# Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 4: The genus *Paracalyptrophora* Kinoshita, 1908

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Abstract.—Previously undocumented from the western Atlantic, three new species of *Paracalyptrophora* are described from this region. In order to facilitate comparisons, all six species in the genus are diagnosed, illustrated, included in a dichotomous key, and compared in a table of distinguishing characteristics. *P. kerberti* is herein designated the type species of *Paracalyptrophora*. Additional specimens are reported of all six species. *Paracalyptrophora* is now know to occur in the central and South Pacific and both sides of the North Atlantic at depths of 150–1480 m.

Kinoshita (1908:58), in his report on Primnoidae from Japanese waters, recognized the sharp distinction between species of Calyptrophora having the large sclerites of the body of the polyp inseparably fused to form solid rings, as in the type species C. japonica Gray, and those in which the large sclerites encircling the body of the polyp remain separable and unfused. For the latter he established the subgenus Paracalyptrophora including Calyptrophora kerberti Versluys, C. mariae Versluys, and C. josephinae (Lindström). This subgenus was not recognized by subsequent authors until it was elevated to generic status in keys but without further description (Bayer 1981:937; Bayer & Stefani 1989:455).

Dredging and trawling in the western Atlantic by several research vessels, including the USFC steamer *Albatross* and R/V *Gerda*, obtained many specimens referable to three species of *Paracalyptrophora*, which are described herein.

#### Material and Methods

Most of the specimens reported in this paper were collected by the R/V *Gerda*, a vessel operated by the University of Miami, the specimens later deposited at the USNM.

Other specimens were collected by the: *Albatross, Oregon, Silver Bay, Chalcal II* (MNHN), and *Atlantis* (MCZ).

Designation of polyp scales follows the terminology used by Versluys (1906) as amplified by Bayer et al. (1983). Synonymies are purported to be complete. The SEM photomicrographs were taken by the authors on a variety of instruments in the SEM Lab at the NMNH.

The following abbreviations are used: Alb—USFWS Albatross; G—R/V Gerda; H:W-height to maximum width of an opercular scale; IL-inner-lateral opercular scale; JSL-I-Johnson Sea-Link-I; MCZ-Museum of Comparative Zoology, Harvard, Cambridge; MNHN-Muséum national d'Histoire naturelle, Paris; MOM-Musée Océanographique, Monaco; NMNH-National Museum of Natural History, Smithsonian, Washington, D.C.; O-R/V Oregon; SB-R/V Silver Bay; OL-outerlateral opercular scale; SEM—Scanning Electron Microscope stub number (unprefaced number in Bayer series, Cairns series prefaced with a C); USNM-United States National Museum (now the NMNH); ZMA—Zöologisch Museum, Amsterdam; ZMB—Zoologisches Museum, Berlin.

Subclass Octocorallia
Order Alcyonacea
Suborder Calcaxonia
Family Primnoidae Gray, 1858
Genus Paracalyptrophora Kinoshita, 1908

Calyptrophora.—Versluys, 1906:104 (part).—Kükenthal, 1919:468 (part); 1924:317 (part).—Aurivillius, 1931:301 (part).—Deichmann, 1936:171 (part).—Bayer, 1956: F221 (part).—Tixier-Durivault, 1987:171 (part).

Calyptrophora (Paracalyptrophora) Kinoshita, 1908:58.

Paracalyptrophora Bayer, 1981:937, 946.—Bayer & Stefani, 1989:455 (in key only).—Bayer, 2001:367.

Type species.—Calyptrophora kerberti Versluys, 1906, here designated.

Diagnosis.—Primnoidae with verticillate polyps directed downward, enclosed in two pairs of large abaxial scales (i.e., basal and buccal) extending around body to form rings, a pair of smaller infrabasals, and in one species a variable number of small adaxial buccals. The two pairs of large body wall scales are never inseparably fused, sometimes not even meeting at adaxial side of body. When present, sclerites of tentacles are few and small, but usually absent entirely. Branching dichotomous, in one or two fans.

Description.—Colonies are dichotomously branched in one plane or in two parallel fan-shaped planes, with polyps always arranged in whorls and directed downward. The polyps are armed with two pairs of large abaxial scales that nearly or completely encircle the body. They may be so firmly wedged together by the complex sculpture along the abaxial midline that a few pairs may remain joined through cleaning and preparation, but they are not inseparably fused abaxially or adaxially to form solid rings; in many cases the members of the buccal pair do not even meet adaxially. One pair of curved infrabasal scales lies between the large basal scales and the sclerites of the coenenchyme. Eight roughly triangular scales/plates fold over the retracted tentacles to form an operculum covering the retracted tentacles and closing the buccal aperture. In one species, small adaxial buccal scales may be developed below the adaxial opercular scales. The tentacles are either without sclerites, or have extremely small scales in such small numbers as to be easily overlooked. The axis is stiff, brittle, heavily calcified, weakly grooved longitudinally, brownish or blackish and sometimes with metallic luster; the holdfast is calcareous, irregularly discoidal, attached to solid substrate.

Distribution.—Southwestern Pacific (Timor Sea, Norfolk Ridge), Japan, Hawaii, and the North Atlantic; 150–1480 m.

Remarks.—So far as known, the correlation of downward facing polyps and two pairs of large, unfused body scales is unique for this genus. Although the members of basal and buccal abaxial body scale pairs are separate and unfused, they sometimes are so tightly interlocked by the complex tubercular sculpture of the margins that meet along the abaxial suture that they remain attached even after maceration in sodium hypochlorite solution. The adaxial processes of the basal pair may meet but are not permanently united, and the abaxial symphysis usually separates during manipulation for mounting.

The following key begins with a determination of the gross colony form; however, if only branch fragments are available, this can be problematic. In that case, the tabular key (Table 1) can be used to distinguish all six species. In fact, the shape, size, and ornamentation of the buccal scales alone are probably adequate to distinguish the six species.

Key to the Six Species of Paracalyptrophora (Atlantic species in bold face)

- 1'. Colonies in the shape of two rounded,

- Distal margin of buccal scales only slightly flared, revealing most of the opercular scales in abaxial view; dorsolateral edge of buccal scales ridged . . . . . . . . . . . P. josephinae (Lindström, 1877)

- 4. Dorso-lateral margin of basal scales not ridged; dorso-lateral margin of buccal scales with one low ridge; tentacular sclerites present . . . . . *P. carinata*, n. sp.
- 4'. Dorso-lateral margin of basal scales having 3 or 4 prominent ridges; dorso-lateral margin of buccal scales with 4 or 5 prominent ridges; tentacular scales absent ...... P. mariae (Versluys, 1906)

### Paracalyptrophora duplex, new species Figs. 1A-D, 2A-D, 3, 4 A-K

Primnoa regularis Duchassaing & Michelotti, 1860:17, pl. 1, figs. 12–13 (see Remarks herein).

Material examined/Types.—Straits of Florida off Cape Canaveral: 28°08′N, 80°04′W, 49 m (depth suspect), O-5191, 14 Jan 1965, one small colony lacking holdfast and most of main stem, USNM 52755, paratype.

Northwest of Little Bahama Bank: 27°37.65′N, 78°58.74′W, 404 m, JSL-I-

3572, 10 Aug 1993, one large colony lacking holdfast, USNM 93960, paratype.

North of Little Bahama Bank: 27°29.5′N, 78°37.5′W, 485–496 m, *G*-252, 5 Feb 1964, one dry specimen with commensal galatheid crab, USNM 52747 (SEM 1744), paratype.

West of Little Bahama Bank: 27°21′N, 79°15″W, 439–503 m, *SB*-440, 29 Dec 1958, 3 damaged colonies, and detached branches, USNM 51264 (SEM C1045), paratypes.

Off Southwest Point, Grand Bahama: 26°35′N, 78°25′W, 329–421 m, *G*-692, 21 Jul 1965, one branch, USNM 52748; one nearly complete small colony lacking holdfast, USNM 52749; one colony, USNM 52752; 3+ broken branches, USNM 52753, paratypes.

Off Southwest Point, Grand Bahama: 26°29′N, 78°39′W, 247–374 m, *G*-697, 22 Jul 1965, one nearly complete small colony with part of holdfast, USNM 52745, paratype.

