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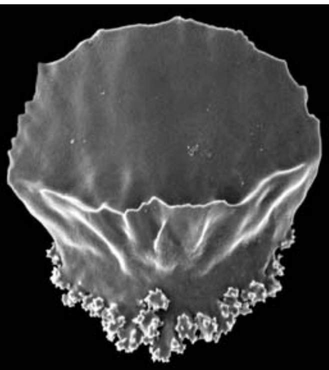

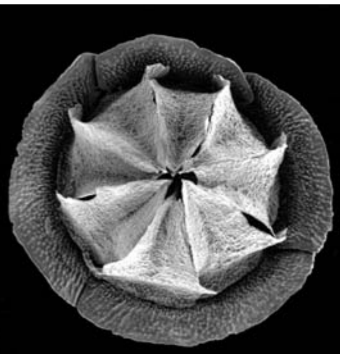

# A Generic Revision and Phylogenetic Analysis of the Primnoidae

## (Cnidaria: Octocorallia)

*Stephen D. Cairns and Frederick M. Bayer*

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ABSTRACT

Cairns, Stephen D., and Frederick M. Bayer. A Generic Revision and Phylogenetic Analysis of the Primnoidae (Cnidaria: Octocorallia). *Smithsonian Contributions to Zoology*, number 629, iv + 79 pages, 19 figures, 4 tables, 2009.—Primnoidae consists of 36 genera, 7 subgenera, and 233 valid species, making it the fourth largest octocorallian family. Species occur in all ocean basins, especially the Antarctic, at depths of 8–5850 m, making primnoids the deepest-living gorgonacean octocorals. Primnoids are common and characteristic of seamounts and deepwater coral banks, often providing habitat for other marine life and serving as proxies for isotopic analyses to determine paleotemperatures. Diagnoses of the primnoid genera and subgenera are based primarily on their type species, and specimens are illustrated by means of scanning electron microscopy, often using stereo images to allow better appreciation of the topology and interconnection of the calycular sclerites. A history of the higher classification of the family is given. Each genus is briefly discussed, and also included are a synonymy of pertinent references, a summary of the geographic and bathymetric ranges, and the deposition of the type specimens of the type species. Four new genera, two new subgenera, one new species, and seven new combinations are proposed. A list of the 233 valid species and the 14 infraspecific taxa is provided along with the purported junior synonyms. An indented dichotomous key is provided for identification of the genera and subgenera. Phylogenetic analysis of the genera and subgenera was performed using 27 morphological characters comprising 94 character states. The cladogram does not consistently support the conventional arrangement of genera into five subfamilies, thus this classification is not followed herein. The origin of the primnoids is inferred to be from an ancestor living in the Antarctic.

Cover images, left to right: Left side detail from stereo images of Figures 8l, 5b, and 16h.

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# Contents

# A Generic Revision and Phylogenetic Analysis of the Primnoidae (Cnidaria: Octocorallia)

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[†] Deceased 2 October 2007.

## INTRODUCTION

Among the 44 families of Octocorallia (Williams and Cairns, 2005, updated), the Primnoidae ranks fourth in number of species (233/3200 = 7.3%, see Tables 1, 4) and third in number of genera (36/340 = 10.6%), resulting in an average of 6.5 species per genus. No confirmed fossil species are known. Primnoids occur worldwide at depths of 8–5,850 m, although they are most common at slope and upper abyssal depths (Table 1), the few shallow records being uncommon. The primnoids thus may be considered to be the quintessential deepwater octocoral family, only some pennatulaceans occurring in deeper water. It is tempting to speculate that the modification of their imbricate external calycular scales is the key adaptation for their success in deep water; however, two isidid subfamilies, many of which occur at shelf depths, also have very similar sclerite morphology.

Aside from the innate taxonomic interest of the family and the beauty of their calycular architecture, primnoids serve important ecological and geophysical roles. Because of their large size (e.g., *Primnoa* occurs up to 2 m in height and 7 m wide) and local abundance (sometimes occurring in large monospecific fields), some primnoids, such as *Primnoa, Narella,* and *Callogorgia,* form habitat for fish (Etnoyer and Morgan, 2005; Stone, 2006; Etnoyer and Warrick, 2007) and other invertebrates (Krieger and Wing, 2002; Buhl-Mortensen and Mortensen, 2004, 2005), especially on seamounts (Cairns and Baco, 2007; Rogers et al., 2007; Cairns and Bayer, 2007 [2008]), and on deepwater coral banks (Cairns and Bayer, 2005). Also, because of their solid, layered axis and purported long life span (Andrews et al., 2002; Risk et al., 2002), various isotopic analyses of their axes can be used to determine paleotemperatures (Heikoop et al., 2002; Sinclair et al., 2005; Sherwood et al., 2005).

The following abbreviations are used in the text.

*Museums*

| | |
|---|---|
| AM | Australian Museum, Sydney |
| BM | The Natural History Museum, London |
| MNHNP | Muséum National d'Histoire Naturelle, Paris |
| NTM | Northern Territories Museum, Darwin |

**TABLE 1.** Distributional characteristics of the primnoid genera and subgenera. The number of valid species plus subtaxa may include subspecies, varieties, and/or forms (see Table 4 for complete list).

| Genus | Distribution | Depth Range (m) | Number of species + subtaxa |
|---|---|---|---|
| *Primnoeides* | Southern Indian Ocean | 400–558 | 1 |
| *Ophidiogorgia* | Antarctica | 27–426 | 2 |
| *Aglaoprimnoa* | Subantarctic South America | 70–686 | 1 |
| *Armadillogorgia* | South Georgia, Scotia Sea | 659–1,886 | 1 |
| *Ainigmaptilon* | Antarctica to South Georgia | 75–550 | 5 |
| *Primnoella* | Western Atlantic, Australia, New Zealand | 8–1,249 | 10 |
| *Convexella* | Antarctic, Kermadec, North Atlantic | 12–5,850 | 5 |
| *Dicholaphis* | Off Japan | 731 | 1 |
| *Callozostron* | Antarctic, New Zealand | 1,354–3,876 | 4 |
| *Arntzia* | Antarctic | 64–604 | 1 |
| *Thouarella* | | | |
| *T. (Thouarella)* | Subantarctic, western Atlantic, North Pacific | 60–1,005 | 14 + 2 |
| *T. (Euthouarella)* | Indo–western Pacific, North Atlantic | 256–1,644 | 10 + 1 |
| *T. (Diplocalyptra)* | Off Japan | 146 | 2 |
| *T. (Epithouarella)* | Antarctic, subantarctic | 106–686 | 3 |
| *Metafannyella* | Antarctic | 265–1,280 | 4 |
| *Fannyella* | | | |
| *F. (Fannyella)* | Antarctic | 46–852 | 2 |
| *F. (Scyphogorgia)* | Antarctic | 100–550 | 1 |
| *F. (Cyathogorgia)* | Antarctic | 55–485 | 1 |
| *Onogorgia* | Antarctic | 22–433 | 1 |
| *Pyrogorgia* | Tierra del Fuego | 384–511 | 1 |
| *Amphilaphis* | Subantarctic, Galapagos, Antarctic, Hawaii | 55–3,182 | 6 |
| *Mirostenella* | Subantarctic | 201–1,647 | 2 |
| *Acanthoprimnoa* | Caribbean, Japan | 45–686 | 4 + 1 |
| *Plumarella* | Western Pacific, Patagonia, northwest Atlantic | 10–1,914 | 21 + 4 |
| *Callogorgia* | Indo-Pacific, North Atlantic | 37–2,472 | 25 + 3 |
| *Fanellia* | Western, central, and northern Pacific | 92–1,028 | 8 |
| *Paranarella* | Northwest Atlantic | 3,855 | 1 |
| *Primnoa* | North Atlantic, North Pacific, subantarctic | 9–1,020 | 4 + 1 |
| *Australogorgia* | Off Tasmania | 987 | 1 |
| *Narella* | Cosmopolitan | 55–4,594 | 38 |
| *Arthrogorgia* | North Pacific | 163–1,127 | 4 |
| *Paracalyptrophora* | Western and central Pacific, North Atlantic | 150–1,480 | 6 |
| *Calyptrophora* | Pacific, western Atlantic | 229–3,107 | 14 + 2 |
| *Tokoprymno* | Subantarctic | 549 | 1 |
| *Parastenella* | Cosmopolitan , except east Atlantic | 567–3,470 | 6 |
| *Candidella* | Atlantic, central Pacific | 378–2,165 | 4 |
| *Microprimnoa* | New Caledonia | 415 | 1 |
| *Pterostenella* | Indo–western Pacific | 60–75 | 2 |
| *Perissogorgia* | New Caledonia | 55–750 | 7 |
| *Dasystenella* | Subantarctic South Atlantic | 300–5,087 | 1 |
| *Pseudoplumarella* | Eastern Australia | 55–115 | 5 |
| Totals | | 8–5,850 | 233 + 14 |

| | |
|---|---|
| NMNH | National Museum of Natural History, Smithsonian, Washington, D.C. |
| USNM | United States National Museum (now the NMNH) |
| ZMA | Zöologisch Museum, Amsterdam |
| ZMB | Zoologisches Museum, Berlin |

*Other Terms*

| | |
|---|---|
| CI | Consistency index |
| Coel. | Coelenterata (term prefaces catalog numbers associated with ZMA) |
| L:W | Ratio of length to width of a sclerite |
| PAUP* | Phylogenetic Analysis Using Parsimony |
| RI | Rescaled consistency index |
| SEM | Scanning electron microscopy |

## A Brief History of the Primnoidae, with Special Emphasis on the Higher Classification

The oldest described primnoid species was *Gorgonia resedaeformis* Gunnerus, 1763 (=*Primnoa resedaeformis*), whereas the earliest described primnoid genus was *Primnoa* Lamouroux, 1816.

Although many have cited Gray (1858) as the author of the family Primnoidae, some even citing this work as published in 1857, his paper was, in fact, published on 23 February 1858. However, one year earlier, Milne Edwards (1857:138) introduced the term Primnoacées to include two genera (*Primnoa* and *Muricea*). Primnoacées was termed an *agèle* by Milne Edwards, a category between subfamily and genus, thus either a tribe or supergenus. We interpret this taxonomic level to be a tribe and thus among the family group names, making it the earliest available name for the family Primnoidae. Gray (1858) referred to the family as Primnoadae (spelling later corrected to Primnoidae by Verrill, 1868) and included three genera: the type genus *Primnoa* and *Callogorgia* and *Primnoella*. Later, Gray (1870) included 13 genera in the family, many of which are now considered to be in different families, and established the family "Calyptrophoradae" for one genus and "Calligorgiadae" for seven genera now assigned to the Primnoidae and Ellisellidae. Verrill (1883) correctly eliminated some of the nonprimnoid genera from the family. In his comprehensive classification of the Alcyonaria, Studer (1887) placed 12 genera in the family, all of which are still considered primnoids, and divided the genera into four subfamilies (Callozostrinae, Calyptrophorinae, Primnoinae, and Primnoeidinae) but did not offer justification for the subfamilies. The classification of the 14 primnoid genera in Wright and Studer's (1889) *Challenger* Expedition report followed that of Studer (1887) but also included diagnoses of the four subfamilies: Callozostrinae was characterized by having a flexible axis; Calyptrophorinae had a rigid axis and a small, fixed number of annular body wall scales; Primnoinae had a rigid axis and a larger, variable number of body wall scales; and Primnoeidinae had a rigid axis but lacked an operculum. Except for Versluys (1906) and Kinoshita (see below), this subfamilial arrangement has been followed until recent times.

Versluys (1906), in his beautifully illustrated revision of the *Siboga* (1902) primnoids, provided the most comprehensive exploration of this family to date. He provided extensive discussion about most of the characters used to differentiate primnoid genera and even suggested a preliminary evolutionary tree of the genera, creating a hypothetical ancestral form ("*Stammform*"), which he called *Proprimnoa,* and then choosing *Primnoeides* as the closest genus to the ancestral form. The ancestral form, as well as *Primnoeides*, was characterized by having all sclerites, both coenenchymal and body wall, of the same shape; a very poorly developed operculum; body wall scales not arranged in rows (except in the juvenile form); uniplanar pinnate colonies; calyces arranged in whorls of two to four; and two layers of coenenchymal sclerites. He concluded by listing the 67 known species and 11 known genera in the family. Although Versluys followed Studer's subfamilial classification for the descriptive part of his paper, saying that he did not want to cause confusion by deviating from previous classifications (Versluys, 1906:158), in the second part of his paper, titled "Comparative Phylogenetic Section," he nonetheless proposed a different organization of the genera into five subfamilies, two of them new (see below).

Subfamily 1: Primnoeidinae (*Primnoeides*): operculum poorly developed, body wall scales not in well-arranged rows.

Subfamily 2: Primnoellinae, new subfamily (*Primnoella*): operculum and circumoperculum developed, adaxial side of body wall exposed.

Subfamily 3: Thouarellinae, new subfamily (*Thouarella, Amphilaphis, Plumarella, Stenella*): eight rows of body wall scales but often indistinct and reduced in size near base, nonetheless, body wall completely covered, operculum well developed.

Subfamily 4: Primnoinae (*Primnoa, Callogorgia, Stachyodes,* and *Calyptrophora*): operculum present but no circumoperculum, body wall scales greatly reduced in number.

Subfamily 5: Callozostroninae (*Callozostron*): axis flexible, eight rows of body wall scales, operculum present.

Kinoshita was also very active at this time, publishing seven papers (Kinoshita, 1907, 1908a, 1908b, 1908c, 1908d, 1908e, 1909) on the primnoids of Japan, as well as discussing general characteristics of the family. He was the only author to adopt Versluys' subfamilial organization of the genera, but most of his papers were in Japanese, which limited their use to many taxonomists. English translations are available at the Smithsonian. At the conclusion of this series of papers, Kinoshita (1909) tabulated 118 species in 13 genera. Much later, Utinomi (1979) resumed the tradition of research on Japanese primnoids.

Nutting was also active in working on the primnoids collected by the USFWS *Albatross* in Pacific waters, reporting new primnoid species from the Hawaiian Islands (Nutting, 1908), off California (Nutting ,1909), and off Japan and the Aleutian Islands (Nutting, 1912). And Thomson and Mackinnon (1911) reported 11 primnoid species (7 new) from off New South Wales, Australia, collected by the *Thetis*.

