branches commonly reach same dimensions as primary branches although they generally are slightly narrower. Secondary branches branch off in pairs at about 51° and join to form polygonal meshwork. Fenestrules vary significantly in size; 2.00–4.55 mm long and 2.50–4.64 mm wide (about three branches across colony per 10 mm, and 2.5–3.0 fenestrules along colony per 10 mm). Branches usually carry four rows of apertures on each side of keel, thickest primary branches carry up to six rows. Secondary and tertiary branches usually have fewer rows of apertures. Apertures circular to slightly oval, commonly

FIGURE 4—*Ramipora hochstetteri* Toula, internal features. All petrographic thin sections. 1, shallow to medium deep tangential section, Festningen, 184.0 m above the base of the Kapp Starostin Formation,  $\times 6$ , PMO A42214; 2, deep tangential section, Festningen, 184.0 m above the base of the Kapp Starostin Formation,  $\times 6$ , PMO A42214; 3, deep tangential section showing typical branching pattern, Festningen, 282.0 m above the base of the Kapp Starostin Formation,  $\times 14$ , PMO A42057; 4, transverse section of thick primary branch, arrow points at large vesicles in endozone, Festningen, 362.0 m above the base of the Kapp Starostin Formation,  $\times 14$ , PMO 138.103/1; 5, tangential section showing apertures (A) with peristome (P) and median mesotheca (M), Festningen, 184.0 m above the base of the Kapp Starostin Formation,  $\times 35$ , PMO A42214; 6, deep tangential section showing chimney-like peristomes around apertures (arrows), Festningen, 184.0 m above the base of the Kapp Starostin Formation,  $\times 35$ , PMO A42214; 7, transverse section of branch near point of branching, Festningen, 362.0 m above the base of the Kapp Starostin Formation,  $\times 14$ , PMO 138.103/1; 8, transverse section of several branches, Festningen, 163.0 m above the base of the Kapp Starostin Formation,  $\times 14$ , PMO A41790.

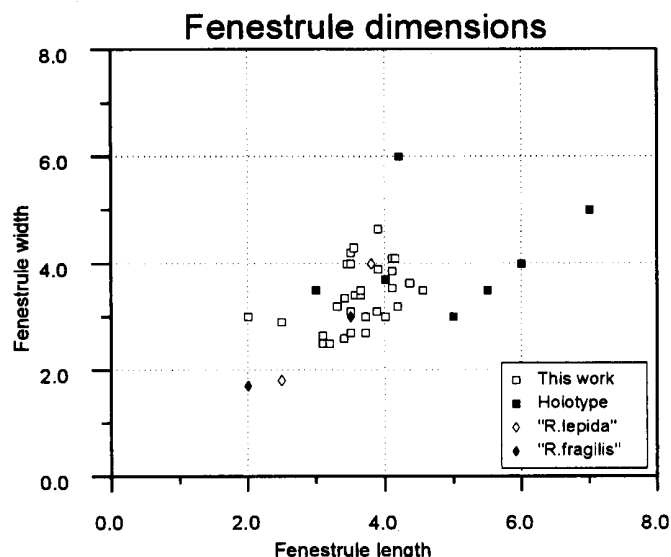


FIGURE 7—Fenestrule dimensions in *Ramipora hochstetteri* Toula.

0.19 mm long and 0.17 mm across, with indistinct lunarium. Apertures have elevated ridges causing chimney-like appearance. Distance between aperture centers averages 0.45 mm (equals 10–11 per 5 mm).

Autozoecia originate close to mesotheca, being slightly curved in their proximal part, more or less elongated in middle part and sharply bent to meet colony surface at almost right angles. Clear calcitic peristome, 0.018–0.020 mm wide, developed in autozoecial walls near colony surface. Diaphragms not observed in autozoecial tubes. Individual tubes separated by vesicular tissue in endozone. Blister-like vesicles vary significantly in size, 0.09–0.13 mm in diameter and 0.06–0.08 mm in height. Vesicles less common in exozone, which is characterized by laminated stereom pierced by stylets. Exozonal vesicles low, and commonly accumulated at certain levels. Mesotheca composed of three layers with granular microstructure, about 0.036–0.055 mm thick in central parts of branches. Zoarial and autozoecial characters are sketched in Figure 5.

**Discussion.**—Morozova and Kruchinina (1986, p. 40) correctly reassigned *Septopora phyllata* from Bjørnøya to *Ramipora*, but retained the species name. Study of Malecki's specimens, however, revealed sufficient similarities in external features and dimensions for inclusion in *R. hochstetteri*. New collections made at Bjørnøya have provided additional support for the above conclusion. The identification of *R. hochstetteri* by Nikiforova (1936) from Spitsbergen was discussed by Morozova and Kruchinina (1986), who concluded that Nikiforova's specimens are not conspecific with Toula's holotype. They included her species in their new species *R. lepidi*, based on additional material derived from the Kapp Starostin Formation (=Starostinskaya Svita in Russian usage) of Spitsbergen. The reassignment was based on the absence of a main (primary) branch, the width of the branches, and the size of the fenestrules. Because Nikiforova's figure 1 clearly exhibits the presence of a primary branch (left-most branch in her illustration) and the dimensions of branches and fenestrules fall within the variation of new material of *R. hochstetteri* investigated, *R. lepidi* is a synonym. In the original description, *R. fragilis* was distinguished from *R. lepidi* by the wider branches as well as the circular shape of autozoecial apertures. The latter character of size and shape