Off Southwest Point, Grand Bahama: 26°28′N, 78°37′W, 555–575 m, *G*-695, 22 Jul 1965, one branch, USNM 52756, paratype.

Off Southwest Point, Grand Bahama: 26°27′N, 78°43′W, 522–489 m, *G*-706, 22 Jul 1965, one young colony lacking hold-fast, USNM 52746 (SEM 1752); 3 more or less complete colonies and detached branches, USNM 52754 (SEM 263, 1755, 1756), paratypes.

Off Southwest Point, Grand Bahama: 26°27′N, 78°43′W, 384–403 m, *G*-533, 4 Mar 1965, one colony, USNM 52751 (SEM C1046–47), holotype; 2 damaged colonies, one denuded incomplete axis, and detached branches, USNM 52750 (SEM 1753, 1754, C1042); one young colony, USNM 100773, paratypes.

Off Havana: 23°10′39″N, 82°20′21″W, 389 m, *Alb*-2350, 20 Jan 1885, one intact colony and many damaged branches, USNM 17314, paratype.

South of Great Inagua Island: 20°43′N, 73°29′W, 448 m, *O*-5416 24 May 1965, one

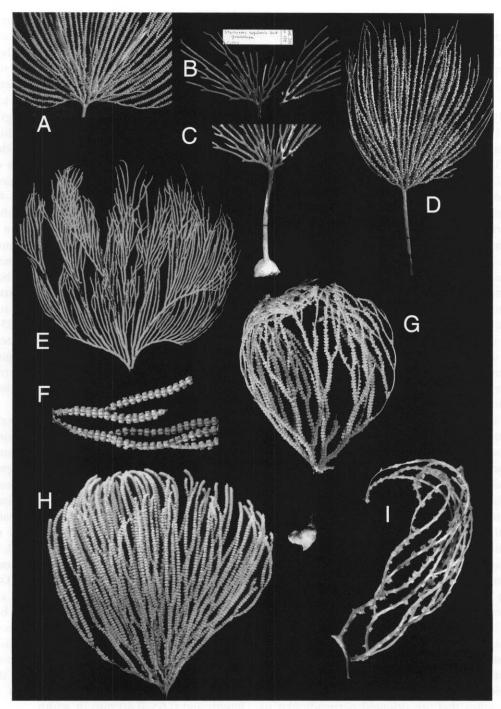


Fig. 1. A–D, *Paracalyptrophora duplex* (A, paratype from G-252, USNM 52747; B, C, holotype of *Primnoa regularis*, Turin Coel. 275; D, holotype, USNM 52751): A, base of double fan showing enclosed galatheid crab, × 0.36; B, upper part of colony with broken branch in place, × 0.25; C, lower part of colony showing calcified holdfast, × 0.25; D, complete holotype, × 0.31. E, *P. simplex*, holotype USNM 52767, × 0.15. F, *P. josephinae*, *Atlantis* 23-152, USNM 100788, branch fragment, × 1.0. G, *P. carinata*, holotype, USNM 49948, complete colony and holdfast, × 0.33. H, *P. mariae*, Chalcal II, CP25 (MNHNP), colony, × 0.25. I, *P. kerberti*, *Alb*-5093, USNM 30105, × 1.0.

colony without holdfast (dry), USNM 1008871, paratype.

Holotype of *Primnoa regularis*, Guadeloupe, Museo Regionale di Scienze Naturali, Turin, Coel. 275 (ex. 175), 1 complete dry colony and several broken branches, all polyps lost (SEM C1043–44).

Type locality.—26°27′N, 78°43′W (off Southwest Point, Grand Bahama), 384–403 m.

Description.—Colonies consist of a robust, vertical main stem and a pair of parallel, dichotomously branching fans. The stem is anchored in a dense, white, calcareous, semi-hemispherical holdfast, the largest known 32 mm in diameter. Most damaged specimens are broken above the holdfast; only four of the specimens reported herein are complete in this regard. The main stem is inflexible, 7-10 cm in height, up to 8 mm in diameter, and usually round in cross section, although in large specimens the stem is slightly compressed in a direction perpendicular to the fan. In large colonies, the main stem constitutes about 35% of the height of the colony. The underlying stem axis is golden or blackbrown, faintly longitudinally striate, and, when dried, often splits longitudinally to reveal a lighter colored central core. The first bifurcation of the main stem, which results in two branches, is in the plane of the eventual fans; the second series of bifurcations, which results in four branches, is perpendicular to the fans; and the third and all remaining bifurcations are in the plane of the fans. The length of the internode between the first and second bifurcations is quite short (e.g., 1.5 mm) and in most colonies, except for small ones, this internode is subsumed into the second internode, such that it would appear as though the first division of the main stem is into four robust branches that are oriented perpendicular to the fans. All higher order branching is dichotomous and equal such that both branches are of the same diameter, neither one seeming to dominate (and thus not lyriform). In some cases, one half of a dichotomy remains simple or divides at a much wider interval than usual so that adjacent branches do not interfere with one another, but in general, most of the branching occurs within 5 cm of the top of the main stem, resulting in many elongate, unbranched terminal branches up to 11-13 cm in length. Rarely are there more than 7 nodes leading to a terminal branch, the most highly divided branches being those on the margin of the colony fans. A large colony might have 23-30 terminal branches per fan, or 46-60 terminal branches in the colony. The distance between adjacent branches of a fan is usually only 2-4 mm, whereas the distance between the two parallel fans is 12–15 mm. A fully developed fan is usually wider than tall, large fans measuring 21-25 cm across and 15-16 cm tall, thus occupying the top <sup>2</sup>/<sub>3</sub> of the colony height. The holotype is 23.5 cm tall and 14 cm wide, with a main stem length (broken) of 7.6 cm, but the largest known specimen (holotype of *P. regularis*) is 27 cm tall, 25 cm wide, with a complete main stem length of 10 cm.

Polyps are arranged in regular whorls and directed downward. Usually the whorls are composed of three polyps, but whorls of 4 or 5 may occur on the proximal part of the branches; in some colonies, whorls of 4 or even 5 predominate; 14-20 whorls occupy 3 cm of axial length, but the variation in any one colony is not usually so great. In general, polyps are well spaced, in that polyps within a whorl do not touch one another and there is a distance of 0.40-0.45 mm between adjacent whorls. Polyps are present on the stalk in small colonies, but in large specimens they are absent from both stalk and the lower part of major branches; polyps are also often missing from the side of the branches that face the opposite fan. Polyps are 1.0-1.2 mm in length and 0.65-0.80 mm in width.

Each polyp is protected by two pairs of large abaxial body scales and a smaller pair of infrabasals. The infrabasal scales are the smallest of the body wall sclerites, only about 0.20 mm in maximum height, cres-

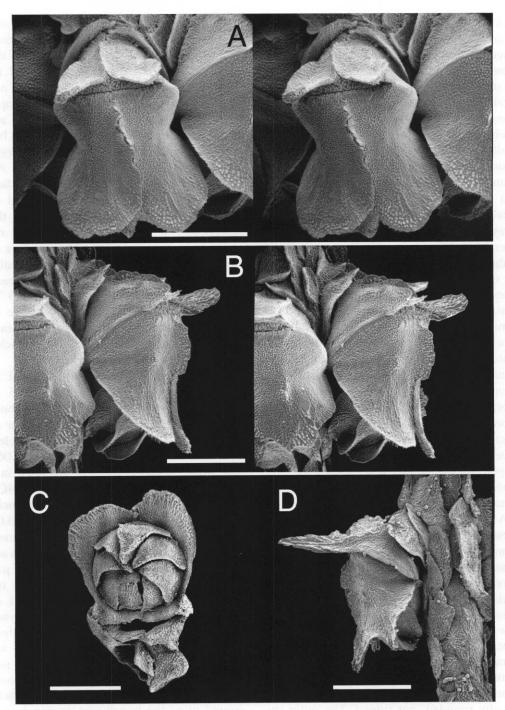


Fig. 2. Paracalyptrophora duplex (A, B, D, paratype from G-706, USNM 52754; C, holotype, USNM 52751): A, abaxial stereo view of polyp; B, lateral stereo view of polyps; C, opercular view of a polyp; D, lateral view of a polyp with jagged-edged buccal scales. Scale bars 0.5 mm.