Willi Kükenthal, undoubtedly the most prolific octocoral researcher of all time, published four papers on the primnoids of Japan (Kükenthal, 1907, 1908; Kükenthal and Gorzawsky, 1908a, 1908b); he (Kükenthal, 1912) also reported the primnoids of the German South Polar Expedition of 1901–1903, making the six-year period of 1907–1912 an incredibly active one for the study of this family! Kükenthal (1915) later revised the family, providing keys to the genera and all 126 known species at that time. Perhaps on the basis of this rash of papers, Kükenthal (1915:142) stated that Primnoidae may be the most thoroughly investigated family in the order Gorgonacea, a perception that holds true even today.

In his monumental work on the gorgonians of the German deep-sea expedition of the *Valdivia* (1898–1899), Kükenthal (1919) devoted 185 pages to a revision of the family Primnoidae, including descriptions of all species and dichotomous as well as indented keys to all genera and the 138 species. His treatment of the Primnoidae in his landmark revision of Gorgonaria (Kükenthal, 1924) is largely derivative of this earlier 1919 work. In general, Kükenthal followed the same higher classification of the primnoid genera and subfamilies as suggested by Studer (1887). Kükenthal (1919) also rigorously analyzed Versluys' phylogenetic analysis of the genera, strongly disagreeing with the interpretation of many of the characters he used (see below). For instance, although Kükenthal agreed with Versluys that two layers of coenenchymal sclerites and similar types of sclerites in the coenenchyme and calyx were primitive states, contrary to Versluys, he thought that calyces arranged in whorls, body wall scales not in rows, a rudimentary operculum, and unbranched colonies were derived states rather than primitive. He implied that Versluys did not give adequate explanation for his choice of ancestral states and then went on to didactically list what he thought were the primitive states. Ironically, after this rather harsh criticism, Kükenthal agreed with Versluys that *Primnoeides* was the most primitive of the primnoid genera.

Other expeditionary reports that included the description of deepwater primnoids include Thomson and Richie (1906), the Scottish National Antarctic Expedition of 1903; Molander (1929), the Swedish Antarctic Expedition of 1901–1903; Aurivillius (1931), the gorgonians of Sixten Bock's expedition to the Bonin Islands in 1914; Thomson and Rennet (1931), the Australasian Antarctic Expedition of 1911–1914; Deichmann (1936), the *Blake* expeditions in the western Atlantic; and Madsen (1944), the Danish *Ingolf* Expedition in the boreal North Atlantic.

Subsequent to 1950, the major contributions to primnoid taxonomy were made by F. M. Bayer and coauthors (1950–2004, see References), and they tend to concentrate on taxa from the western Atlantic and Antarctic. Most notable was his revision of the octocoral genera in the *Treatise on Invertebrate Paleontology* (Bayer, 1956), in which all primnoid genera were diagnosed and placed in four subfamilies, *Ainigmaptilon* being placed in a family of its own. The four subfamilies were distinguished on only three characters: Primnoeidinae (one genus) had a poorly developed operculum, body wall scales not arranged in rows, and polyps that inclined toward the branch axis; Primnoinae (six genera) had a well-developed operculum, eight rows of body wall scales, and inclined polyps; Calyptrophorinae (three genera) had a well-developed operculum, two rows of body wall scales that wrapped around the polyp, and inclined polyps; and Callozostrinae (three genera) had a well-developed operculum, five to eight rows of body wall scales, and polyps that stood perpendicular to the branch. Bayer (1956) was the last published subfamilial listing of the primnoid genera and thus the model that will be compared in the phylogenetic analysis, although not much evolved since the original model proposed by Studer (1887). Bayer (1961) also published the first of his keys to the primnoid genera, this one an illustrated dichotomous key. His second key to the primnoid genera (Bayer, 1981b) was part of a larger key to all octocoral genera. His third key (Bayer and Stefani, 1989) was in French and was published in the context of the description of new primnoid species and genera from New Caledonia. Significant morphological and historical remarks on the family are also made in Bayer (1982, 1988). A series of seven papers were published by Cairns and Bayer (2002, 2003, 2004b, 2004c, 2005) and Cairns (2006, 2007a) that revise the primnoid species from the western Atlantic.

Finally, a new primnoid genus was described by López-González et al. (2002) from the Southern Ocean.

A total of 233 valid primnoid species are now known (Table 4).

### ACKNOWLEDGMENTS

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## MATERIAL AND METHODS

### MATERIAL

This study was based primarily on the collections of the NMNH, which currently must be considered the most comprehensive in the world for this family. Of the 41 higher taxa included in the revision, the NMNH contains representatives of the type species of 39 of them, and 15 of those 39 are represented by the type specimens of the type species. The type of *Pseudoplumarella* (*P. thetis*) was borrowed from the AM. No original material of *Dicholaphis* Kinoshita, 1907 could be obtained; thus, that taxon is described and figured from the literature. Although emphasis was given to the type species in defining the genera and subgenera, as many species as possible were examined within each taxon to fully describe its variation and to properly code for phylogenetic analysis. Representatives of the out-group were obtained from the NTM.

*Eogorgia* Hickson, 1938, described from the Eocene of Mississippi, was tentatively placed in the Primnoidae by Bayer (1956) solely on the basis of its size. Hickson had considered it to be a scleraxonian. On the basis of its spindle- and needle-shaped sclerites and general lack of any other information, it is not considered to be a primnoid in this revision. Two putative fossil species of *Primnoa* are listed in Table 4 but are considered highly doubtful for the family.

### DESCRIPTIVE METHODOLOGY

Genera are arranged in an order of roughly less to more derived as determined from the cladogram. The generic synonymies include the original descriptions as well as other references that include useful descriptive or illustrative information, with special mention of any keys to the generic or specific levels. Generic diagnoses are telegraphic in style and consistent in order of characters to facilitate comparison among genera. The deposition of the type specimens of the type species are given when known. The terminology for the calyces and sclerites follows that developed by Versluys (1906) as modified by Bayer et al. (1983).

With primnoids, it is important to be able to distinguish and count the scales on various rows on a calyx, especially those on the adaxial side. This requires careful dissection of a calyx from the branch in order to see the inner (=adaxial) face. Distinguishing scale rows is most easily accomplished by mounting entire calyces for SEM photography, stereo views being most helpful in viewing scales, especially those of the operculum and marginal scales, which are sometimes similar in shape and size. However, if an SEM view is not practical, one may allow the calyx to dry, mount it on a small piece of clay on a glass slide (for stability), and then progressively touch the calyx with a fine-tipped colored marker. The ink of the marker will provide excellent contrast, allowing one to see the outlines and texture of the scales. One can even mark specific scales prior to dissolution by bleach and thus trace specific scales for later description.

### PHYLOGENETIC ANALYSIS METHODOLOGY

#### *Remarks on the Choice of Out-Group and Evidence for Monophyly*

The Primnoidae is one of five gorgonacean families constituting the suborder Calcaxonia, a suborder characterized by having a solid (nonloculated) axis composed of calcium carbonate that is embedded in a gorgonin matrix, the latter giving the branch a variable degree of flexibility. Two of the other four calcaxonian families, the Ellisellidae and Ifalukellidae, have very different sclerite compositions (i.e., spindles, dumbbells, and small discs), which easily distinguish them from the Primnoidae. One of the other calcaxonian families, the Chrysogorgiidae, has many similarities with the primnoids, including the possession of scales in their sclerite complement; a flexible, metallic-colored axis; and an axis composed of concentric layers. However, the chrysogorgiid sclerites do not form an external squamous protective armor as they do in all primnoids, many chrysogorgiids have rod-shaped body wall sclerites (which do not occur in primnoids), and the crystal orientation in the chrysogorgiid scales is longitudinal, which produces a circular extinction pattern under polarized light (Figure 3c), whereas the crystal orientation of all primnoids is radial, which leads to a distinctive cruciform extinction pattern. The remaining calcaxonian family, the Isididae, also has many similarities with the Primnoidae, particularly the subfamilies Mopseinae and Circinisidinae, both of which have external squamous protective scales very similar to that of the primnoids. Indeed, it would appear that the two families underwent separate but parallel adaptive radiations, solving all the problems of having external plate-like armor, but often in slightly different ways (Alderslade, 1998). Traditionally, the isidids were differentiated from the other calcaxonians by their jointed axis, their axes composed of rigid, solid calcareous nodes joined together with slightly flexible gorgonin internodes. However, Bayer (1988) described a jointed primnoid, *Mirostenella*, which seemed to bridge the gap between isidids and primnoids or at least to blur the distinction. Bayer (1988) did not make any phylogenetic speculations regarding this anomalous genus, but later, in an unpublished manuscript, he described a second species of *Mirostenella* that did not have a jointed axis, implying that having joints was not even of generic importance. Furthermore, Bayer (1988) pointed out that Kükenthal (1919) hypothesized that the jointed isidid axis may have evolved four times, thus minimizing its potential for phylogenetic signal. Isidids also differ from primnoids in a fundamental way in the structure of their axis (Table 2, character 24), which is composed of radial crystallization, not longitudinal (Bayer, 1955, 1961). Lesser differences between the isidids and primnoids are that the isidids have large tentacular sclerites (Table 2, character 25), sometimes have opercular octants composed of multiple sclerites (Table 2, character 26), and have rooted heads in the coenenchyme (Table 2, character 27). A final major character that had been used to distinguish the Primnoidae from all other genera was the cruciform extinction pattern of its scales in polarized light, which results from radial crystal orientation. However, Alderslade (Northern Territories Museum, Darwin, personal communication, 2007) affirms that genera of the isidid subfamily Circinisidinae also yield a cruciform pattern, which would make them the most similar subfamily to the primnoids and thus a logical choice for an out-group. The Circinisidinae consists of seven genera, all restricted to southern Australia and New Zealand at depths of 12–146 m. Instead of choosing one genus as an out-group, as that genus may have evolved in various ways, the entire subfamily was used as the out-group. Characteristics of all seven genera were coded for the phylogenetic analysis, even though that meant using multiple states for many of the characters. Nonetheless, it is interesting to note that the circinisidinine genus *Plexipomisis* is remarkably similar to the least derived primnoid genus, as determined by Versluys (1906), Kükenthal (1919), and our phylogenetic analysis. Also, Alderslade (pers. comm., 2007), in examining an unidentified *Primnoeides*-like primnoid, stated that "if it had an isidid axis then it would fit perfectly in the Circinisidinae."

It is reassuring to know that of the few molecular studies that have included primnoid genera (Berntson et al., 1999, 2001; McFadden et al., 2006), which were based on18S nuclear and msh1 and ND2 mt markers, the isidids (albeit of the subfamily Keratoisidinae) were always the sister group of the primnoids. Furthermore, the McFadden et al. (2006) analysis showed the Chrysogorgiidae to be sister to the Primnoidae + Isididae, consistent with the morphological analysis presented above. The phylogenetic tree presented by McFadden et al. (2006) also supported the monophyly of the Primnoidae (based on four genera) but showed the suborder Calcaxonia to be paraphyletic with the order Pennatulacea, implying that the calcaxonian family Ellisellidae was the sister group of the pennatulids.

In summary, an assertion of the monophyly of the Primnoidae is based on a combination of morphological characters, i.e., a solid axis having concentric layers of calcified material embedded in gorgonin, calyces and branches heavily armored with imbricating scales, a cruciform extinction pattern of the scales, longitudinal crystallization of the branch axes, lack of tentacular sclerites, polyps often arranged in whorls, and opercular scales often keeled, as well as molecular evidence based on two mitochondrial genes. Although few of the morphological characters are unique to the family, the combination of characters defines the family. As more characters are compared between Isididae and Primnoidae, the gap between these two families seems to decrease, but it would appear

**TABLE 2.** Characters and character states used in the phylogenetic analysis of the primnoid genera; CI = consistency index for each character per the 50% majority rule tree.

| Character | Character state |
|---|---|
| | **Morphology of the Colony** |
| 1. Colony shape | 0, unbranched (flagelliform) (Figure 3h); 1, dichotomous (planar); 2, dichotomous (lyriform); 3, dichotomous (bushy); 4, dichotomous (sparse); 5, sympodial; 6, pinnate (opposite); 7, pinnate (alternate); 8, bottlebrush (CI = 0.368) |
| 2. Shape of base | 0, discoidal or dendritic (attached); 1, funnel shaped (free) (CI = 1) |
| 3. Branch nodes | 0, present; 1, absent (CI = 0.5) |
| | **Morphology of Calyces** |
| 4. Basal fusion of calyces | 0, not fused (Figure 17j); 1, fused (Figure 3i) (CI = 0.33) |
| 5. Coordination of polyps | 0, isolated (irregular, on all sides but without order) (Figure 6g); 1, spirals; 2, biserial (alternate or opposite) (Figure 11k); 3, paired (Figure 17a); 4, in whorls (verticillate) (Figures 9j, 10a); 5, on leaves (Figure 4p) (CI = 0.545) |
| 6. Proximity of calyces to stem | 0, inclined (Figure 5c) to perpendicular (Figure 17a); 1, appressed (Figure 10a, d); 2, adnate (Figure 4b) (CI = 0.222) |
| 7. Orientation of calyces | 0, up (distad) (Figure 15i); 1, perpendicular (Figure 17a); 2, down (proximad) (Figure14g) (CI = 0.333) |
| | **Morphology of Sclerites** |
| | Operculars |
| 8. Operculum | 0, absent (or poorly developed) (Figure 3a); 1, present (Figure 16h) (CI = 1) |
| 9. Distal inner surface of opercular scales | 0, tuberculate (Figure 12g); 1, smooth (Figure 5f); 2, single medial keel (Figure 15g); 3, multiridged (Figure 12g); 4, spinose (Figure 11c) (CI = 0.4) |
| 10. Correspondence of opercular and marginal scales | 0, correspond (Figures 6o, 7i); 1, no correspondence (e.g., may not be same number of marginals and operculars) (Figures 16h, 17i); 2, regular offset (Figure 16a) (CI = 0.67) |
| | Marginals (= Circumoperculars, Buccals) |
| 11. Number of marginals | 0, seven; 1, eight (Figure 6o); 2, more than eight (Figure 3s); 3, six (Figure 13s); 4, five (Figure 18j); 5, four (Figure 16h); 6, two (Figure 14g) (CI = 0.714) |
| 12. Circumoperculum | 0, present (Figure 7i); 1, absent (Figure 18j) (CI = 0.2) |
| 13. Distal margin of marginal scales | 0, rounded (Figure 13m) or straight; 1, pectinate (ctenate) (Figure 11g–h); 2, serrate (Figure 11s); 3, pointed (Figure 5h–i); 4, spinose (Figures 5p, 8k) (CI = 0.2) |
| | Body Wall Sclerites |
| 14. Body wall sclerite imbrication | 0, imbricate (usually thin) (Figures 3e, 4q); 1, mosaic (thick) (Figure 17a) (CI = 1) |
| 15. Body wall sclerite shape | 0, elliptical (Figure 16e), oval (Figure 3e), or rectangular (Figure 18e); 1, triangular (Figure 4m–n); 2, polygonal (figure 17e–f); 3, sickle shaped (Figure 4e); 4, ascus shaped (Figure 8l) (CI = 0.8). |
| 16. Number of longitudinal rows of body wall scales | 0, not arranged in rows as adult; 1, 8 (Figure 3s); 2, 7; 3, 6 (Figure 8b); 4, 5 (Figure 18i); 5, 3; 6, 2 (figure 14g); 7, 1 (CI = 0.7) |
| 17. Coverage of adaxial body wall | 0, naked (Figure 4r) or few vestigial sclerites (Figures. 8b, 13i); 1, narrow bare strip (Figure 6a); 2, completely covered (Figures 3a, 5a) (CI = 0.33) |
| 18. Number of abaxial rows of body wall scales | 0, two rows (Figure 4q); 1, one row (Figure 41a) (CI = 1) |
| 19. Number of scales in each abaxial body wall row or on the abaxial face | 0, variable (usually >5) (Figure 12e); 1, fixed (3 or 4) (Figure 14b); 2, fixed (5) (Figure 13b); 3, fixed (2) (Figure 15a) (CI = 1) |