TABLE 1—Measured characters in *Ramipora hochstetteri* Toula. Abbreviations: BW, branch width; BT, branch thickness; AL, aperture length; AW, aperture width; AAD, distance between aperture centers; FL, fenestrule length; FW, fenestrule width; BA, branching angle between primary and secondary branches; n, number of measurements; N, number of specimens measured; MIN, minimum value; MAX, maximum value; AVG, average value; STD, standard deviation; CVi, range in intracolony coefficient of variation; CVr, intercolony coefficient of variation between all measured specimens. All measurements in millimeters.

	N	n	MIN	MAX	AVG	STD	CVi	CVr
BW	4	17	0.73	2.73	1.35	0.51	12.39–42.04	37.75
BT	4	17	1.27	3.50	2.47	0.69	3.57–23.80	27.82
AL	4	43	0.15	0.22	0.19	0.02	2.81–7.36	11.91
AW	4	43	0.14	0.19	0.17	0.02	3.10–7.12	9.15
AAD	2	28	0.36	0.53	0.45	0.04	4.80–10.45	8.17
FL	3	30	2.00	4.55	3.62	0.52	9.45–17.74	14.25
FW	3	30	2.50	4.64	3.39	0.59	11.19–16.80	17.39
BA	3	52	34	73	51	7.1	9.79–21.05	13.86

variation lies within the range of variation of *R. hochstetteri*. Figures 6 and 7 show a plot of branch and fenestrule dimensions in *R. hochstetteri*, *R. lepidi*, and *R. fragilis*. They show that *R. lepidi* and *R. fragilis* lie within the range of variation of *R. hochstetteri*, and hence these two species are regarded as junior synonyms of *R. hochstetteri*. Few measurements were recorded for *R. cf. R. hochstetteri*, from the Lower Permian of the Pamirs (Reed, 1925), but branch dimensions account for inclusion in *R. hochstetteri*. *Ramipora ambrosioides*, from the Lower Permian of Western Australia (Crockford, 1944), is separated from *R. hochstetteri* in possessing thinner primary branches (1.1–1.5 mm wide and 1.5 mm thick) and more widely separated apertures (distance between successive centers averages 0.56 mm), as well as having secondary branches diverging from primary branch at higher angles (50–90°).

*Ramipora hochstetteri* var. *carinata* Etheridge, described by Etheridge (1879) from Ordovician rocks of north-east Wales, was recently a subject of discussion by Spjeldnæs (1984, p. 18). Here it was proposed as the type species for *Pinnatopora* (order Fenestrata), as it was published prior to *Pinnatopora sedwicki* by Shrubsole and Vine (1884). *Ramipora* sp., from the Devonian of south England (Whidborne, 1895), also most probably belongs to *Pinnatopora*, judging from published illustrations.

**Measurements.**—See Table 1.

**Occurrence.**—*Ramipora hochstetteri* has been collected from many Upper Permian outcrops in Svalbard (including Bjørnøya) during the present study. The age of these beds, which belong to the Kapp Starostin Formation (Spitsbergen) and Miseryfjellet Formation (Bjørnøya), is latest Early Permian (Kungurian) through Late Permian (Ufimian–Kazanian) (Cutbill and Challenor, 1965; Nakrem et al., 1992). In Novaya Zemlya (Arctic Russia), this species is present in the Upper Permian (Ufimian–Kazanian) Gerke and Savina Groups (Morozova and Kruchinina 1986). The only non-Arctic occurrence of *R. hochstetteri* is in northern Tibet (Metz, 1946). The age of the latter record is ?Late Permian.

**Material.**—Holotype: Naturhistorisches Museum, Wien, number 1875/XLI/40; type locality: Akseloya (77°44'N, 14°40'E), Svalbard; type horizon: Upper part of the Kapp Starostin Formation of the Tempelfjorden Group. Permian, ?Ufimian–Kazanian. On the same slab, with the same museum number, is also the holotype of *Polypora grandis* Toula, 1875 (p. 238, Pl. 9, fig. 7a, b).

Measurements were taken from the following specimens (all from the Kapp Starostin Formation of Svalbard; meters indicate position above the base of the formation): Austjökeltinden, 5.4

m (PMO 138.129); Austjøkelinden, top of formation (PMO 138.128); Festningen, 161.0 m (PMO A41987); Festningen, 163.0 m (PMO A41789); Festningen, 164.0 m (PMO A41792); Festningen, 180.0 m (PMO A42082); Festningen, 184.0 m (PMO A42214); Festningen, 362.0 m (PMO A42235, 138.102/1-2, 138.103/1-3); Mariaholmen, 172.0 m (PMO 118.227); Mariaholmen, 208.0 m (PMO 138.107).

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