cent-shaped, and anchor the polyp to the branch coenenchyme. The basal scales are much larger, up to 1.1 mm, and project perpendicular to the branch. Each basal bears a serrate, projecting spine at its dorso-lateral margin, the spine variable in shape ranging from short and broad to tall and slender, the latter constituting slightly over half the height of the scale. These spines usually bear one finely serrate ridge on their outer side, which is continuous with a ridge on the dorso-lateral margin of the basal scale and which extends only about half way to the base of the basal scale. Tall, slender basal spines also have three more ridges separated by 90°, whereas broad basal spines have 8-10 small parallel ridges on their inner face. The upper, inner face of the basals has a small ridge that hinges with the straight proximal margin of the adjacent buccal scale. The buccal scales are slightly shorter (0.9-1.0 mm) but much broader than the basals, and have a free, flared distal margin (0.15-0.25 mm) that encloses the opercular scales and obstructs a view of the operculars from the adaxial side. The projecting buccal margin, which is translucent due to a thinning of the scale as well as a replacement of the inner tubercles with short spines, may be evenly rounded, produced as a broad lobe on each side (Figs. 2A-C), or divided into 2 or 3 more or less acute, flat lobes, the latter condition more common in young colonies (Fig. 2D). This character varies to a considerable extent even in a single specimen. Whereas the abaxial margins of the basal scales meet as a sharp, raised crest along the abaxial suture, the buccal scales overlap one another at the abaxial midline, often in one direction along half the length, and in the opposite direction along the other half (Fig. 2A). The dorso-lateral margins of the buccals are evenly rounded, not ridged. The outer surfaces of the body scales and operculars are uniformly covered with small (8-10 µm diameter), rounded to sharp granules, and their inner surfaces by crowded, complexly ornamented tubercles also 8-10 µm in di-

ameter. The opercular scales are triangular in shape, decreasing in size from the abaxials (length = 0.48 mm, H:W 1.55) to the adaxials (length = 0.29 mm, H:W = 1.1). As is typical for many primnoids, the adand abaxials are symmetrical in shape, whereas the outer- and inner-laterals are asymmetrical, each class of operculars being more developed on their abaxial margin and thus having an off-centered keel. All operculars bear a prominent keel on their distal, inner surface as well as a field of crowded tubercles that concentrate on the central and basal regions. The lateral regions under the opercular scales are bare or covered with short spines and opercular margins are usually finely dentate, each equilateral triangular tooth being about 3 °m in height (Fig. 4E). The upper surface of the operculars is covered with smooth granules like the body wall scales. The tentacles appear to be devoid of sclerites.

Coenenchymal scales are polygonal to elongate in shape, ranging from 0.15 to 0.80 mm in length, but on average about 0.4 mm. Those on the main stem occur as two layers, a lower layer of flattened sclerites, and an upper layer of thicker (0.06-0.10 mm), rotund scales that are fitted in a closely abutted, mosaic pattern (Fig. 4G-H). The coenenchymal scales of the branches occur in one layer and are flattened (0.02 mm thick), with slightly overlapping margins. Both types of coenenchymal scales are covered exteriorly with small (10-12 µm diameter) granules, most of which are independent but occasionally are linked in short rows that appear to radiate outward from near the center of the scale, but ridges are never present. Their inner surfaces are covered with complex tubercles 8-12 µm in diameter. Coenenchymal scales also cover the basal holdfast. The black axial background gives the translucent coenenchymal scales a milky white color.

Etymology.—Latin duplex = double or twofold, an allusion to the double fan-shape of the colonies.

Comparisons.—Paracalyptrophora du-

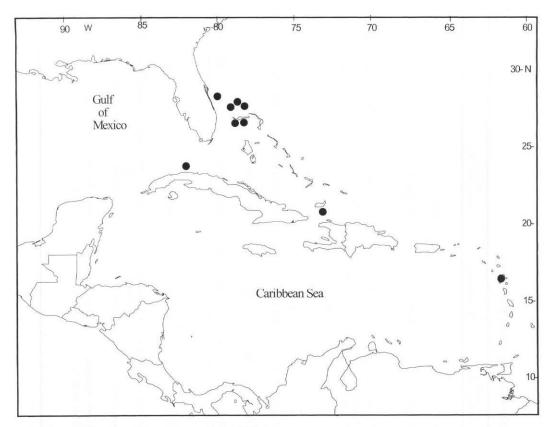


Fig. 3. Distribution of Paracalyptrophora duplex.

plex is compared to *P. simplex* in the account of that species and to other congenerics in Table 1.

Distribution.—Straits of Florida from off Cape Canaveral to Havana; Bahamas (Grand Bahama Island and south of Inagua); Lesser Antilles (Guadeloupe) (Fig. 3); 374–555 m.

Remarks.—The convex space between the two parallel fans appears to provide an ideal niche for galatheid crabs, one of which in each colony may place its abdomen in the region of dense branching at the top of the main stem, and orient its claws along the branching orientation of the fans (Fig. 1A). Coral and crab appear to be the same color.

Examination of the dry, somewhat damaged holotype (deposited at the Turin Museum) of *Primnoa regularis* Duchassaing & Michelotti, 1860 (Figs. 1B–C), which was

designated as the type species of the genus Narella by Gray (1870), shows it to be conspecific with P. duplex. Even though this specimen no longer retains any polyps or polyp sclerites, the branching of the colony and the coenenchymal sclerites are perfectly consistent with this species, and thus logically would have nomenclatural priority. However, following strict nomenclatural priority would cause widespread confusion within primnoid taxonomy. For instance, because P. regularis was chosen as the type of Narella, the three species heretofore placed in Paracalyptrophora would now be placed in the genus Narella, and the 25 species heretofore placed in Narella would have to be transferred to the next available generic name, i.e., Calypterinus Studer, 1887. Furthermore, the morphological relationship implied by the names Calyptrophora and Paracalyptrophora would be

Table 1.—Distinguishing characteristics of the six species of Paracalyptrophora (Atlantic species in bold face).

Paracalyptrophora	P. duplex, n. sp.	P. simplex, n. sp.	P. josephinae (Lindström, 1877)	P. carinata, n. sp.	P. mariae (Versluys, 1906)	Versluys, 1906)
Number of Fans	2	1	-	2	2	2
Maximum Colony Height	27	41	55	23	27.5	24
(cm)						
Maximum Main Stem	10 (37%)	11 (22%)	20 (36%)	5 (22%)	5.5 (18%)	9 (37%)
Height (cm); % of total						
Height						
Branching	Dichotomous (not	Dichotomous (ly-	Dichotomous (not	Dichotomous (not	Dichotomous (not	Dichotomous (not
	lyrate)	rate)	lyrate)	lyrate)	lyrate)	lyrate)
Polyp Length/Width (mm)	1.0-1.2/0.65-0.80	1.3-1.5/0.80-0.95	1.3-1.5/0.75-0.90	1.50-1.75/0.80-0.92	1.4-1.8/0.90	2.0-3.0/1.20-1.25
Separation of Adjacent	0.4-0.45	0.10-0.25	0.4-0.6	0.60-0.65	0.5-1.0	0.5-2.0
whorls (mm)						
Polyps/Whorl	3–5	4-6-8	4-6-7	4-6-8	4-5-7	4-5-8
Whorls/3 cm	14-18-20	14-17-20	13-14-17	12-14-16	11–15	8-10-13
Dorso-lateral Edge of Bas-	Short ridge	Short ridge	Prominent ridge	Not ridged	3-4 prominent	Smooth
al Scale					ridges	
Dorso-lateral Edge of	Evenly rounded	Rounded, but with	Multiple low ridges	Low ridge	4-5 prominent	Smooth
Buccal Scale		aligned granules	,	)	ridges	
Distal Edges of Buccal	Flared; usually lo-	Flared; lobate or di-	Slightly flared;	Not flared: straight:	Slightly flared:	Slightly flared; even
Scales	bate, sometimes	vided	evenly rounded	serrate	curved outward	to spinose
	divided		•			
Abaxial Buccal Scales	0	0	0	0	0	0-5
Max. Length of Abaxial	0.48 mm	0.56 mm	0.57 mm	0.85 mm	0.83 mm	1.10 mm
Opercular Scales						
Branch Coenenchyme Scales	Granular, not ridged	Granular, not ridged	Granular, not ridged	Granular and prominent ridges	Granular and prominent ridges	Granular, not ridged
Max. Length of Tentacular Sclerites	None noted	None noted	None noted	82 µm	None noted	92 µm
Distribution	Straits of Florida,	Insular side of	Eastern Atlantic;	Lesser Antilles;	South Pacific; 418-	Japan; 150–731 m
	Bahamas, Lesser Antilles; 374– 555 m	Straits of Florida; 165–706 m	214–1480 m	514 m	520 m	

lost. To avoid this widespread changing of generic combinations and the confusion that it would cause, we will suggest to the ICZN that the type of *Primnoa regularis* be suppressed and a neotype be designated (ICZN, 1999: article 75.6, conservation of prevailing usage by a neotype), a specimen that is consistent with the current understanding of the genus *Narella* and with the species *N. regularis* as described by Cairns & Bayer (2003).