*continued*

**TABLE 2.** (*Continued*)

| Character | Character state |
|---|---|
| 20. Fusion of body wall sclerites | 0, not fused (Figure 16i); 1, fused ab- and adaxially into continuous rings (Figure 15k–m) (CI = 1) |
| 21. External sculpture of body wall sclerites | 0, smooth (Figure 3f); 1, granular (Figure 18l); 2, longitudinal or radiating ridges (Figure 10b–c); 3, nodular (Figure 11i); 4, spiny (Figure 14f); 5, two types (transverse ridge separating smooth distal portion from tuberculate proximal portion, the ascus scale) (Figure 8l); 6, tuberculate ridges (Figure 12j) (CI = 0.429). |
| 22. Infrabasals | 0, none; 1, one pair (Figure 15i); 2, two or more pairs (Figure 14g) (CI = 1) |
| | COENENCHYMAL SCLERITES |
| 23. Number of coenenchymal layers | 0, two layers (inner layer composed of small tuberculate spheroids that compose the walls of longitudinal stem canals) (Figure 4x–y); 1, one layer of scales (CI = 0.2) |
| | **Characters Used to Distinguish the Out-group** |
| 24. Axis calcification pattern | 0, radial; 1, longitudinal (CI = 1) |
| 25. Large tentacular sclerites | 0, present; 1, absent (CI = 1) |
| 26. Operculum or anthopoma | 0, eight or more scales; 1, only eight scales (CI = 1). |
| 27. Coenenchymal sclerites | 0, scales and rooted heads; 1, scales and tuberculate spheroids (CI = 1) |

that the genera of the subfamily Circinisidinae are morphologically closest to the primnoids, and the isidid family to which it belongs is customarily considered to be the sister group to the Primnoidae.

### *Analysis of Primnoid Genera and the Characters Used*

Phylogenetic trees were generated using the principle of parsimony implemented in PAUP* (Beta version 4b10; Swofford, 1998). Characters were coded as binary variables or as multistate characters as discussed below (Table 2). All multistate characters were treated as unordered. If a genus contained species with two states of a character, the state of the type species was used in the analysis, but either the data matrix (Table 3) was footnoted to indicate the other state(s), or the other states are listed in the generic diagnoses. In the rare case (i.e., character 21 of *Ainigmaptilon* and many characters of the out-group) when the type species was polymorphic for a character, both states were included in the data matrix. A question mark was used in only two instances (character 2 of *Australogorgia* and character 7 of *Paranarella*) to indicate that the character state was unknown; dashes were used to indicate that a character was inapplicable to that taxon. A heuristic search was carried out using 117 random addition sequences followed by branch swapping using the tree bisection-reconnection algorithm. Characters were optimized using the Acctran algorithm. The 50% majority rule tree is shown in Figures 1 and 2), the former showing the percentage of most parsimonious trees containing each node as well as bootstrap support. Bootstrap indices were calculated from 2000 modified replicate searches. The phylogenetic and character analyses were based on the 50% majority rule tree (Figures 1, 2). For each bootstrap replicate, 10 heuristic searches were conducted, with a maximum of 1000 most parsimonious trees held for each. This approach served to accelerate the bootstrap analysis, which took nearly three days to complete. Twenty-seven characters, consisting of 94 character states, were employed in the analysis. The characters used in the analysis include all those that have traditionally been used to define and distinguish genera (see above) as well as some characters not used before (e.g., characters 7, 13, 23), realizing that some of these characters may occur in two states in a single genus. The following characters were used in the analysis (Table 2), with specific character states noted in the discussion of each character.

1. COLONY SHAPE. Primnoids may occur in eight types of branching patterns, which lead to eight colony shapes (Table 2); a ninth pattern (sympodial, state 5) was included to fully score the out-group. Kükenthal (1919:312–314) did not consider this character to be significant at the generic level, and it is true that many genera have more than one colony shape (Table 3). However, colony shape is one of the most easily distinguished characters of a specimen and is thus often used in the key to

**TABLE 3.** Character matrix used in phylogenetic analysis, as defined by Table 2. A question mark indicates the state was unknown; a dash indicates the character was inapplicable. If more than one state is present in the genus, state of the type species is given, and that character is footnoted.</tab title>

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Taxon** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** | **27** |
| Circinisidinae (outgroup) | 0–5 | 0 | 0 | 0 | 0,2 | 0–2 | 0,1 | 0,1 | 0 | 0,1 | 0–2 | 0,1 | 0,2 | 0 | 0 | 0,2 | 0–2 | 0 | 0 | 0 | 0–2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Primnoeides* | 6 | 0 | 1 | 0 | 4 | 0 | 0 | 0[a] | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0[b] | 2 | – | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Ophidiogorgia* | 0 | 0 | 1 | 1 | 4 | 1 | 0 | 0 | – | – | 2 | 1 | 0 | 0 | 0 | 0 | 1 | – | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Aglaoprimnoa* | 4 | 0 | 1 | 0 | 4 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0[b] | 2 | – | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Armadillogorgia* | 4 | 0 | 1 | 0 | 4 | 2 | 0 | 0 | – | – | – | – | – | 0 | 3 | 0[c] | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Ainigmaptilon* | 0 | 1 | 1 | 0 | 5 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0[d] | 2 | – | 0 | 0 | 0,4 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Primnoella* | 0[e] | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Convexella* | 0[e] | 0 | 1 | 0 | 4 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Dicholaphis* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Callozostron* | 0[e] | 0 | 1 | 1 | 4 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Arntzia* | 0 | 0 | 1 | 1 | 4 | 0 | 1 | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Thouarella (Thouarella)* | 8[e] | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3[f] | 0 | 1[g] | 0 | 4 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *T. (Euthouarella)* | 7[e] | 0 | 1 | 0 | 4 | 0 | 0 | 1 | 2 | 0 | 1[g] | 0 | 4 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *T. (Diplocalyptra)* | 1[e] | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 2 | 0 | 1[g] | 0 | 4 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *T. (Epithouarella)* | 8 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1[g] | 0 | 3 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Metafannyella* | 1 | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 4 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Fannyella (Fannyella)* | 2 | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 3 | 0 | 4 | 3 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 1 | 1 |
| *F. (Scyphogorgia)* | 8 | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 4 | 0 | 4 | 1 | 2 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 1 | 1 |
| *F. (Cyathogorgia)* | 1[e] | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 4 | 0 | 4 | 1 | 2 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Onogorgia* | 0 | 0 | 1 | 1 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 3 | 0 | 4 | 1 | 2 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Pyrogorgia* | 2 | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Amphilaphis* | 7 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 3 | 0 | 1[g] | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Mirostenella* | 1[e] | 0 | 0 | 0 | 4 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 4 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Acanthoprimnoa* | 7[e] | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 4 | 0 | 1 | 1 | 4[h] | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Plumarella* | 7 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Callogorgia* | 7[e] | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Fanellia* | 1[e] | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 1 | 1 | 1 |
| *Paranarella* | 1 | 0 | 1 | 0 | 4 | 1 | ? | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 6[i] | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Primnoa* | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Australogorgia* | 1 | ? | 1 | 0 | 6 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Narella* | 1[e] | 0 | 1 | 0 | 4 | 1 | 2 | 1 | 2 | 1 | 5[i] | 1 | 0 | 0 | 0 | 6[i] | 0 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Arthrogorgia* | 7[e] | 0 | 1 | 0 | 4 | 1 | 2 | 1 | 2 | 1 | 6 | 1 | 4 | 0 | 0 | 6 | 0 | 0 | 3 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 |
| *Paracalyptrophora* | 1 | 0 | 1 | 0 | 4 | 1 | 2 | 1 | 2 | 1 | 6 | 1 | 4 | 0 | 0 | 6 | 0[k] | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Calyptrophora* | 1[e] | 0 | 1 | 0 | 4 | 1 | 0[l] | 1 | 2 | 1 | 6 | 1 | 4 | 0 | 0 | 6[m] | 0 | 0[m] | 3 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Tokoprymno* | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Parastenella* | 1 | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 4[n] | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |

*continued*

**TABLE 3.** (*Continued*)

| | Characters | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Taxon** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** | **27** |
| *Candidella* | 1[e] | 0 | 1 | 0 | 4 | 0 | 1 | 1 | 2 | 1 | 5 | 1 | 0 | 0 | 0 | 0 | 2 | – | – | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Microprimnoa* | 4 | 0 | 1 | 0 | 3 | 0 | 1 | 1[o] | 1 | 1 | 5 | 1 | 0 | 1 | 2 | 0 | 2 | – | – | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Pterostenella* | 7 | 0 | 1 | 0 | 4 | 0 | 0 | 1 | 2 | 1 | 4 | 1 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Perissogorgia* | 0[e] | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 2 | 1 | 4 | 1 | 2 | 0 | 0 | 7 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Dasystenella* | 8 | 0 | 1 | 0 | 4 | 0 | 0 | 1 | 2 | 1 | 4 | 1 | 4 | 0 | 0 | 4 | 2 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| *Pseudoplumarella* | 7 | 0 | 1 | 0 | 2 | 2 | 0 | 1 | 2[p] | 1 | 4 | 1 | 0 | 0 | 0 | 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |

[a] Operculum present but rudimentary.

[b] Early in ontogeny, body wall scales arranged in eight rows (state 1), but in adult the row structure is lost (state 0).

[c] Body wall scales in rows on abaxial side but not adaxial side of calyx.

[d] Body wall scales not in rows on type species (state 0) but arranged in eight rows in other species (state 1).

[e] Colony shape of types species indicated, but other shapes may be present in other nontype species (see text).

[f] Opercular keel not present in *T. diadema* (state 1); otherwise, having a foliate keel (state 2).

[g] The eight marginals are arranged in two crowns.

[h] *A. pectinata* has a pectinate tip (state 1).

[i] Vestigial adaxial "rows" not counted.

[j] Adaxial buccals counted.

[k] The type species has a pair of adaxial buccals and thus does not have a naked adaxial side.

[l] The type species and most species have state 0 but two species have state 2.

[m] Two body wall rows present but inseparably fused.

[n] Distal tip both spinose and fluted.

[o] Only five or six of the opercular scales visible when operculum closed.

[p] Opercular locking mechanism unique.

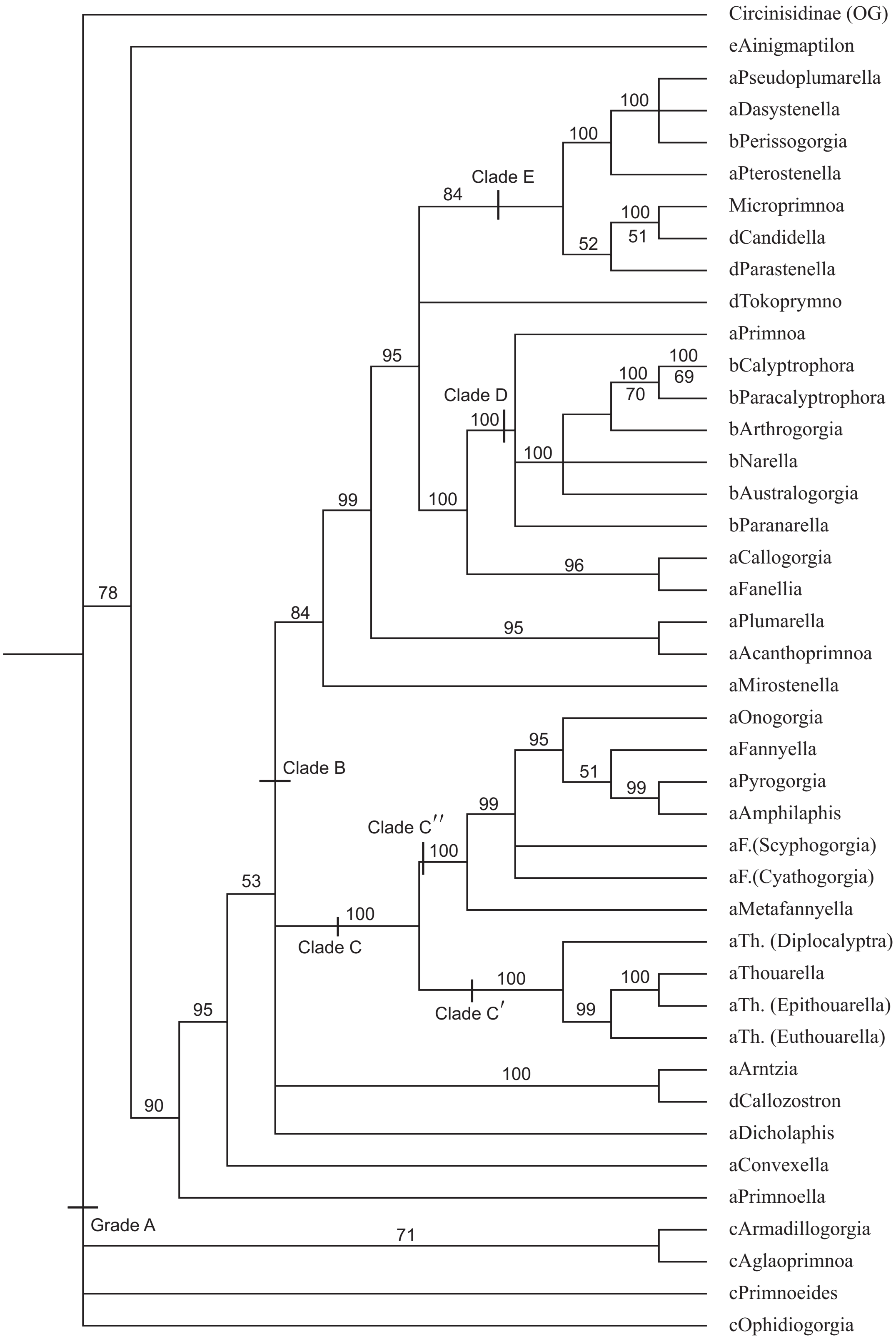

**FIGURE 1.** Fifty percent majority rule cladogram of the primnoid genera, showing clades discussed in text. Percentage of the most parsimonious trees that contain that node is listed above the line, and bootstrap values are below the line. Genera are prefaced with a letter referring to the traditional subfamilial groupings: a, Primnoinae; b, Calyptrophorinae; c, Primnoeidinae; d, Callozostrinae; and e, Ainigmaptilinae. *Microprimnoa* had never been assigned to a subfamily.

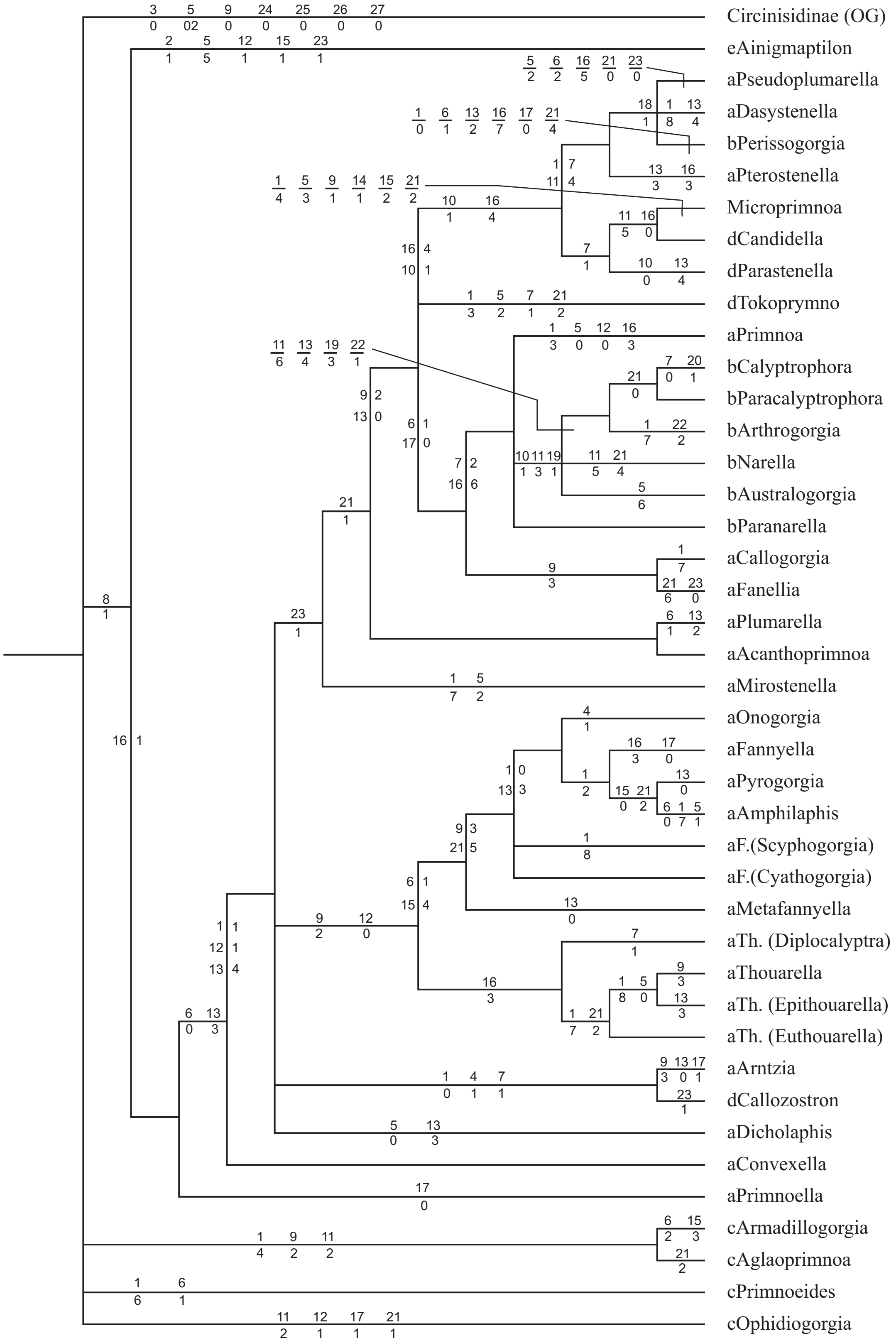

**FIGURE 2.** Fifty percent majority rule cladogram showing all character state changes (see Tables 2 and 3). Character numbers are above (or to the left of) lines, and character state are below (or to the right of) lines.

the genera, even though some genera must be keyed twice to accommodate multiple branching patterns, resulting in different colony shapes. Furthermore, branching pattern is often consistent at the generic level; thus, it was included if only to investigate the distribution of the states on the phylogenetic tree. The out-group has genera with six of the nine growth forms, the only forms not included being pinnate (states 6, 7) and bottlebrush (state 8). Versluys (1906) considered the alternate pinnate (state 7) colony to be the primitive state, but Kükenthal (1919) doubted that supposition, noting that it was a very rare form among primnoids, but did not offer an alternative ancestral form.

2. Shape of Base. The base of all primnoid genera but *Ainigmaptilon*, as well as the base of the out-group taxon, is firmly attached through a discoidal encrustation or dendritic rootlets (state 0), the base of *Ainigmaptilon* being funnel shaped (state 1), adapted to enclose soft mud, like a pennatulacean. This autapomorphic character state (funnel shaped) was included only to indicate the derived position of *Ainigmaptilon* with respect to the out-group.

3. Branch Nodes. The calcified axis of all primnoid genera is continuous, except for the axes of *Mirostenella* and all taxa within the out-group, in which the calcified axis is interrupted by organic nodes at points of bifurcation. The presence of nodes (state 0) in *Mirostenella* was once considered as a possible transition between isidids and primnoids (Bayer, 1988), which is discussed above. This autapomorphic character was included in the analysis to allow for potential affinity with the out-group taxon.

4. Basal Fusion of Calyces. In four primnoid genera the bases of the calyces within each whorl are intimately joined or fused together (state 1), sometimes forming a common atrium for eggs. At first this was scored as one of several character states of character 5 (coordination of polyps), as it could be envisioned as a transition from a whorled arrangement to the leaf arrangement of character 5, but a more conservative scoring would separate this character. None of the out-group genera are arranged in whorls and thus none can be fused.

5. Coordination of Polyps. The polyps/calyces of primnoids may be arranged in six different configurations (Table 2), ranging from irregular (state 0) to whorls (state 4) and even concentrated on specialized leaf-like structures (state 5) as in the pennatulaceans. Although Kükenthal (1919) used this character for species-level discrimination and even "species group" discrimination, he did not believe that it was useful for higher-level classification because of variation within genera. However, we have found this character to be very useful in the key as well as phylogenetic analysis, perhaps because many of the genera that previously contained dual-character states have been split into smaller genera for which the states are uniform. The condition of the out-group is isolated (state 0) or biserial (state 2), implying that the more complex states of paired (state 3), whorled (state 4), and in leaves (state 5) are derived (but see Results). Versluys (1906) considered the whorled state to be primitive, the whorls having only two to four calyces; however, Kükenthal (1919) strongly implied the presence of whorls was an advanced state associated with unbranched colonies.

6. Proximity of Calyces to Stem. The calyces of some primnoid genera stand perpendicular to the branch or are only slightly inclined (state 0) distally or (more rarely) proximally. Such calyces are usually cylindrical and have a uniform number of body wall scale rows on all sides of the calyx. In other genera, the calyces bend close to the branch, such that their adaxial side is almost touching the branch coenenchyme; these calyces are said to be appressed (state 1). In appressed calyces the adaxial body wall row of scales are sometimes reduced in size or not present at all, an adaptation to the smaller surface area presented by the bent calyx and the apparent lack of the need of protective scales for a body region that is appressed to the branch. In the third possibility (adnate, state 2), the calyces are so strongly wedded to the branch coenenchyme that essentially, there is no adaxial side to the calyx and thus no adaxial scales either. Kükenthal (1919) considered this character to have great classificatory significance and used it as a basis for subfamilial classification. Genera in the out-group have all three variations.

7. Orientation of Calyces. As mentioned for character 6, if the calyces are inclined, appressed, or adnate, there is the possibility that the calyces are directed up (state 0; distad) or down (state 2; proximad). Perpendicular (state 1) orientation is also a possibility. The calyces of the out-group genera are oriented up or perpendicular, never downward.

8. Operculum. In most primnoid genera each of the distalmost eight scales of every calyx is highly modified into an isosceles triangle shape, which, when the calyx is closed, forms a tight-fitting, impervious, conical operculum that covers the aboral tentacular region of the polyp (state 1). The opercular scales are usually larger than the adjacent marginals and differently shaped, easily distinguished from all other sclerites of the calyx. The opercular scales usually decrease in size from the ab- to the adaxial position. However, in some genera the distalmost sclerites are similar to the marginals in shape and size, and

although they may fold over the polyp, they are not differentiated as distinctive opercular scales, nor do they form a distinctive operculum (state 0). The presence or absence of an operculum is one of the characters that most have used to help distinguish subfamilies. The out-group may have both states. Versluys (1906) considered the lack of an operculum in *Primnoeides* to be primitive, whereas Kükenthal (1919) disagreed, considering that genus to simply have a rudimentary operculum.

9. Distal Inner Surface of Opercular Scales. The inner basal region of all opercular scales bears numerous small complex tubercles, as is the case of the inner side of most primnoid scales. The tubercles probably function as anchors, securing the sclerite in the underlying mesogloea. However, the inner distal half of opercular scales is often longitudinally convex as well as bearing a prominent keel (state 2) or ridge along that convexity. The musculature required for closing the opercular apparatus attaches to this keel or ridge, the extent and height of the keel presumably reflecting the strength of the attached musculature. When the operculum closes over the polyp, these keels also tend to come together, guiding the operculars into place. Other forms of internal sculpture include multiple ridges (state 3), a uniformly spinose (state 4) surface, or a smooth (state 1) surface. The out-group is unique in having tubercles (state 0) on both proximal and distal ends.

10. Correspondence of Opercular and Marginal Scales. In all primnoid and isidid genera that have opercula, the operculum consists of eight scales or, in the case of some isidids, seven or eight anthopoma octant regions (Alderslade, 1998). In most cases these eight scales are directly aligned (correspond, state 0) with eight subadjacent marginal scales; however, in those genera with fewer than eight marginal scales there cannot be a 1:1 correspondence (state 1). Furthermore, in one genus (*Parastenella*), the marginal scales are offset (state 2) from the operculars, each overlapping half of two adjacent opercular scales. The out-group has two of these states, lacking the offset state.

11. Number of Marginals. As mentioned for character 10, many primnoid genera have eight marginal scales (state 1), which is probably the ancestral state of this character. However, some genera have more or less than eight marginals, and a group of genera (Figure 1: clade D) is characterized by having only two marginal scales (state 6), which, in this case, are termed the buccal scales. Marginal scales are also sometimes called circumopercular scales (see character 12). The out-group genera may have more than eight (state 2), eight (state 1), or seven (state 0) marginals, the latter state being unique to the out-group.

12. Circumoperculum. In some primnoid genera the marginal scales are capable of folding over the opercular scales, or at least over the bases of the opercular scales, providing additional protection for the vulnerable distal end of the polyp. This infolding, of usually eight marginals, was termed the circumoperculum (state 0) by Kükenthal (1919:329). This character is used as a higher-level discriminating character in the key to the genera in this report. In other genera, the marginal scales do not fold over the operculum (state 1). The out-group taxa have both states. Versluys (1906) considered the circumoperculum to be primitive, whereas Kükenthal (1919) considered it to be advanced.

13. Distal Margin of Marginal Scales. The distal margin of the marginal scales has a variety of shapes (Table 2), ranging from straight (state 0) to prominently spinose (state 4); these shapes are usually consistent at the genus level. The architecture of this region probably has some relation to the amount of protection afforded to the polyp within the calyx, as does the circumoperculum. The genera in the out-group taxa have only two of these states: straight (state 0) and serrate (state 2).

14. Body Wall Sclerite Imbrication. In the out-group and all primnoid genera but *Microprimnoa* the body wall scales are relatively thin and arranged in an imbricate (state 0) fashion, the free end being distal. However, in *Microprimnoa* the body wall scales are extremely thick and placed in a mosaic (state 1) arrangement (not imbricate). This autapomorphic character state (mosaic) was included only to indicate the derived position of *Microprimnoa* with respect to the out-group.

15. Body Wall Sclerite Shape. Most primnoid genera and the out-group have body wall scales that are elliptical, oval, or somewhat rectangular in shape, which are all considered to be the same state, called elliptical (state 0); however, several genera have uniquely shaped body wall scales (Table 2). Except for the ascus-shaped scales (state 4) of *Fannyella* and related genera (Figure 1: clade C″), the shape of the body wall scales is autapomorphic and does not contribute to phylogenetic structure. In general, Kükenthal (1919) suggested that body wall sclerite shape, number, and arrangement are important at the species and generic levels; these attributes have been divided into characters 15–19 in our analysis.