## *Paracalyptrophora simplex,* new species Figs. 1E, 4L–T, 5A–C, 9

Material examined/Types.—North of Little Bahama Bank: 27°34.5′N, 78°49′W, 488–516 m, *G*-254, 6 Feb 1964, broken branches probably of a single colony, USNM 52769, paratype.

North of Little Bahama Bank: 27°29.5′N, 78°37.5′W, 485–496 m, *G*-252, 5 Feb 1964: one large dry colony (holotype), USNM 52767 (SEM 1757, 1758, C1049–51); 5 branches, USNM 52757; one colony, USNM 52763; one large dry colony, USNM 52764; one large dry colony, USNM 52765; one large dry colony, USNM 52766; four dry branches, USNM 52768, paratypes.

Off Settlement Point, Grand Bahama: 26°45′N, 79°05′W, 494–530 m, *G*-1125, 13 Jun 1969, 6 branches and fragments, USNM 52762 (SEM 265, 267, 1731), paratypes.

Straits of Florida: 26°38′N, 79°02′W, 516 m, *G*-1312, 31 Mar 1971, detached branches, USNM 57556, paratypes.

Off Southwest Point, Grand Bahama: 26°31′N, 78°51′W, 366 m, *G*-503, 4 Feb 1965, 3 dry colonies, USNM 52770 (SEM 1760, 1761, 1771), paratypes.

North of North Bimini, Bahamas: 25°59′N, 79°19′W, 439–458 m, *G*-633, 30 Jun 1965, 5 broken branches, USNM 52759 (SEM 1721, 1722, 1747), paratypes.

North of North Bimini, Bahamas: 25°56′N, 79°22′W, 402 m, *G*-798, 12 Sep

1966, 2 incomplete colonies, USNM 52760 (SEM C1048), paratypes.

Off Havana, Cuba: 23°09′10″N, 82°23′W, 706 m, *Alb*-2152, 30 Apr 1884, 2 branches, USNM 7166, paratypes.

Yucatan Channel: 20°59′N, 86°23′00″W, 305 m, bottom temp. 17.1°C, *Alb*-2353, 22 Jan 1885, 2 dichotomous branches in poor condition, USNM 50087, paratypes.

Arrowsmith Bank, Yucatan: 20°57′N, 86°34′W, 165–140 m, *G*-899, 10 Sep 1967, one colony, USNM 52761, paratype.

Type locality.—27°29.5′N, 78°37.5′W (north of Little Bahama Bank), 485–496 m.

Description.—Colonies consist of a robust, vertical main stem, which gives rise to a fan that is uniplanar and consists of dichotomously branching elements. The stem is anchored in a white calcareous holdfast, although only one specimen was collected with the base intact. The main stem is inflexible, up to 11 cm in height and 9.6 mm in basal diameter, in large specimens compressed in the branching plane. In large colonies, the main stem constitutes about 22% of the height of the colony. The stem axis is golden or dark brown with a slightly lighter colored core, and faintly longitudinally striate. All branching is dichotomous and equal, except for the two outermost branches of the fan of larger colonies, which are often twice the diameter of the inward branching stems as well as being straight, which confers a lyrate shape to the colony. Although long end branches up to 12 cm length occur, in general, branching occurs throughout the fan at intervals of about every 1.5 cm, sometimes resulting in terminal branching that have resulted from 15 previous bifurcations. The distance between adjacent branches is about 4-5 mm. The fan is roughly the same height as width. The largest colony (the holotype) is 41 cm tall, with a fan 38 cm in height and 34 cm in width, and a broken main stem only 3 cm long.

Polyps are arranged in regular whorls consisting of 4–8 polyps (usually 6); 14–20 whorls occur in 3 cm of axial length,

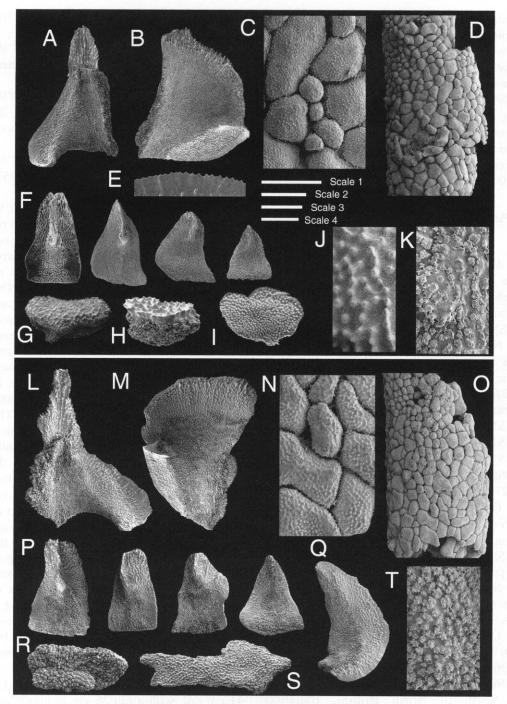


Fig. 4. A–K, *Paracalyptrophora duplex* (A, B, E, F, holotype; C, D, paratype, *SB*-1440; G, J, K, paratype, *G*-533; H, I, holotype of *Primnoa regularis*, Turin Museum): A, basal scale; B, buccal scale; C, D, main stem coenenchymal scales in situ; E, distal margin of opercular scale; F, ad-, OL-, IL- and adaxial operculars; G, H, side views of coenenchymal scales from stalk; I, top of coenenchymal scale from branch; J, K, upper granular and lower warty sides of coenenchymal scales. L–T, *Paracalyptrophora simplex* (L, M, P–T, holotype; N, O, paratype from G-798): L, basal scale; M, buccal scale; N, O, main stem coenenchymal scales in situ; P, ad-, OL, IL, and adaxial operculars; Q, infrabasal scale; R, S, lower and upper views of coenenchymal scales;

and although this range may be present within a single colony, 17 seems to be the predominant number. In general, polyps are closely spaced, i.e., adjacent polyps in a whorl are usually directly adjacent or even overlapping, and the distance between adjacent whorls is quite small (0.10–0.25 mm), such that the tip of the buccal scales of the polyps of one whorl almost touch the buccal spines of the polyp of an adjacent whorl. Polyps occur on the main stem of small colonies. Polyps are 1.3–1.5 mm in length and 0.8–0.95 mm in width.

Each polyp is protected by two pairs of large abaxial body scales and a pair of narrow, curved infrabasal scales situated between the coenenchymal sclerites and the basal pair. The body wall scales are virtually identical in shape and ornamentation to those described for P. duplex, differing primarily in size, those of P. simplex being slightly larger, i.e., the infrabasals are up to 0.33 mm in height, the basals up to 1.15 mm, and the buccals up to 1.05 mm, the latter with a flared distal margin 0.25 mm in extent, which, like that of P. duplex, may be produced as a single broad lobe (Figs. 4M, 5C) or divided into 2-4 acute teeth. Furthermore, the dorso-lateral margins of the basals bear only short ridges (Fig. 5B), whereas the dorso-lateral margins of the buccals often bear parallel, aligned rows of surface granules (Fig. 5A). The opercular scales are also similar in shape but slightly larger, the abaxial operculars up to 0.56 mm in length and the adaxials 0.34 mm in length, but all operculars having slightly serrate margins and a H:W ratio of 1.4-1.6, similar to that of P. duplex. The coenenchymal sclerites are also quite similar in size and shape to those of P. duplex; however, the surface granules are somewhat larger, up to 18 µm in diameter.

Etymology.—Latin simplex = simple,

single, or onefold, an allusion to the colonies in the shape of a single fan.

Comparisons.—The shape of the polyps of P. simplex is virtually identical with those of C. duplex, differing primarily in having slightly larger (20-25%) sclerites and thus larger polyps. But, even though the polyps are larger, both species have the same range of polyps per cm, this because the distance between polyp whorls of P. simplex is shorter. In general, the polyps of P. simplex are more crowded, having more polyps per whorl as well as having more closely spaced whorls, these characters serving to distinguish isolated branches. Characters at the grosser (colonial) level that distinguish P. simplex from P. duplex are that it produces only one fan, it attains a larger colony size, branching occurs throughout the fan with as many as 15 nodes, and large colonies tend to have a lyrate branching pattern (Table 1).

Distribution.—Known only from the insular side of the Straits of Florida from the Yucatan Channel to north of Little Bahama Bank, Bahamas (Fig. 9); 165–706 m.

Paracalyptrophora josephinae (Lindström, 1877) Figs. 1F, 6A–C, 7A–G

Calyptrophora josephinae Lindström, 1877:6, pl. 1, figs. 1–3 (Josephine Bank).—Versluys, 1906:109 (re-examination of type and Studer's specimen).— Kükenthal, 1919:474 (diagnosis); 1924: 319 (diagnosis and key).—Thomson, 1927:29 (Alice Bank).—Aurivillius, 1931:301, fig. 60, pl. 6, fig. 5 (re-description of type, key to species in genus).—Deichmann, 1936:172 (remarks).—Grasshoff & Zibrowius, 1983:119, pl. 1, figs. 5, 6 (Josephine Bank).—Carpine & Grasshoff, 1985:33 (MOM deposition).—

T, lower view of coenenchymal scale. Scale bar 1: R=0.20 mm; 2: F, G, I, P, Q, S=0.25 mm, H=0.083 mm; 3: E, J, K, T=0.05 mm; 4: A-C, L-N=0.25 mm.

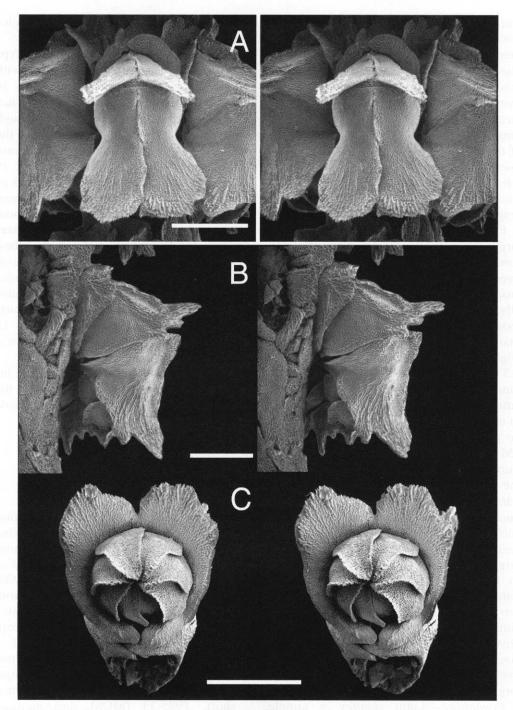


Fig. 5. Paracalyptrophora simplex (A, C, holotype; B, paratype from G-633, USNM 52759): A, abaxial stereo view of a whorl; B, lateral stereo view of a polyp; C, opercular stereo view of a polyp. Scale bars 0.5 mm.

Grasshoff, 1985a:305 (*Talisman* specimens from Biskaya); 1985b:73 (Josephine and Great Meteor Banks); 1986:27 (remarks).

Stachyodes Josephinae.—Studer, 1901:41 (Azores).

Calyptrophora (Paracalyptrophora) josephine.—Kinoshita, 1908:58 (taxonomic reassignment).

Paracalyptrophora josephinae.—Bayer, 1981:938, text-fig. 77 (new comb.).—Grasshoff, 1989:219 (listed).—Bayer, 2001:367 (mentioned).

Material examined.—Atlantis Seamount: 34°05′N, 30°15′W, 293 m, R/V Atlantis cruise 152, station 23, 26 Aug 1948, 2 dichotomous branches (MCZ, in alcohol; fragment USNM 100788) (SEM 1719).

Fragment of holotype (SEM C1052–54). *Types*.—The holotype is deposited at the Swedish Museum of Natural History (1113). Type Locality: Josephine Bank (36°46′N, 14°07′W), 201–214 m, station 36n.

Diagnosis.—This species has been described three times before, the first being the detailed original description of Lindström, the second by Versluys (1906), and the third and by far the most detailed by Aurivillius (1931), all three based on the holotype or fragments of it. We have also examined a small fragment of the holotype but can add little to the previous descriptions except for what can be illustrated by SEM. Thus, only a diagnosis for this species is presented herein:

Colonies uniplanar, one of the largest (the holotype) 55 cm in height. Branching dichotomous, occurring throughout colony at intervals of 20–35 mm. Stem axis bronze to golden yellow. Polyp whorls consist of 4–7 polyps (the average being 6); 13–17 (usually 14) whorls occur over 3 cm axial length; adjacent whorls separated by 0.4–0.6 mm, depending on branch diameter. Polyps 1.3–1.5 mm in length (not 1.6 mm, as stated by Lindström) and 0.75–0.90 mm in width. Infrabasals typically crescent

shaped, 0.25–0.30 mm in height. Basals 0.75-0.90 mm in height, the distal 0.17-0.20 mm (20%) being a short, quite broad, blunt distal "spine", which on the exposed interior face is covered with 10-12 parallel, serrate ridges (Figs. 7A-B). Each basal scale also bears one prominent ridge on its exterior dorso-lateral margin. Buccal scales up to 1.0 mm in length, having very slightly flared, evenly rounded distal margins that envelop only the proximal 0.07-0.09 mm of the opercular scales; however, the dorsolateral margins of buccal scales usually bear 2-4 low ridges. Opercular scales typical in shape for the genus, the abaxial up to 0.57 mm, the outer- and inner laterals equal to or longer than the abaxials (0.54–0.69 mm), and adaxials up to 0.43 mm in length, all operculars having a H:W of 1.4-1.5. Coenenchymal sclerites irregular in shape, up to 0.76 mm in length, but mostly 0.4 mm in length. These scales, like those of the polyps, bear small (10 µm diameter) blunt granules exteriorly, which are occasionally linked in short rows but never formed into ridges. Inner faces of coenenchymal scales as well as those of polyp scales bear complexly ornamented tubercles about 10 µm in diameter. Tentacular sclerites not observed.

Comparisons.—C. josephinae is quite similar to P. simplex, as can be seen in the comparison of characters in Table 1, but differs from both P. simplex and P. duplex in having less flared and less projecting buccal scales (Figs. 6A-C), which allows a view of most of the opercular scales in abaxial view. P. josephinae also has fewer polyp whorls per cm because the average spacing between whorls is higher. The dorso-lateral ridges on the buccal and basal scales are more prominent than those of P. simplex. Finally, the short, broad basal "spines" of P. josephinae may be unique, these spines more accurately called a flattened lobe.