16. Number of Longitudinal Rows of Body Wall Scales. Many primnoid genera have eight longitudinal rows of body wall scales (state 1), but in genera in which the calyces become appressed or ad-

nate to the branches, there is a tendency to have fewer and/or smaller scales on the adaxial side of the polyp (e.g., *Thouarella*) or to completely eliminate the adaxial rows (e.g., *Narella*), resulting in six rows (state 3) or less. In the latter case, there results a partially unprotected adaxial region (see character 17). Some genera (e.g., Figure 1, clade D) have an even farther reduction to a small, fixed number (two to five) of scales in only two rows (state 6), and the calyces of one genus (*Perissogorgia*) are reduced to only one row of scales (state 7). On the other hand, in some genera the scales are not arranged in rows but are small and appear to occur randomly (state 0). In the case of *Aglaoprimnoa* and *Primnoeides*, however, this random stage ontogenetically proceeds through a stage having eight longitudinal rows, which is probably the ancestral state for the primnoids. A similar reduction in number of longitudinal rows in response to polyp bending is documented for the out-group isidids (Alderslade, 1998). The number of longitudinal rows of scales was considered to be of great classificatory value by Kükenthal (1919) and has been used by most authors to help distinguish subfamilies and define the genera. Unfortunately, it is one of the characters that is hardest to observe, in that a calyx must be carefully dissected from the branch in order to examine the adaxial side and then the longitudinal rows must be carefully analyzed. Stereo SEM views are of great help. Versluys (1906) considers the lack of row structure (state 0) to be primitive, whereas Kükenthal (1919) considered eight body wall rows (state 1) to be the primitive state, the unordered state proceeding from the octameral one, and he viewed the fewer number of rows as a reduction from eight.

17. COVERAGE OF ADAXIAL BODY WALL. As mentioned above (characters 6 and 16), when the calyx is appressed or adnate to the branch, the adaxial body wall is reduced in surface area and may not need a covering of sclerites because of its proximity to the branch, which would also allow greater flexibility for bending. If the calyx is not completely covered (state 2) with scales, it may be completely bare (state 0) or be covered with a random covering of very small scales or, in two cases, reveal a narrow bare strip (state 1). All of these adaptations are present in the out-group. Kükenthal (1919) considered the modification of the adaxial face by lacking scales or having modified scales to be a derived state.

18. NUMBER OF ABAXIAL ROWS OF BODY WALL SCALES. In most primnoid genera there are two (state 0) abaxial rows of body wall scales, which are relatively easily visible in abaxial view of a calyx in situ. In several genera, the abaxial rows are reduced to one (state 1), and in those genera without row structure, this state is entered with a dash. Most genera in the out-group do not have scales arranged in rows, but when they are, there are two abaxial rows.

19. NUMBER OF SCALES IN EACH ABAXIAL BODY WALL ROW OR ON THE ABAXIAL FACE. Most primnoid genera, as well as the out-group genera, have a variable (state 0) number of scales in each abaxial body wall row: usually over 5 and up to 70. Included in this tabulation are genera that may not have their scales ordered in rows but nonetheless have over five tiers of scales on the abaxial face of the calyx. In three genera (Table 3) there is a fixed number of two (state 3) scales in each abaxial row, in one genus (*Narella*) there are three or four scales per row (usually 3, state 1), and in one genus (*Paranarella*) there are five scales per row (state 2).

20. FUSION OF BODY WALL SCLERITES. In the out-group and all primnoid genera except for *Calyptrophora,* all body wall scales are independent of one another (state 0), but in *Calyptrophora* both pairs of body wall scales (buccal and basal) are inseparably fused on both the ab- and adaxial sides of the calyx, forming two ring-shaped structures that do not disarticulate after bleaching. The sclerites of the genus have been prosaically described by Deichmann (1936:172) as "joined angularly to each other like the elbows of a stove pipe downward bent." This autapomorphic character state (fused, state 1) was included only to indicate the derived position of *Calyptrophora* with respect to the out-group.

21. EXTERNAL SCULPTURE OF BODY WALL SCLERITES. The outer surface of the body wall scales are either smooth (state 0) or sculptured in various ways (Table 2), this character usually being consistent within a genus. If granular (state 1) or ridged (state 2), the granules and ridges appear to radiate from a central nucleus located near the center of the scale. The out-group taxa have three of the seven known ornamentations.

22. INFRABASALS. Some primnoid genera have a pair (state 1) of distinctive crescent-shaped sclerites at the base of the calyx that appear to help anchor the calyx to the coenenchymal sclerites. These sclerites are called infrabasals. In one genus (*Arthrogorgia*) there are multiple pairs (state 2) of these scales, but in most genera as well as the out-group, they do not occur at all (state 0).

23. NUMBER OF COENENCHYMAL LAYERS. Many primnoid genera have only one layer of coenenchymal sclerites (state 1), the combined layer of sclerites and underlying tissue being quite thin. In other genera there is a second underlying component of sclerites (state 0) consisting of longitudinal tracks of small irregularly shaped

tuberculate spheroids, which separate the stem canals that run along the branch axis (Bayer, 1980). The out-group also appears to have this secondary layer. The shape and size of the outer coenenchymal scales, while useful at species differentiation, were found to be too variable to be used as a genus-level character; however, a different type is found in the out-group (see character 29). Both Versluys (1906) and Kükenthal (1919) considered the two-layer coenenchyme to be ancestral.

24. AXIS CALCIFICATION PATTERN. As Bayer (1955) described and illustrated, a cross section of the axis of a primnoid reveals a concentric pattern of calcification resulting from longitudinal crystallization (state 1), whereas an axial cross section of an isidid reveals a radial pattern, with wedge-shaped sectors of crystals radiating outward from the center of the branch (state 0).

25. LARGE TENTACULAR SCLERITES. The genera of the out-group all have large crescent-shaped tentacular sclerites (state 0) that give rigidity and protection to the tentacles (Alderslade, 1998), whereas there are no large sclerites in the tentacles of primnoids (state 1).

26. OPERCULUM OR ANTHOPOMA. When primnoid genera have an operculum, it is composed of eight discrete opercular scales (state 1). However, in the out-group, each homologous region corresponding to an opercular scale of the operculum, called an octant of the anthopoma (Alderslade, 1998), may be composed of one or a series of smaller crescent- to club-shaped sclerites (state 0).

27. COENENCHYMAL SCLERITES. The coenenchymal sclerites of the primnoids consist of thin scales or thick plates (*Microprimnoa*) or, sometimes, an inner layer of tuberculate spheroids (state 1). It is common in the out-group to also have rooted heads as a component (state 0).

Few phylogenetic analyses of octocorallian taxa have been performed on the basis of morphological characters. Those that we know of include Williams (1993, 1995, 1997) on various pennatulacean genera and Sánchez (2005) on the species of the Pargorgiidae.

## RESULTS AND DISCUSSION OF CHARACTER EVOLUTION AND THE EVOLUTIONARY TREE

### TREE ANALYSIS

The unweighted analysis of the data matrix (Table 3) yielded 137,408 equally most parsimonious trees, and, not unexpectedly, the strict consensus tree of those trees shows little resolution. Thus, for the purposes of establishing working relationships among taxa and subsequent hypotheses of character evolution, a 50% majority rule consensus tree was used (Figures 1, 2). This tree has a length of 144 steps, CI = 0.472, and RI = 0.642. Figure 1 also shows bootstrap support for several branches, based on 2000 replicates, and indicates some of the clades referred to in the text. Figure 2 indicates all of the inferred character state changes. Both Figures 1 and 2 are used as the basis for the following discussion of phylogeny and character analysis with the caveat that the character state transformations are not necessarily optimal since the analysis is based on only a subset of the data, i.e., the 50% majority rule tree.

The 50% majority rule consensus tree does not lend strong support to the five traditionally established subfamilies, either the classification of Wright and Studer (1889) as amended by Kükenthal (1919) and Bayer (1956) or the alternate classification of Versluys (1906), but it does show deep structure and groups some genera in clades that are close to the composition of some of the subfamilies as well as showing evidence of other potential classificatory groupings. For instance, the four genera of the subfamily Primnoeidinae, including that genus Versluys (1906) and Kükenthal (1919) thought to be the most plesiomorphic, *Primnoeides,* group together (Figure 1: grade A, four genera prefaced with the letter c) in a basal polychotomy with the out-group. They share the characteristics of having a poor or absent operculum and body wall scales not arranged in rows. *Primnoeides* shows the shortest patristic distance from the out-group (nine steps), justifying Versluys' use of that genus as the most primitive primnoid. It is interesting to note that the genus having the second shortest patristic distance to the out-group (10 steps), *Primnoella* was the second genus derived by Versluys (1906:155), although there is little resemblance of our tree to the rest of his evolutionary hypothesis. This clade and the earliest diverging genus among the rest of the primnoids, *Ainigmaptilon*, are all restricted to the Antarctic, suggesting that the origin of the Primnoidae may have been from that region.

*Ainigmaptilon*, constituting the subfamily Ainigmaptilinae, is indicated to be derived just after the basal polychotomy but is also in a very isolated position, probably justifying a separate subfamilial placement. Unique features of that family are its discoidal base and placement of calyces on polyp leaves.

The Callozostrinae (Figure 1: four genera prefaced with the letter d), which had been grouped on the basis that its calyces are oriented perpendicular to the branch axis, does not form a natural grouping; thus, contrary to

Kükenthal's (1919) suggestion that it be used as the basis for subfamilial differentiation, this character appears to have little taxonomic weight and no classification value.

The Calyptrophorinae (Figure 1: clade D, six genera prefaced with the letter b and one prefaced with the letter a) form a cohesive unit defined by having calyces that point downward and having only two rows of body wall scales. *Primnoa* is indicated to be a part of this clade, which is consistent with its close morphological affinity, some species of *Primnoa* having a "*Narella*"-type polyp (Cairns and Bayer, 2005). The placement of *Perissogorgia* in the adjacent clade E may well be correct.

The remaining subfamily, Primnoinae (24 genera prefaced with letter the letter a), is a highly polyphyletic and unnatural grouping, but nonetheless, several clades appear to have cohesion among these genera. These genera are roughly divided in half depending on whether the coenenchyme occurs in two layers (clade C) or in one layer (clade B). Within clade C, clade C′ contains *Thouarella* and its subgenera, characterized by having only six rows of body wall scales, and clade C″ contains *Fannyella* and its subgenera and associated genera, characterized by having the ascus-type body wall scale. Most of the genera in clade C occur in the Antarctic, especially those in clade C″, whereas some genera in clade C′ also occur in the Atlantic and Pacific. Clade B, on the other hand, contains few genera that occur in the Antarctic, most being found in the Atlantic and Indo-Pacific, two genera (*Parastenella* and *Narella*) being cosmopolitan. Clade B contains clade D (see above) and also clade E, consisting of seven genera characterized by the lack of a correspondence between marginal and opercular scales. Within this group is *Microprimnoa*, the only genus that previously could not be placed in a subfamily.

Although some subfamilies and grouping are defined by the consensus tree, we do not recommend basing a classification on it, as there is still much work needed on character analysis and interpretation, not to mention corroboration by molecular methods. For now, we recommend not using subfamilial divisions since the traditional groupings are not supported by our phylogenetic hypothesis and our hypothesis does not produce compelling evidence for homogeneously monophyletic clades.

## CHARACTER ANALYSIS

CHARACTER 1 (COLONY SHAPE). As Kükenthal (1919) suggested, colony shape and branching pattern are highly variable, sometimes even within a genus (Table 3), and may not be of much use for determining phylogeny, its CI being only 0.368. The tree shows that the ancestral state (unbranched, state 0) may evolve into four other states including various dichotomous states (states 1, 2, and 4) and opposite pinnate (state 6), whereas the planar dichotomous state (state 1) may evolve into an equal number of variations, including alternate pinnate (state 7) and other dichotomous forms (states 3 and 4). The most common transition in this character is planar dichotomous to alternate pinnate, which occurs five times on the tree. The bottlebrush state (8) is derived three times: twice from alternate pinnate and once from planar dichotomous. Transitions in colony shape occur most commonly on stems leading to terminal taxa.

CHARACTER 3 (BRANCH NODES). The tree implies that, notwithstanding the out-group having nodes, the ancestral state for the primnoids was lacking nodes (state 1), the single primnoid genus having nodes (state 0) being deeply buried in the tree without close affinity to the out-group.

CHARACTER 4 (BASAL FUSION OF CALYCES). Basal fusion gives little structure to the tree except to help unite *Arntzia* and *Callozostron*.

CHARACTER 5 (COORDINATION OF POLYPS). The tree implies that, notwithstanding the out-group having isolated and biserially arranged polyps, the ancestral state for the primnoids was in whorls (state 4), as Versluys (1906) suggested. The most parsimonious interpretation of the majority rule tree is that the whorled state gave rise to every other state, the biserial and isolated states, three times each. For the most part, this character does not give much structure to the tree, occurring mainly on stems leading to terminal taxa.

CHARACTER 6 (PROXIMITY OF CALYCES TO STEM). The tree implies that state 1 (appressed) is ancestral in the primnoids. Although this character has a very low CI (0.222), showing many transitions between states 0 (inclined) and state 1, some of the changes help to support cladistic structure within clade B.

CHARACTER 7 (ORIENTATION OF CALYCES). This character is labile on the tree, with the upward directed calyces (state 0, ancestral) changing to perpendicular (state 1) four times, but the transition from upward (state 0) to downward (state 2) occurs only once and helps to define clade D.

CHARACTER 8 (OPERCULUM). The presence of an operculum (state 1) serves as the unique synapomorphy that separates most of the primnoid genera from the four least derived genera (clade A), all of which branch in a basal polytomy along with the out-group. The cladogram thus suggests that the operculum is a character that was derived early in primnoid evolution and was never lost once evolved, having a robust CI of 1. Thus, Versluys (1906) was likely correct to have suggested that the lack of an operculum was a primitive state.

CHARACTER 9 (DISTAL INNER SURFACE OF OPERCULAR SCALES). The tree implies that, notwithstanding the out-group having a tuberculate inner surface (state 0), the ancestral state for the primnoids was smooth (state 1); however, fairly early in the diversification of the family, the smooth state changed to keeled (state 2), and the keels then transformed to multiple ridges (state 3), both of these transitions happening three convergent times. The keeled and spinose nature of the opercular scales helps to define clade C.

CHARACTER 10 (CORRESPONDENCE OF OPERCULAR AND MARGINAL SCALES). The cladistic hypothesis suggests that correspondence of operculars and marginals (state 0) was the ancestral state, a state that twice lost this correspondence (state 1), and one taxon (*Parastenella*) evolved an offset arrangement (state 2) from the random state (state 1). The character has a fairly high CI of 0.667 and helps to define clade E.

CHARACTER 11 (NUMBER OF MARGINALS). The tree suggests that the ancestral number of primnoid marginals was eight (state 1), from which independent increases (state 2, occurring in the least derived genera) and decreases of scales (states 3, 4, and 5) occurred. Furthermore, it suggests that the reduction to four (state 5) and two (state 6) marginal scales proceeded through a stage having six marginals (state 3). The CI for this character is fairly high (0.714) and can be used to help justify groupings within clades E and D.