Remarks.—Apart from having "erect and regularly dichotomizing branches" (Lindström 1877:6), the form of Lindström's

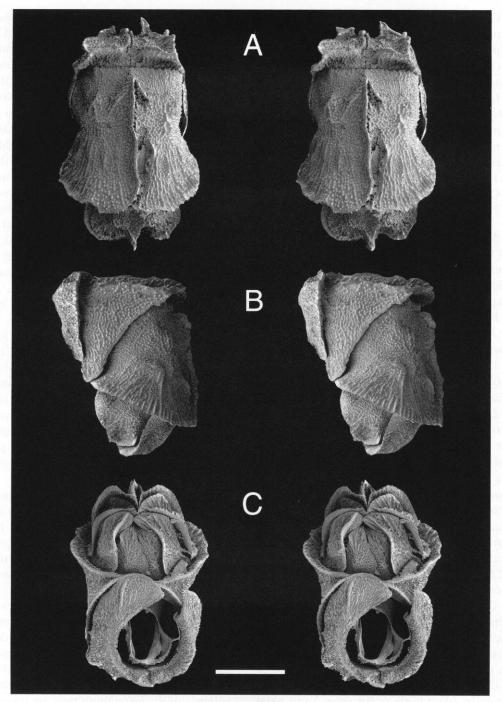


Fig. 6. Paracalyptrophora josephinae, holotype, Swedish Museum of Natural History 1113: A, abaxial stereo view of a polyp; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

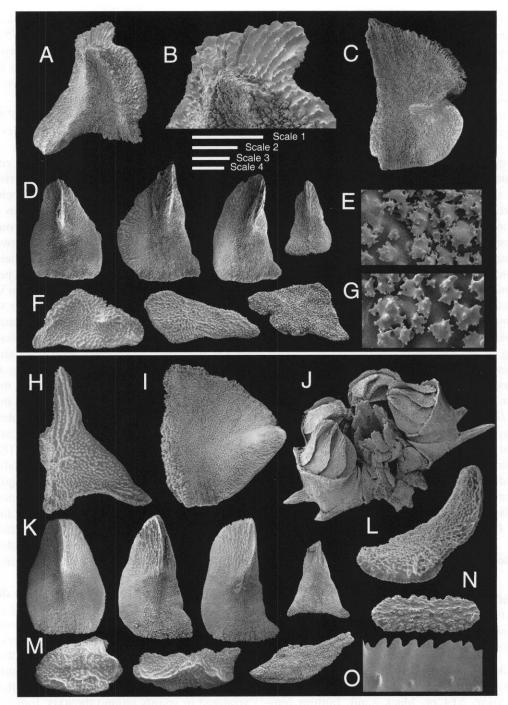


Fig. 7. A–G, *Paracalyptrophora josephinae*, holotype: A, B, inner side of basal scale, B showing the finely ridged projecting spine; C, buccal scale; D, ad-, OL, IL, and adaxial operculars; E, G, opercular and coenenchymal tubercles on lower side of opercular and coenenchymal scales, respectively; F, upper and lower faces of 3 coenenchymal scales. H–O, *Paracalyptrophora carinata*, holotype: H, basal scale; I, buccal scale; J, whorl of 4 polyps; K, ab-, OL, IL, and adaxial opercular scales; L, infrabasal scale; M, 3 coenenchymal scales showing ridging; N, tentacular scale; O, margin of opercular scale. Scale bar 1: E, G, N, O = 25 μm; 2: D, F = 0.25 mm; J = 0.75 mm; L = 0.125 mm; 3: A, C, I, K, M = 0.25 mm; B = 0.083 mm; 4: H = 0.25 mm.

eastern Atlantic holotype and subsequently reported colonies has not been described. Evidently the "splendid specimen" 5.5 decimeters long was not available to Versluys (1906) or Aurivillius (1931:301) for their re-description of Lindström's type, as Aurivillius reported only "a number of fragments, about 5-8 mm long", and we received on loan only a small branch for comparison. The size stated by Aurivillius must be centimeters rather than millimeters, as some of the pieces had one or two bifurcations. Nonetheless, Lindström's allusion to the diameter of the "basis" (=main stem) indicates that he probably had a complete colony, and, had it been a biplanar colony, Lindström surely would have mentioned this fact. Observation of the type specimen by Stockholm curator Björn Sohlenius (pers. comm., 2002) confirms that the holotype is uniplanar. Furthermore, according to M. Grasshoff (pers. comm., 2002), most of the specimens he collected and observed in situ (see synonymy) were uniplanar.

Distribution.—Eastern and mid-Atlantic: Bay of Biscay; Josephine, Great Meteor, and Atlantis Seamounts; Azores (south of Flores and Alice Bank); 214–1480 m. The undocumented references of *P. josephinae* from the western Atlantic (Grasshoff 1985b, 1986) probably pertain to the types of *P. carinata*.

### Paracalyptrophora carinata, new species Figs. 1G, 7H–O, 8A–C, 9

Calyptrophora josephinae.—Grasshoff, 1985b:73 (in part: western Atlantic reference); 1986:27 (in part: western Atlantic reference).

Material examined/Types.—Lesser Antilles, southwest of St. Lucia: 13°34′N, 61°04W, 514 m, black sand, bottom temperature 8.4°C, Alb-2752, 4 Dec 1886, one colony (holotype) with part of holdfast, and 5 detached branches, USNM 49948 (SEM 264, C1055–56, 63), paratypes.

Lesser Antilles, between St. Lucia and

St. Vincent: 13°34′N, 61°03W, 514 m, black sand, bottom temperature 8.4°C, *Alb*-2753, 4 Dec 1886, one incomplete colony with part of holdfast and tangled with hemp fibers from the tangle-bar, USNM 49968, paratype.

Type locality.—13°34′N, 61°04′W (southwest of St. Lucia, Lesser Antilles), 514 m.

Description.—Colonies consist of a robust, vertical main stem, which gives rise to a pair of parallel, dichotomously branching fans. The main stem is anchored in a dense, white, irregularly-shaped calcareous mass—the holdfast—the largest of the two observed being 18 mm in width. The main stem of the larger specimen (the holotype) is inflexible, 5 cm in height, and 4.4 mm in maximum diameter, supporting fans up to 18 cm in height and 8 cm broad, the entire colony being 23 cm in height. The stem axis is golden-yellow to bronze in color and faintly longitudinally striate. Branching is uniformly dichotomous (but not lyrate), the first two internodes being quite short, the remaining internodes, which may number up to 10 for certain terminal branches, are spaced fairly uniformly at intervals of 18-21 mm throughout the colony. Occasionally terminal branches are up to 8 cm in length. A slight irregularity in the branching pattern of the paratype has led to three of the first four branches contributing to one fan, the opposite, parallel fan being smaller, originating from only one of the original four branches.

Polyps are arranged in whorls and directed downward, each whorl consisting of 4–8 polyps (usually 6); 12–14–16 whorls occupy 3 cm of axial length. In general, polyp whorls are well spaced, such that each whorl is separated by 0.60–0.65 mm. Polyps are common on the main stem, often arranged in spirals around the axis. Individual polyps are 1.50–1.75 mm in length and 0.80–0.92 mm in width.

Each polyp is protected by two pairs of large abaxial body wall scales and a pair of smaller crescent-shaped infrabasals, which

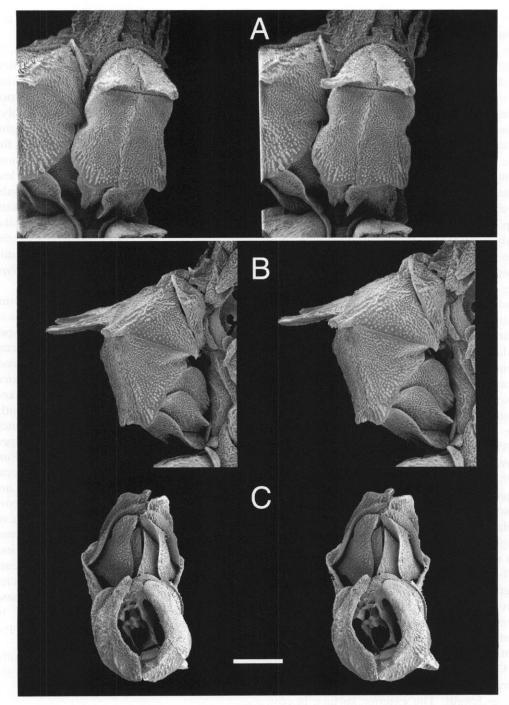


Fig. 8. Paracalyptrophora carinata, holotype, USNM 49948: A, abaxial stereo view of polyps; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

are about 0.30 mm in height and typical in shape for the genus. The basal scales are the largest sclerites, up to 1.2 mm in height, the distalmost 0.45-0.50 mm consisting of a prominent, pointed, finely serrated spine. Each spine is covered with several rows of closely spaced teeth. The dorso-lateral margins of the basal scales are not ridged, but acutely curved to cover the lateral sides of the polyp. The buccal scales are 0.9-1.0 mm long and have fairly straight, finely serrate (apices of triangles about 6 µm tall) distal margins that are not flared and overlap the basal margins of the operculars by only 0.10-0.15 mm, which exposes most of the opercular scales in lateral or adaxial views (Figs. 8A-B). There is a slight swelling on the center of the proximal third of each buccal from which a low ridge originates and continues along the dorso-lateral margin of the sclerite (Fig. 8A). The opercular scales are triangular in shape, and, in general, decrease in size and H:W ratio from ab- to adaxial direction. Of the two abaxial operculars, usually only one is symmetrical, the other being more developed on the adaxial side. These operculars are up to 0.85 mm in height, the symmetrical one having a H:W of 1.58, the asymmetrical of 1.9. The outer-lateral operculars are of equal height but similar to the asymmetrical abaxials in shape. The inner-lateral operculars are also asymmetrical in shape but slightly smaller and squatter in shape, only up to 0.7 mm in height, having a H:W of 1.7-1.8. The adaxial operculars are symmetrical, rarely over 0.55 mm in height, and have a broad base with a H:W of 1.2-1.4. Tentacular sclerites are very rare, shaped as flattened rods up to 82 µm in length and 26 μm in width.