CHARACTER 12 (CIRCUMOPERCULUM). The ancestral state is implied to be the presence of a circumoperculum (state 0), but this state is independently lost (state 1) three times and purportedly regained twice, contributing to a very low CI (0.200). Nonetheless, the presence of a circumoperculum helps to justify clade C, and its absence helps to differentiate *Ainigmaptilon*.

CHARACTER 13 (DISTAL MARGIN OF MARGINAL SCALES). Although the ancestral state is considered to be rounded (state 0), the distribution of the other states are quite labile/homoplastic, resulting in a low CI (0.2). In general, this character was of limited value in the analysis.

CHARACTER 15 (BODY WALL SCLERITE SHAPE). Although the CI is high (0.8), most of the character states (states 1, 2, and 3) are autapomorphic, so that the only real structure provided by this character is uniting the genera that had been split (clade C″) from *Fannyella*, i.e., those having an ascus-type body wall scale (state 4). Kükenthal's (1919) suggestion that number of body wall scale rows and scale shape and arrangement are important at the genus level is thus only partly accurate, with characters 15 and 17 being poorly supported but characters 16, 18, and 19 being useful in providing structure.

CHARACTER 16 (NUMBER OF LONGITUDINAL ROWS OF BODY WALL SCALES). The ancestral state is inferred to be that the body wall scales are not arranged in longitudinal rows (state 0), a condition shared with the primitive genera that stem from the basal polytomy, as Versluys (1906) suggested. Early in evolution, eight rows (state 1) becomes the standard, which then goes through a series of reductions from eight to five (state 4) or two (state 6) and then from five to one (state 7), two (state 6), three (state 5), or six (state 3) and from two (state 6) to six (state 3). The CI is relatively high (0.7), showing just one reversal and one convergence. This character is useful in distinguishing several clades, such as clades C′, D, and E, as well as *Ainigmaptilon*.

CHARACTER 17 (COVERAGE OF ADAXIAL BODY WALL). The ancestral primnoid state is inferred to be completely covered (state 2), this state changing to naked (state 0) four times and to a bare strip (state 1) twice. The only topological structure provided for the tree is to reinforce monophyletic support for an unnamed clade consisting of clade D (= Calyptrophorinae) and three other taxa. Otherwise, the character state changes lead to terminal taxa and are spread throughout the tree.

CHARACTER 18 (NUMBER OF ABAXIAL ROWS OF BODY WALL SCALES). The presumed ancestral state is to have two abaxial body wall rows of sclerites (state 0), this state changing only once to code for the three genera having only one abaxial row (state 1); thus, it helps to distinguish genera in clade E. Its CI is 1.

CHARACTER 19 (NUMBER OF BODY WALL SCALES ON ABAXIAL FACE). Most primnoid genera have a variable number of scales (usually over five) in their abaxial rows, which is inferred from the cladogram to be the ancestral state (state 0). Within clade D (Calyptrophorinae) there is a gradual reduction from a high variable number to a low fixed number of three or four (state 1) and then to only two (state 3), and there is an independent reduction for *Parastenella* to a fixed number of five (state 2). The CI for this character is 1.

CHARACTER 21 (EXTERNAL SCULPTURE OF BODY WALL SCLERITES). The ancestral state is presumed to be smooth (state 0), a state shared with the out-group and many of the lesser derived genera. The smooth state transforms to granular (state 1) from which the spiny (state 4), nodular (state 3), ridged (state 2), and tuberculate ridge (state 6) states evolved; however, there is rampant homoplasy among these character states, resulting in a low CI (0.429). Nonetheless, at least one of the transitions to the ascus scale morphology helps to define clade C″, the *Fannyella*-type genera.

CHARACTER 22 (INFRABASALS). The state of the out-group and most primnoid taxa, including the ancestral state, is to lack infrabasal scales (state 0). But within clade D (Calyptrophorinae) there is a progression from none (state 0) to one pair (state 1) to more than one pair (state 2), which gives some resolution within this clade. The CI is 1 for this character.

CHARACTER 23 (NUMBER OF COENENCHYMAL LAYERS). The ancestral state as well as that of the out-group is to have two layers of sclerites (state 0), as suggested by Versluys (1906). Although the CI for this character is low, it does serve to distinguish the two largest clades within the family (clades B and C) and is still considered to be significant.

Characters 2, 14, and 20 are autapomorphic and thus do not contribute to tree topology. Likewise, characters 24–27 were included to show how the Primnoidae differ from the out-group and thus show evidence of the monophyly of the Primnoidae. They do not contribute to tree structure.

In summary, the characters that show high CI and/or significant support for clades are 8 (presence or absence of an operculum), 10 (correspondence of marginal and opercular scales), 16 (the number of longitudinal body wall scales), 18 (the number of adaxial rows of body wall scales), and 19 (the number of scales in each body wall row). Characters of little value in illustrating generic affinities include 1 (colony shape), 4 (basal fusion of calyces), 6 (proximity of calyces to stem), 13 (distal margin of marginal scales), and 21 (external sculpture of body wall scales).

## SYSTEMATIC ACCOUNT

### SUBCLASS OCTOCORALLIA

### ORDER GORGONACEA

### SUBORDER CALCAXONIA GRASSHOFF, 1999

### FAMILY PRIMNOIDAE MILNE EDWARDS, 1857

DIAGNOSIS. Cross section of axis reveals undulating concentric layers of calcified material embedded in gorgonin, resulting from a longitudinal (not radial) pattern of calcification (Bayer, 1955:pls. 4e–f). This arrangement usually results in a longitudinally striate (or grooved) outer axial surface; axis solid and continuous (with only one exception, *Mirostenella,* which has a jointed axis), without a chambered central core. Colonies branched in a variety of manners or unbranched, usually firmly attached to substrate by a calcareous discoidal holdfast. Polyps nonretractile, the calyces occurring in a variety of arrangements and orientations, in one case (*Ainigmaptilon*) arranged in clusters on leaf-like structures. Polyps heavily armored with calcareous scales that are usually arranged in an imbricate manner: each calyx has eight triangular opercular scales forming a closeable operculum, a variable number of marginal (also called buccal or circumopercular) scales (usually eight), and a variable number of rows of longitudinal body wall scales (often eight). Scales distinguished by the cruciform extinction pattern (Figure 3c), revealed in polarized light (dark field or crossed Nicol filter), that results from a radial crystal orientation (Bayer, 1956:F221, fig. 158-5). Coenenchymal sclerites also predominantly imbricate scales, but some genera also have an inner layer of tuberculate spheroids that compose the walls of the longitudinal canals.

TYPE GENUS. *Primnoa* Lamouroux, 1812.

DISTRIBUTION. Worldwide (especially common in Antarctic region), occurring predominantly at slope depths, but ranging from 8 to 5,850 m.

## ARTIFICIAL INDENTED KEY TO THE GENERA OF PRIMNOIDAE

I. Polyps united in groups forming polyp leaves [Figure 4p] placed along axis as in some pennatulaceans: “**Subfamily Ainigmaptilinae**”: ***Ainigmaptilon***

II. Polyps individually distinct or united basally [Figure 3i], but not united in groups forming polyp leaves: **“Subfamily Primnoinae”**

  A. Polyps adnate [Figure 4b] to coenenchyme except for oral region.

    1. Colonies dichotomous, large, and robust, terminal branches long and flexible; polyps large, arranged in close-set whorls, abaxial side covered by two rows [Figure 4a] of narrow, sickle-blade-shaped sclerites [Figure 4e]; distalmost polyp scales not differentiated as operculum [Figure 4b]: ***Armadillogorgia***

2. Colonies closely pinnate, slender and plumose, side branches short and stiff; polyps small, not in whorls, biserial, or in close spirals [Figure 19a], directed obliquely upward, abaxial side with only one longitudinal row of scales, adaxial side extremely short and adnate to coenenchyme, lacking scales below marginals; operculum well developed, tall, conical [Figure 19b], the triangular opercular scales fitting closely together [Figure 19c–e]: ***Pseudoplumarella***

B. Polyps not adnate to coenenchyme (e.g., appressed [Figure 10a], inclined [Figure 5c], or perpendicular [Figure 17a]).
  1. Polyps having sclerites in the form of thick plates [Figure 17e–g], not imbricating but closely fitted as in mosaic [Figure 17a], not aligned in regular rows: ***Microprimnoa***
  2. Polyps having sclerites in the form of scales [Figure 3f], thin or thick, clearly imbricating and aligned in regular rows [Figure 4q], at least on immature polyps; adaxial body wall rows may be missing [Figure 4r] or vestigial [Figure 8b].
    a. Polyps having sclerites aligned in five to eight or more complete, well-developed rows on all sides of polyp or randomly, at least on immature polyps, resulting in adaxial side of polyp being completely covered with scales [Figure 3a].
      1′. Sclerites of mature polyps in multiple (more than eight) rows [Figure 3s], the longitudinal alignment of eight regular rows present only in immature polyps; distalmost scales not differentiated as well-organized operculum [Figure 3a].
        a′. Colonies robust, dichotomous; polyps large, curved inward toward axis; polyps arranged in whorls; numerous distal body scales with strong apical keel [Figure 3p]: ***Aglaoprimnoa***
        b′. Colonies small, delicate, pinnate; polyps small, not curved inward; polyps arranged biserially (not in whorls) [Figure 3b]; distal body scales lack keel [Figure 3f] but close over retracted tentacles and mouth [Figure 3a]: ***Primnoeides***
      2′. Sclerites of polyps in five to eight longitudinal rows; distalmost scales differentiated as operculum [Figure 5p].
        a′. Marginal scales of polyps form a circumoperculum [Figure 7i] that folds over bases of opercular scales.
          1″. Outer surface of abaxial and lateral body scales, including marginals and submarginals, with a well-defined, transverse [Figure 9c], serrate [Figure 8l], spinose, or granular [Figure 7o] ridge extending across the greatest width of the sclerite, separating the exposed distal part from the proximal part covered by the distal margin of the next lower scale. The transverse ridge is continuous with lateral and distal margins and forms a shallow concavity (the ascus scale) on upper surface of sclerite.
            a″. Exposed outer surface of body wall scales sculptured with a serrate or spinose transverse ridge [Figure 8l]; inner surface of opercular scales ridged [Figure 9m].
              1‴. Colonies flagelliform; marginal scales without apical spine: ***Onogorgia***
              2‴. Colonies branched; marginal and sometimes submarginal scales with a strong, smooth apical spine.
                a‴. Colonies bottle-brush shaped, with numerous simple twigs arising from all sides of main stems: ***Fannyella*** (***Scyphogorgia***), new subgenus
                b‴. Colonies dichotomously to quasi-pinnately branched: ***Fannyella*** (***Cyathogorgia***), new subgenus
            b″. Exposed outer surface of body scales sculptured with low, smooth projections and distinguished from the covered portion by a transverse row of granules or tubercles along a more or less thickened boundary between exposed and concealed part of scale [Figure 7o]; inner surface of opercular scales with a strong apical keel most prominent on abaxial [Figure 7u] and outer laterals: ***Metafannyella,*** new genus
          2″. No distinct boundary separating exposed distal part of body scales from proximal part covered by scale below [Figure 6i].
            a″. Colonies flagelliform (unbranched), sometimes unattached: ***Convexella***
            b″. Colonies abundantly branched.
              1‴. Calyces with eight rows of equal-sized body wall scales [Figure10d].

        - a‴. Branching dichotomous: ***Pyrogorgia***, new genus
        - b‴. Branching pinnate: ***Amphilaphis***
      - 2‴. Calyces with eight rows of body wall scales, the two adaxial rows having smaller scales especially near calyx base, these rows being covered by broadened adjacent inner laterals: ***Thouarella*** sensu lato
        - a‴. Marginal scales lacking or without short distal spine [Figure 7k]: ***Thourella*** (***Epithouarella***)
        - b‴. Marginals with well-developed distal spine [Figure 6p].
          - 1⁗. Polyps arranged in pairs or whorls [Figure 7b].
            - a⁗. Colonies pinnate or bottlebrush: ***Thouarella*** (***Euthouarella***)
            - b⁗. Colonies dichotomous branched: ***Thouarella*** (***Diplocalyptra***)
          - 2⁗. Polyps isolated [Figure 6g]: ***Thourella*** (***Thouarella***)
- b′. Marginal scales of polyps do not fold over bases of opercular scales [Figure 10s].
  - 1″. Colonies unbranched or very sparsely branched.
    - a″. Polyps with eight marginal scales [Figure 5p]; polyps fused basally [Figure 5o]: ***Callozostron***
    - b″. Polyps with four marginal scales [Figure 16h]; polyp bases not fused [Figure 16i]: ***Candidella*** (in part)
  - 2″. Colonies abundantly branched.
    - a″. Branching closely pinnate.
      - 1‴. Polyps biserial [Figure 11k] or isolated, directed strongly upward; body scales in eight longitudinal rows; eight marginal scales [Figure 10s].
        - a‴. Distal edges of body wall scales spinose [Figure 10x–y] or serrate [Figure 11q–r]; inner face of sclerites tuberculate [Figure 10w, y]: ***Plumarella*** (in part)
        - b‴. Distal edges of body wall scales pectinate [Figure 11e–f]; inner faces of sclerites smooth [Figure 11j] (not tuberculate): ***Acanthoprimnoa*** (in part)
      - 2‴. Polyps in whorls, directed weakly upward [Figure 17j].
        - a‴. Body scales in five longitudinal rows [Figure 17h]; five marginal scales [Figure 17i]: ***Pterostenella***
        - b‴. Body scales in eight longitudinal rows; eight marginal scales [Figure 10s]: ***Mirostenella*** (in part)
    - b″. Branching dichotomous or bottlebrush.
      - 1‴. Eight marginal scales [Figure 10s].
        - a‴. Polyps arranged biserially [Figure 11k].
          - 1⁗. Inner surface of operculars keeled [Figure 15u]; brood polyps common [Figure 15q]: ***Tokoprymno***
          - 2⁗. Inner surface of operculars not keeled [Figure 11c]; brood polyps rare.
            - a⁗. Distal edges of body wall scales spinose or serrate [Figure 11q–r]; inner face of sclerites tuberculate [Figure 11r]: ***Plumarella*** (in part)
            - b⁗. Distal edges of body wall scales pectinate [Figure 11e–f]; inner faces of sclerites smooth [Figure 11c, j] (not tuberculate): ***Acanthoprimnoa*** (in part)
        - b‴. Polyps arranged in whorls [Figure 10s], pairs [Figure 16c], or isolated [Figure 5j].
          - 1⁗. Polyps isolated [Figure 5j]: ***Dicholaphis***
          - 2⁗. Polyps arranged in pairs [Figure 16c] and whorls [Figure 10s].
            - a⁗. Marginal scales offset from opercular scales [Figure 16a]; inner face of operculars keeled [Figure 16f]: ***Parastenella***
            - b⁗. Marginal scales align with opercular scales [Figure 10s]; inner face of operculars smooth [Figure 10v]: ***Mirostenella*** (in part)
      - 2‴. Four [Figure 16h] or five [Figure 18j] marginal scales.
        - a‴. Four marginal scales [Figure 16h]; colonies uniplanar dichotomous: ***Candidella*** (in part)
        - b‴. Five marginal scales [Figure 18j]; colonies bottlebrush in shape: ***Dasystenella***