Coenenchymal sclerites are elongate to irregular in shape, up to 0.87 mm in maximum length. The exterior surface is covered by small granules (14–15 µm in diameter) and prominent longitudinal or reticulately arranged ridges (Fig. 7M). The inner surface of the coenenchymal scales, as well as those of the polyps, are covered with

complexly ornamented tubercles  $10-12 \mu m$  in diameter.

*Etymology*.—Latin *carinata* = keeled, an allusion to the ridged coenenchymal scales.

Comparisons.—Paracalyptrophora carinata is easily distinguished from the two other western Atlantic species by its polyp morphology: having non-flared, straightedged buccal sclerites that cover only the bases of the opercular scales. In addition, P. carinata has larger polyps and thus less whorls per axis length, non-ridged basals, ridged coenenchymal scales, and small tentacular scales (see Table 1). Tentacular scales are also present in Japanese material of P. kerberti (Versluys) but the taxonomic significance of this character in Paracalyptrophora has yet to be determined.

Paracalyptrophora carinata is most similar to the eastern Atlantic P. josephinae, especially in polyp morphology, both species having very similarly-shaped buccal scales with non- or only slightly flared, straight distal margins. However, P. carinata differs in having a biplanar colony and having larger polyps with consequently larger opercular scales. It also has much taller basal spines and a lesser developed dorso-lateral ridge of the basal scales. Furthermore, P. carinata has non-flared buccal scales, whereas those of P. josephinae are slightly flared, and the operculars of P. carinata are pointed outward, whereas those of P. josephinae are usually pointed downward toward the branch axis. Each of these differences taken separately might indicate range of variation or perhaps a subspecies of P. josephinae, but taken together these consistent differences are considered to warrant differentiation as a different species.

Distribution.—Known only from southwest of St. Lucia, Lesser Antilles (Fig. 9); 514 m.

Paracalyptrophora mariae (Versluys, 1906) Figs. 1H, 10A–C

Calyptrophora mariae Versluys, 1906:107–109, pl. 9, fig. 25, text-figs. 140–145 (Ti-

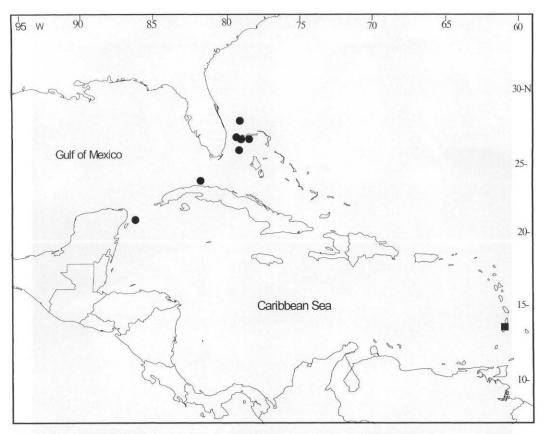


Fig. 9. Distribution of Paracalyptrophora simplex (circles) and P. carinata (square).

mor Sea).—Kükenthal, 1919:474 (diagnosis); 1924:317, 318–319 (key, diagnosis).—Aurivillius, 1931:301 (key).—van Soest, 1979:103 (type deposition).

Calyptrophora (Paracalyptrophora) mariae.—Kinoshita, 1908:58 (listed).

Paracalyptrophora mariae.—Bargibant in Forges, Grandperrin & Laboute, 1987:34 (listed).—Bayer, 2001:367 (listed).

Material examined.—Chalcal II, CP25 (HGP-44), 23°38.6′S, 167°43.12′E (Stylaster Bank, on Norfolk Ridge just southeast of New Caledonia), 418 m, 1 large colony (NMNH) and SEM stubs 1202–1204 (USNM).

Types.—A fragment of the holotype is deposited at the ZMA (Coel. 7414), but the larger colony is missing (van Soest 1979). Type Locality: 10°39′S, 123°E (Roti Strait between Timor and Roti), 520 m.

Diagnosis.—Colonies biplanar, the largest of the two known specimens (the holotype) 27.5 cm in height, consisting of a main stem 5.5 cm in height and two parallel fans, each about 22 cm in height and 16 cm in width. Branching dichotomous (equal, not lyrate), occurring every 2-3.5 cm in the lower half of fan, the distal branches often over 10 cm in length and rarely the result of more than 5 bifurcations. Stem axis black; branches often a metallic gold. Polyp whorls consist of 4-7 polyps, the larger number on thicker branches; 11-15 whorls occur over 3 cm branch axial length; adjacent whorls separated by 0.5-1.0 mm, depending on branch diameter. Polyps 1.4-1.8 mm in length and about 0.9 mm in width. Infrabasal scales crescent shaped and about 0.15 mm in height, each bearing one prominent longitudinal ridge. Basals about 0.85

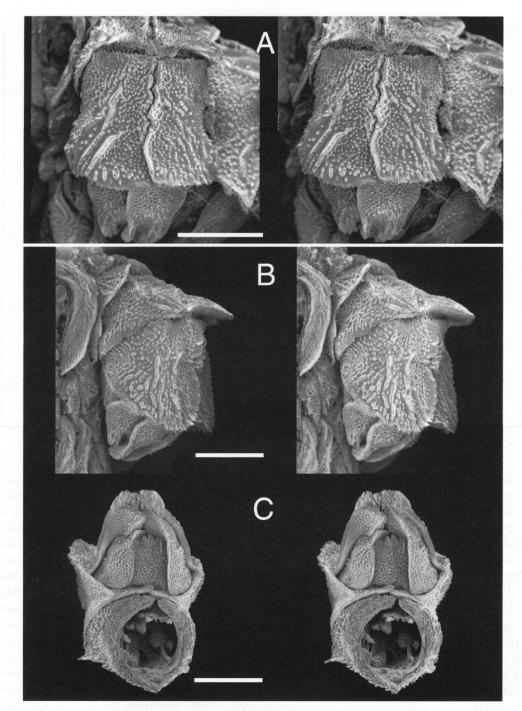


Fig. 10. Paracalyptrophora mariae, Chalcal II, CP 25, USNM Stub 1202, 1204: A, abaxial stereo view of a polyp; B, lateral stereo view of a polyp; C, adaxial stereo view of a polyp. Scale bars 0.5 mm.

mm in height, the distal 0.20 mm being a robust, projecting spine. Dorso-lateral margins of basals bear 3 or 4 prominent, serrate ridges (Fig. 10B). Buccal scales about 0.85 mm in length and have a slightly flared and slightly projecting dorso-lateral distal margin, which nonetheless covers only the basal part (about 0.2 mm) of the opercular scales. Dorso-lateral margin of each buccal scale bears 4 or 5 prominent ridges (Fig. 10A). Operculars typical for the genus, the abaxial operculars up to 0.83 mm in height and adaxials only 0.36 mm, but most operculars maintaining a H:W of 1.5-1.7. Tentacular scales not noted. Coenenchymal branch sclerites irregular in shape, rarely more than 0.5 mm in maximum length, and covered externally with granules and prominent ridges (Fig. 10B).

Comparisons.—Paracalyptrophora mariae is distinguished from all other species by having prominently and multiply-ridged body wall scales (Table 1), including the infrabasals, as well as ridged coenenchymal scales.