b. Polyps having sclerites aligned in complete, well-developed rows only on abaxial and sometimes outer-lateral sides [Figure 4p], the adaxial side having a few [Figure 8b], small (vestigial) [Figures 13i, 14a] or no (naked) [Figures 4r, 15b] sclerites below the adaxial marginal scales.
  1′. Abaxial side of polyps protected by large scales [Figure 15i]; distalmost eight scales form a well-differentiated operculum [Figure 13s].
    a′. Polyps crowded irregularly around stems, not in regular whorls: ***Primnoa***
    b′. Polyps arranged in pairs or whorls [Figure 14b] around stems.
      1″. Abaxial body wall scales arranged in a single longitudinal row of large scales [Figure 18b]: ***Perissogorgia***
      2″. Abaxial body wall scales arranged in two or more longitudinal rows [Figure 15a].
        a″. Body wall scales in two rows [Figure 15a, i] (no adaxial or outer- and inner-lateral rows of scales, although one pair of outer- and inner-lateral marginal scales may be present [Figure 13a]): **“Subfamily Calyptrophorinae”**
          1‴. Two pairs of large abaxial body wall scales [Figure 15a].
            a‴. Both pairs of abaxial plates extend around body as a solid ring, the members inseparably fused along abaxial and adaxial symphysis [Figure 15k–m]: ***Calyptrophora***
            b‴. Abaxial plates extend around body but are not solidly fused along abaxial and adaxial symphysis [Figure 15b].
              1⁗. One pair of infrabasal scales [Figure 15h]: ***Paracalyptrophora***
              2⁗. Two or more pairs of infrabasal scales [Figure 14h]: ***Arthrogorgia***
          2‴. Three [Figure 14c] to five [Figure 13b] pairs of abaxial body wall scales.
            a‴. Three [Figure 14c] or four pairs of abaxial scales enclose body; no inner- or outer-lateral scales [Figure 14a].
              1⁗. Six marginal scales [Figure 13s]; calyces arranged unilinearly: ***Australogorgia***
              2⁗. Four [Figure 14a] marginal scales (including two small adaxial scales); calyces arranged in downward pointing whorls [Figure 14b]: ***Narella***
            b‴. Five pairs of abaxial body wall scales [Figure 13b]; one pair of both inner- and outer-laterals present [Figure 13a]: ***Paranarella***
        b″. Body scales in four, six [Figure 4r], or eight longitudinal rows.
          1‴. Circumopercular scales (marginals) fold over bases of opercular scales [Figure 4r].
            a‴. Colonies unbranched (flagelliform) or weakly branched with long whip-like branches; body sclerites are thin, smooth [Figure 4t, u], imbricating scales: ***Primnoella***
            b‴. Colonies dichotomously branched (lyriform), end branches long; body sclerites are thick ascus scales [Figure 8c–d]: ***Fannyella*** **(Fannyella)**
          2‴. Circumopercular scales (marginals) do not fold over bases of opercular scales [Figure 12c, e].
            a‴. Colonies unbranched; polyps stand perpendicular to branch: ***Arntzia***
            b‴. Colonies branched (pinnate, dichotomous); polyps appressed to branch [Figure 12a, e], inclined upward.
              1⁗. Body scales sculptured with ridges, crests, or smooth granules [Figure 12c]; coenenchymal scales nearly smooth or sculptured by radial or anastomosing ridges; colonies mostly pinnate, plumose, rarely dichotomous: ***Callogorgia***
              2⁗. Body scales sculptured with finely serrate or tuberculate crests closely radiating from depositional center [Figure 12h, j–k]; coenenchymal scales sculptured with crowded tubercles; colonies mostly dichotomous, sometimes openly pinnate or quasi-dichotomous: ***Fanellia***
  2′. Abaxial side of polyps covered by numerous small warty plates [Figure 3j–l] not aligned in regular longitudinal rows except in small, immature individuals; distalmost sclerites not differentiated as opercular scales [Figure 3g]: ***Ophidiogorgia***

## 1. *Primnoeides* Studer and Wright in Studer, 1887

FIGURE 3A–F

*Primnoeides* Studer and Wright in Studer, 1887:52.—Bayer, 1956:F220; 1961:292 [illustrated key to genus]; 1981b:934 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Williams, 1992:276.

*Primnoides* Wright and Studer, 1889:90 [incorrect subsequent spelling].—Versluys, 1906:9.—Kükenthal, 1915:142, 144 [key to genus]; 1919:339; 1924:253.

DIAGNOSIS. Colonies uniplanar, branching in an opposite, pinnate manner. Calyces arranged in pairs (Figure 3b) or whorls of three, the calyces inclined upward; brood chambers in base of calyx common. Rudimentary operculum present, composed of small rounded scales not keeled on inner surface, in the closed position usually completed overshadowed by adjacent marginals (Figure 3a); operculars usually do not entirely cover the distal polyp. Body wall, marginal, and opercular scales similar in shape, becoming progressively smaller distally. Small calyces completely covered with eight longitudinal rows of body wall scales, but larger calyces add additional scales in an irregular manner, resulting in nonlinear arrangement of body wall scales. Outer surface of scales smooth, inner surface bearing only sparse tubercles. Coenenchymal scales in two layers: outer layer consists of smooth, flat, circular to elliptical scales; inner layer consists of small tuberculate spheroids (see Versluys, 1906:fig. 4).

DISCUSSION. *Primnoeides* bears resemblance to *Aglaoprimnoa* but differs in branching pattern, having a tendency to form only pairs (not whorls) of calyces, and in lacking keels on the opercular scales.

Williams (1992) implied that a second, undescribed species in the genus exits from off southwestern South Africa (400–450 m), but it has not yet been described.

DISTRIBUTION. Prince Edward Island, off South Africa (Williams, 1992, and herein), Indian Ocean, 400–558 m. This infrequently collected genus is known only from the type locality and generalized localities from off southwestern South Africa (Williams, 1992). Another record of *P. sertularoides* is reported herein: Gilchrist station 70: 33°16′13″S, 17°28′10″E (off Cape Town, South Africa), 413 m, 7 May 1920, USNM 58601 (ex BM 1933.12.1.9).

TYPE SPECIES. *P. sertularoides* Wright and Studer, 1889, by subsequent monotypy. The holotype (in alcohol) is deposited at the BM (1889.05.27.62 and 1922.1.21.1), and a fragment of the type is deposited at the ZMA (Coel. 3085) (van Soest, 1979).

## 2. *Ophidiogorgia* Bayer, 1980

FIGURE 3G–L

*Ophidiogorgia* Bayer, 1980:223–225; 1981b:934 [key to genus].—Bayer and Stefani, 1989:455.—Bayer, 1996b:179–180.

DIAGNOSIS. Colonies unbranched (flagelliform). Calyces arranged in whorls of up to 21, the polyp bases within a whorl often fused (Figure 3i); the strongly appressed calyces face upward. Operculum and distinctive marginals absent, all body wall scales being the same size and shape: small discoidal scales (Figure 3j–l). Body wall scales numerous but not arranged in longitudinal rows, except on young calyces, occurring as two imbricate layers on abaxial and lateral body walls, leaving a narrow strip on the adaxial face bare. Coenenchymal scales in two layers, including an inner layer of tuberculate spheroids that separate the stem canals. All sclerites have a coarsely granular outer surface.

DISCUSSION. *Ophidiogorgia* is distinctive among the primnoids in having several characters found in few, if any other, primnoid genera (Table 3): i.e., multilayered body wall sclerites, no operculum, and nonaligned body wall scales (except in juvenile calyces). Bayer (1996b) suggested that *Ophidiogorgia* may have evolved from *Primnoella* since they are morphologically similar: *Primnoella* has very reduced opercular scales, both genera have reduced adaxial sclerite coverage, and ontogenetically, *Ophidiogorgia* does have longitudinal rows of body wall scales in its early stages (Bayer, 1996b). Nonetheless, *Ophidiogorgia* differs in having fused basal calyces, more than eight marginal scales, granular sculpture on its body wall scales, and multiple layers of sclerites on the body wall and coenenchyme.

DISTRIBUTION. Antarctic waters: Bouvet Island, South Orkney, continental Antarctica, 27–426 m.

TYPE SPECIES. *O. paradoxa* Bayer, 1980, by original designation. The holotype is deposited at the USNM (58165).

## 3. *Aglaoprimnoa* Bayer, 1996

FIGURE 3M–S

?*Amphilaphis*.—Stibane, 1987:25, pl. 1, fig. 2.

*Aglaoprimnoa* Bayer, 1996a:516.

DIAGNOSIS. Colonies uniplanar, sparsely dichotomously branched, with long terminal branches. Calyces arranged in closely placed whorls of up to 10, the appressed calyces directed upward; calyces cylindrical to cone shaped; brood chambers common. Poorly developed, almost flat operculum present; inner face of opercular scales longitudinally keeled. Marginal scales not differentiated from other body wall scales, folding over bases of opercular scales (Figure 3r). Small calyces covered with eight longitudinal rows of scales, the adaxial rows somewhat shorter; however, larger calyces intercalate additional body wall scales, making the longitudinal row structure indistinct and even appear to spiral (Figure 3s). Outer face of body wall scales smooth but with radiating ridges near distal edge, which interlock with similarly sized ridges on inner distal face of the more proximal scale, preventing lateral displacement of scales as calyx opens and closes (Bayer, 1996a). Coenenchymal scales in two layers: outermost layer consists of highly concave, saucer-like plates (Figure 3q), the inner layer composed of small tuberculate spheroids (Figure 3m).

DISCUSSION. Bayer (1996a) stated that this genus does not have an operculum; however, calyces from the type series and even one figured by him (Bayer, 1996a: fig. 10, bottom) show a distinct, if somewhat ill defined, operculum composed of eight triangular, keeled, opercular scales.

DISTRIBUTION. South Georgia and Burdwood Bank, 70–686 m.

TYPE SPECIES. *A. stefanii* Bayer, 1996a, by original designation. The holotype is deposited at the USNM (81289).

## 4. *Armadillogorgia* Bayer, 1980

FIGURE 4A–G

*Armadillogorgia* Bayer, 1980:217; 1981b:934 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1996a:527.

DIAGNOSIS. Colonies sparsely dichotomously branched. Calyces arranged in whorls of up to 20 calyces, facing upward in the holotype but downward in other specimens; adaxial side of calyces adnate to branch. Operculum not present nor are distinctive marginal scales; calycular aperture (mouth) a simple, unadorned pore (Figure 4b). Polyp completely covered by sclerites, the abaxial body wall covered by two rows of up to 70 broad, smooth, sickle-shaped sclerites that meet in an alternating (zigzag) pattern on calyx midline (Figure 4a, e). Sclerites on adaxial and circumoral region scale-like but not arranged in rows or in any order. Coenenchyme composed of two layers of sclerites, an outer layer of goblet-shaped sclerites (Figure 4f–g) and an inner layer of tuberculate spheroids.

DISCUSSION. Although Bayer (1980) compared *Armadillogorgia* to certain species of *Primnoella*, it is difficult to even consider its placement within the family Primnoidae. It lacks opercular and marginal scales, its body wall sclerites are not scales but a uniquely shaped sickle-like sclerite, its lateral and adaxial sclerites are not arranged in rows whereas the abaxial rows have up to 70 sclerites, and its sclerites do not demonstrate the characteristic cruciform extinction pattern under crossed Nicols. If this is a primnoid, it is a very highly derived genus.

DISTRIBUTION. South Georgia, Scotia Sea, 659–1,886 m.

TYPE SPECIES. *A. cyathella* Bayer, 1980, by original designation. The holotype is deposited at the USNM (58166).

## 5. *Ainigmaptilon* Dean, 1926

FIGURE 4H–P

*Ainigmaptilon* Dean, 1926:337.—Carlgren, 1943:1–7.—Bayer, 1950:295–296 [key to species]; 1956:F222; 1981b:936 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1996b:151.

*Lycurus* Molander, 1929:66–70.

DIAGNOSIS. Colonies unbranched (flagelliform), the stem terminating proximally in a funnel-shaped base, which, when filled with mud, functions as an anchor in soft sediment. Calyces arranged in terminal clusters of up to 30 on unsupported, simple, or branched fleshy lobes, called polyp leaves (Figure 4o, p) by previous authors. Polyp leaves arranged in an alternate biserially manner on the branch. Well-developed operculum present, each opercular having an extremely long, smooth apical spine (Figure 4h–j), so long that they cannot close over the tentacles of the polyp; inner face of operculars not keeled. Eight marginal scales present but not differentiated from other body wall scales, the latter arranged randomly (type species) or in eight longitudinal rows (e.g., *A. edisto*). Body wall scales irregular in shape or triangular shaped, with a broad, notched distal end (arrowhead shaped; Figure 4m–n), having a spiny or smooth outer surface. Coenenchymal plates on branch surface as well as leaf surface fusiform in shape, having an L:W of up to 10; outer surface smooth, inner surface tuberculate; no inner layer of specialized coenenchymal sclerites.

Discussion. *Ainigmaptilon* has such an unusual mixture of characters that Dean (1926:337) remarked that it "differs so extraordinarily from any other Alcyonarian so far described that one finds it difficult to assign it to even any of the five large orders." She was referring not only to the leaf-like arrangement of the polyps and axial canal structure, which allied it to the order Pennatulacea, but also to the scale-like sclerites and lack of siphonozooids, which allied it more to the family Primnoidae of the order Gorgonacea. She finally provisionally placed the new genus in the pennatulacean, with affinities to the Virgulariidae. Perhaps unaware of Dean's work, Molander (1929) described two new species with similar morphology, but after going through much the same soul-searching as Dean, he concluded that his two species belonged in a new primnoid genus (*Lycurus*) and new subfamily (Lycurinae), having affinities to the primnoid *Callozostron*. Hickson (1930) also favored a placement of *Ainigmaptilon* as a primnoid, but Thomson and Rennet (1931) reverted to Dean's logic in placing it as a pennatulacean genus "*Incertae sedis*." Carlgren (1943) described yet a fourth species, synonymized *Ainigmaptilon* and *Lycurus*, and raised Molander's subfamily to family rank: Ainigmaptilonidae, with suggested affinities to the Primnoidae. Bayer (1950) described the fifth species (Table 4) and maintained the taxon as a separate family (but corrected the spelling of the family name to Ainigmaptilidae), as he (Bayer, 1956) did in the Treatise revision; however, in Bayer (1981b) and subsequent papers (see synonymy above), without explanation he considered *Ainigmaptilon* as a genus in the Primnoidae. Bayer (1996b) compared *Ainigmaptilon* to *Callozostron*, summarized in the discussion of the latter genus herein.