Remarks.—Despite a moderate synonymy, this species is known from only two specimens, the holotype and the specimen listed without comment by Bargibant (1987), illustrated herein, who must also be credited with the new combination. The New Caledonian specimen is similar to the description of the holotype, differing primarily in having slightly smaller polyps (1.4 mm vs. 1.6–1.8 mm) and thus more whorls per 3 cm (14–15 vs. 11–12).

Distribution.—Timor Sea and southeast of New Caledonia; 418–520 m.

Paracalyptrophora kerberti (Versluys, 1906) Figs. 1I, 11A–C, 12A–J

Calyptrophora japonica.—Studer, 1878: 642 (Japan).

Calyptrophora kerberti Versluys, 1906: 105–107, text-figs. 134–139 (Japan).—Nutting, 1912:59 (Japan).—Kükenthal, 1919:472–473, text-figs. 223–226 (Ja-

pan); 1924:318, text-fig. 173 (key, diagnosis).—Aurivillius, 1931:301 (key).—van Soest, 1979:103 (type deposition).—Utinomi, 1979:1011–1013, fig. 2a–i (Sagami Bay).

Calyptrophora (Paracalyptrophora) kerberti.—Kinoshita, 1908:58, 63–65, pl. 4, fig. 29 (Japan).

Calyptrophora (Paracalyptrophora) Kerbeti (sic).—Kinoshita, 1909:8–9, pl. 1, fig. 2, 2 text-figs. (Japan).

Paracalyptrophora kerberti.—Bayer, 2001: 367 (listed, new comb.).

*Material examined.*—Japan: *Alb*-5093, 1 colony, USNM 30105 (reported by Nutting, 1912), SEM C1058–62, 1064.

Types.—The holotype is deposited at the ZMA (Coel. 2294) (van Soest 1979). The second specimen described by Versluys, also from Japan (Hilgendorf collection), is interpreted as a paratype, and is deposited at the ZMB (2065). Type Locality: "Japan", depth unknown (Bloemhoff collection), although Utinomi (1979) suggests that the specific type locality is Sagami Bay.

Diagnosis.—Colonies biplanar, the largest known colony (Kükenthal 1919) 24 cm in height and 11 cm in fan width; greatest stem length (Versluys 1906) 9 cm. Branching dichotomous (equal, not lyrate), most branching occurring in lower half of fan, the distal branches rarely over 6.5 cm in length are rarely the result of more than 6 or 7 bifurcations. Stem axis brown, black, or golden. Polyp whorls consist of 4-8 (usually 5) polyps; 8-13 (usually 10) whorls occur over 3 cm branch length; adjacent whorls widely spaced, 0.5-2.0 mm. Polyps 2.0-3.0 mm in length and about 1.2 mm in width. Infrabasals crescent shaped, about 0.35 mm in height. Basals 1.4-1.5 mm in height, the distalmost 0.6-0.8 mm a prominent sharp spine, which bears one finely serrate ridge on its outer surface; otherwise the basal scales are unridged and fairly smooth. Buccal scales 1.3-1.9 mm in length, the longer scales those having a dis-

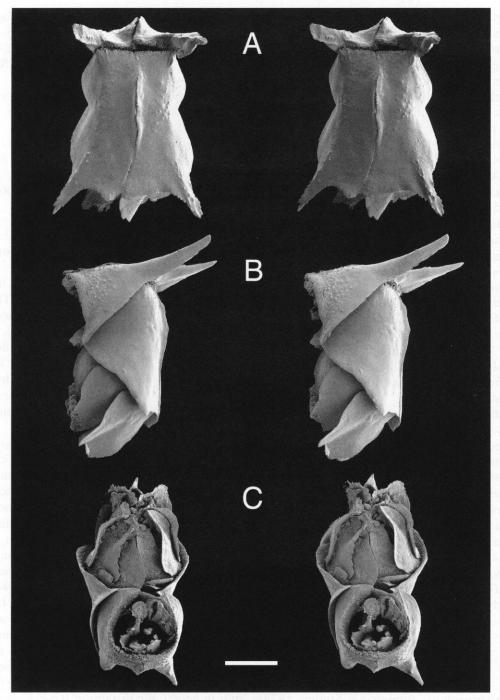


Fig. 11. Paracalyptrophora kerberti, Alb-5093, USNM 30105: A, abaxial stereo view of a polyp with spinose buccal scales; B, lateral stereo view of a polyp with straight-margins buccal scales; C, adaxial stereo view of a polyp. Scale bar 0.5 mm.

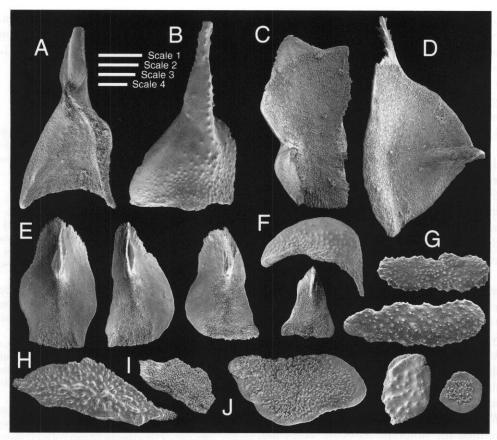


Fig. 12. Paracalyptrophora kerberti, Alb-5093, USNM 30105: A, B, inner and outer view of a basal scale; C, buccal scale with a small distal, triangular distal margin; D, buccal scale with a prominent distal spine; E, ab-, OL, IL, and adaxial operculars; F, infrabasal scale; G, 2 tentacular scales; H–I, upper and lower views of coenenchymal scales; J, 3 adaxial buccal scales. Scale bar 1: H, I = 0.25 mm; 2: G = 25  $\mu$ m; 3: J = 0.125 mm; 4: A–F = 0.25 mm.

tal spine; only slightly flared at distal margin, which covers only the basal part of the opercular scales; and relatively smooth, without any ridges and with only sparse granulation. Distal margin of buccals may be straight (Fig. 11C), jagged (Figs. 11B, 12C), or bear a prominent, serrate spine up to 0.35 mm in length projecting from the dorso-lateral margin (Figs. 11A, 12D), all variations present on the same colony. One to five small (up to 0.47 mm in length and 0.22 mm in width), flat, elliptical to ovalshaped adaxial buccal scales often present between the interior, adaxial ridge of the buccal scales and the adjacent adaxial and inner-lateral operculars. These scales usually are not paired. Abaxial operculars symmetrical, up to 1.10 mm in height, having a H:W of 1.4-1.7. Outer-lateral operculars equal in height but usually slightly narrower than abaxials and asymmetrical, having a H:W of 1.7–2.3. Inner-laterals up to 0.92 mm in height, asymmetrical; H:W = 1.8. Adaxial operculars almost equilateral in shape (H:W = 1.1-1.2), and much smaller (only up to 0.7 mm in length). Distal margins of the abaxials and outer-laterals are coarsely serrate. All operculars bear prominent keels on their distal, inner surfaces, those on the larger operculars (e.g., abaxials and outer-laterals) sometimes divided into 3 or 4 parallel crests (Fig. 12E). Outer faces

of all operculars fairly smooth, like the other body wall sclerites; inner surface tuberculate, but tubercles restricted to the central region, the margins fairly smooth. Tentacular sclerites flattened rods up to 92  $\mu m$  in length and 26  $\mu m$  in width. Coenenchymal sclerites elongate but irregular in shape, up to 1.0 mm in length but usually only about 0.5 mm. Their upper surfaces are covered with low granules 12–14  $\mu m$  in diameter; there are no ridges.

Comparisons.—Paracalyptrophora kerberti is the most distinctive species in the genus, having several unique characters. It is the only species known to have adaxial buccal scales. It is also distinctive in having the largest polyp size and thus the smallest number of polyp whorls per cm (Table 1). Furthermore, as mentioned by Nutting (1912), it is distinctive in often, but not always, having one prominent spine on the distal dorso-lateral margin of each buccal scale. Finally, the exterior sculpture of all scales is extremely reduced, the body wall scales almost appearing as smooth.

Remarks.—Although Versluys (1906) described the holotype as being uniplanar, he qualified his description as being based on a small damaged specimen, and also reported a paratype that was biplanar. It was Kinoshita's (1908:63) opinion, based on "several" specimens, that the species bears two parallel fans, and all subsequent records of this species were based on biplanar colonies.

Distribution.—Off Honshu, Japan; 150–731 m.

### Acknowledgments

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