The crystal orientation of the scales of *Ainigmaptilon edisto* is radial, producing the characteristic primnoid cruciform extinction pattern under crossed Nicols. The position of polyps on a leaf-like structure and the funnel-shaped base are unique characters for this genus.

Distribution. Antarctica to South Georgia, 75–550 m.

Type Species. *Ainigmaptilon*: *A. haswelli* Dean, 1926, by monotypy. Type reputed to be deposited at the University Museum, Sydney. The type species is best described by Dean (1926); Thomson and Rennet (1931) inexplicably repeated her description with virtually no changes, using Dean's figures as well.

*Lycurus*: *L. virgularoides* Molander, 1929, here designated. The type is reputedly deposited at the Stockholm Museum of Natural History.

## 6. *Primnoella* Gray, 1858

FIGURE 4Q–Z

*Primnoella* Gray, 1858:286.—Studer, 1887:51 [in part].—Wright and Studer, 1889:80–83 [in part: group *Convexae* in part and group *Carinatae*].—Versluys, 1906:48–51 [in part: group *Carinatae*].—Kükenthal, 1908:12–13 [in part: *Compressae*]; 1912:311–320 [in part]; 1915:143, 148–149 [in part: *Compressae,* key to genus and species]; 1919:384–387 [in part: key to species]; 1924:279–281 [in part: key to genus and species].—Bayer, 1956:F220 [in part]; 1961 [illustrated key to genus]; 1981b:not 936 [= *Convexella*], 938 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1996b:165–167 [not *Caligorgia gracilis* Thomson and Mackinnon, rather *Caligorgia laevis*; not *P. gracilis* Molander, 1929].—Cairns, 2006:162–163 [key to west Atlantic species].

*Callirrhabdos* Philippi, 1894:211–213.

Diagnosis. Colonies usually unbranched (flagelliform), although two species display sparse dichotomous branching. Calyces arranged in whorls of up to 15, each calyx strongly flattened in cross section and strongly appressed to branch, facing upward. An inconspicuous operculum is present, often hidden from view by infolded marginal scales (Figure 4r); operculars smooth on inner surface (not keeled or ridged). Polyps protected by two abaxial rows of large body wall scales (Figure 4q), which are only scales visible in abaxial view; up to 32 scales occur per abaxial row, which alternate in position with their adjacent scales. Shorter, less conspicuous inner- and outer-lateral longitudinal scale rows usually present, as well as some pairs of vestigial adaxial scales, resulting in six or eight longitudinal body wall scale rows. Lateral and adaxial scales much smaller than abaxials, resulting in a naked adaxial body wall (Figure 4r). Coenenchymal scales in two layers, including an inner layer of tuberculate spheroids (Figure 4x–y) that compose the walls of the longitudinal stem canals.

Discussion. Species from at least three genera were at one time grouped in *Primnoella*, these subgroups recognized as early as 1889 by Wright and Studer, but not formally and nomenclaturally recognized until 1996 (*Convexella* of Bayer, 1996b) and 2002 (*Arntzia* of López-González et al., 2002). As explained more fully by Bayer (1996b) and Cairns (2006), *Primnoella* differs from *Convexella* in having calyces flattened in cross section, body wall scales of different sizes (the abaxial scales being by far the largest and only ones visible in abaxial view), a naked adaxial body wall region, and appressed calyces (not inclined). *Primnoella* differs from *Arntzia* in having compressed polyps, nonfused basally fused polyps, a smooth inner opercular surface, and a circumoperculum that folds over the operculars (Table 3). The 10 species currently attributed to *Primnoella* are listed in Table 4. Characters used to distinguish species include number of polyps per whorl, number of abaxial body wall scales, number of adaxial body wall scales, size and shape of marginal scales, and size of polyps (Cairns, 2006).

The generic placement of *P. antarctica* Kükenthal, 1907 is problematic. Kükenthal (1919) placed it in the *Convexae* section of the genus *Primnoella* (later called *Convexella* by Bayer, 1996b) because of its round-in-cross-section calyces, but Bayer removed it from that genus in 1996 because it had a bare adaxial body wall. He suggested an affinity with *Ophidiogorgia* but did not elaborate. Because it appears to have a distinct, if small, operculum, and its body scales are arranged in longitudinal rows, it does not seem to belong in *Ophidiogorgia*. Short of describing a separate genus for this species, we suggest a tentative placement in *Primnoella*, but differing from that genus in having a calyx round in cross section and thus having four body wall scale rows visible in abaxial view.

DISTRIBUTION. Lesser Antilles, entire eastern and southwestern coasts of South America, southeastern Australia, New Zealand, Tasmania, 8–1,249 m (Cairns, 2006).

TYPE SPECIES. *Primnoella*: *Primnoa australasiae* Gray, 1850, by monotypy. Dry syntypes deposited at the BM (1850.1.21.1, 6, and 10; 1983.3.2.13–14) (Bayer, 1996b).

*Callirrhabdos*: *C. chilensis* Philippi, 1894, by monotypy. Type not located.

## 7. *Convexella* Bayer, 1996

FIGURE 5A–I

*Primnoella*.—Studer, 1887:51 [in part].—Wright and Studer, 1889:83–84 [in part: *Convexae*].—Versluys, 1906:51 [in part: *Convexae*].—Kükenthal, 1908:12–13 [in part: *Convexae*]; 1915:148 [in part: *Convexae*, in part, key to genus and species]; 1919:384–386 [in part: *Convexae*, in part, key to species]; 1924:279–280 [in part].—Madsen, 1944:39.—Bayer, 1956:F220 [in part]; 1981b:936, not 938 [= *Primnoella*] [key to genus].—Bayer and Stefani, 1989:455 [in part: key to genus].

*Convexella* Bayer, 1996b:171–180.

DIAGNOSIS. Colonies usually unbranched (flagelliform) or sparsely dichotomously branched. Calyces arranged in whorls of up to 15 (Figure 5b), each calyx round in cross section and inclined upward or perpendicular to axis. An inconspicuous operculum consisting of 6–10 opercular scales is present (Figure 5a, f–g), often hidden from view by the eight infolded marginal (= circumopercular) scales; operculars smooth on inner surface. Marginals arranged in two circles of four that alternate with one another, the circumference of the distal polyp not being large enough to accommodate eight marginal scales. Polyps protected by eight complete longitudinal rows of body wall scales, four of which can be seen in abaxial view. Body wall scales not paired but alternate with those of adjacent rows, appearing to spiral around calyx. Coenenchymal scales in two layers: outer layer composed of smooth, rounded scales; inner layer composed of small, irregularly shaped tuberculate rods.

DISCUSSION. As mentioned in the discussion of the genus *Primnoella* as well as in the publications of Bayer (1996b) and Cairns (2006), species now placed in the genus *Convexella* had been placed in the species group "*Convexae*" of *Primnoella*. Bayer (1996b) finally separated five species (Table 4) from *Primnoella* to form the basis of *Convexella*, the latter differing in having calyces round in cross section, eight rows of equal-sized body wall scales and thus no naked adaxial region, four rows of body wall visible in abaxial view, and calyces inclined (not appressed) upward. The species are briefly reviewed by Bayer (1996b).

DISTRIBUTION. Antarctic, subantarctic South America, Kermadec Trench, North Atlantic, 12–5,850 m, *C. krampi* being the deepest known primnoid.

TYPE SPECIES. *Primnoella magelhaenica* Studer, 1879, by original designation. Type assumed to be deposited at the ZMB. The type species is well described and copiously illustrated by Bayer (1996b).

## 8. *Dicholaphis* Kinoshita, 1907

FIGURE 5J–N

*Dicholaphis* Kinoshita, 1907:230–231; 1908a [27 Jul]:24–27 [best description of genus and species]; 1908c [15 Nov]:57 [key to genus, in Japanese]; 1908d [15 Dec]:524 [in Japanese]; 1908e:50 [key to genus].

*Primnoella*.—Kükenthal, 1919:404 [in part: *P. delicata*]; 1924:279, 287.

DIAGNOSIS. Colonies branch in a regular, planar, dichotomous manner. Calyces occur without order on branches (not in pairs, whorls, or rows) and are inclined upward. A tall, well-developed operculum present, the operculars smooth on their distal inner face (not

**TABLE 4.** List of the 36 genera, 7 subgenera, 233 species, 4 subspecies, and 10 forms or varieties of the Primnoidae Milne Edwards, 1857, including purported junior synonyms and junior homonyms. Type species are indicated by an asterisk and listed first, other species are listed chronologically; a plus sign (+) indicates a fossil species; a dash precedes a form, variety, or subspecies. Order of genera reflects cladogram (Figures 1, 2).

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| *Primnoeides* Studer and Wright in Studer, 1887 | **P. sertularoides* Wright and Studer, 1889 |
| *Ophidiogorgia* Bayer, 1980 | **O. paradoxa* Bayer, 1980 |
| | *O. kuekenthali* (Gravier, 1913) |
| *Aglaoprimnoa* Bayer, 1996a | **A. stefanii* Bayer, 1996a |
| *Armadillogorgia* Bayer, 1980 | **A. cyathella* Bayer, 1980 |
| *Ainigmaptilon* Dean, 1926 (= *Lycurus* Molander, 1929) | **A. haswelli* Dean, 1926 |
| | *A. antarcticum* (Molander, 1929) |
| | *A. virgularoides* (Molander, 1929) |
| | *A. wallini* Carlgren, 1943 |
| | *A. edisto* Bayer, 1950 |
| *Primnoella* Gray, 1858 (= *Callirrhabdos* Philippi, 1894) | **P. australasiae* (Gray, 1850) |
| | *P. divaricata* (Studer, 1879) |
| | *P. distans* Studer, 1879 |
| | *P. grandisquamis* Wright and Studer, 1889 |
| | *P. chilensis* (Philippi, 1894) |
| | = *P. philippii* Aurivillius, 1931 |
| | = *P. biserialis* Wright and Studer, 1889 |
| | *P. scotiae* Thomson and Richie, 1906 |
| | = *P. compressa* Kükenthal, 1908 |
| | ?*P. antarctica* Kükenthal, 1907 |
| | *P. delicatissima* Kükenthal, 1909 |
| | *P. laevis* (Thomson and Mackinnon, 1911) |
| | *P. polita* Deichmann, 1936 |
| *Convexella* Bayer, 1996b | **C. magelhaenica* (Studer, 1879) |
| | = *Primnoella flagellum* Studer, 1878 |
| | =? *P. vanhoeffeni* Kükenthal, 1909 |
| | *C. murrayi* (Wright and Studer, 1889) |
| | *C. divergens* (Hickson, 1907) |
| | *C. jungerseni* (Madsen, 1944) |
| | *C. krampi* (Madsen, 1956) |
| *Dicholaphis* Kinoshita, 1907 | **D. delicata* Kinoshita, 1907 |
| *Callozostron* Wright, 1885 | **C. mirabile* Wright, 1885 |
| | = *C. horridum* Kükenthal, 1909 |
| | *C. carlottae* Kükenthal, 1909 |
| | *C. acanthodes* Bayer, 1996b |
| | *C. diplodiadema* Bayer, 1996b |
| *Arntzia* López-González, Gili and Orejas, 2002 | **A. gracilis* (Molander, 1929) |
| *Thouarella (Thouarella)* Gray, 1870 (= *Rhopalonella* Roule, 1908; = *Primnodendron* Nutting, 1912; = *Parathouarella* Kükenthal, 1915) | *T. *antarctica* (Valenciennes, 1846) |
| | *T. variabilis typica* Wright and Studer, 1889 |
| | – var. *brevispinosa* Wright and Studer, 1889 |
| | – var. *gracilis* Wright and Studer, 1889 |
| | *T. koellikeri* Wright and Studer, 1889 |
| | *T. brucei* (Thomson and Richie, 1906) |
| | *T. versluysi* Kükenthal, 1907 |
| | *T. striata* Kükenthal, 1907 |
| | *T. pendulina* (Roule, 1908) |
| | *T. clavata* Kükenthal, 1908 |
| | *T. hicksoni* Thomson, J.S., 1911 |
| | *T. alternata* Nutting, 1912 |
| | = *P. attenuate* Kükenthal, 1924:301 (misspelling of *alternata*) |

*continued*

TABLE 4. (*Continued*)

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| | *T. recta* Nutting, 1912 |
| | *T. superba* (Nutting, 1912) |
| | *T. bipinnata* Cairns, 2006 |
| | *T. diadema* Cairns, 2006 |
| *Thouarella (Euthouarella)* Kükenthal, 1915 | **T. hilgendorfi* (Studer, 1878) |
| | – *T. h.* forma *plumatilis* Aurivillius, 1931 |
| | *T. moseleyi* Wright and Studer, 1889 |
| | *T. laxa* Versluys, 1906 |
| | *T. tydemani* Versluys, 1906 |
| | = *?Hookerella pulchella* Gray, 1870 |
| | *T. typica* Kinoshita, 1907 |
| | *T. flabellata* Kükenthal, 1907 |
| | *T. carinata* Kükenthal, 1908 |
| | *T. tenuisquamis* Kükenthal, 1908 |
| | = *T. regularis* Kükenthal, 1907 (junior homonym) |
| | ?*T. longispinosa* Kükenthal,1912 |
| | *T. grasshoffi* Cairns, 2006 |
| *Thouarella (Diplocalyptra)* Kinoshita, 1908e | **D. coronata* Kinoshita, 1908e |
| | *D. parva* Kinoshita, 1908e |
| *Thouarella (Epithouarella*) Kükenthal, 1915 | **T. crenelata* Kükenthal, 1907 |
| | *T. affinis* Wright and Studer, 1889 |
| | *T. chilensis* Kükenthal, 1908 |
| *Metafannyella,* new genus | **F. lepidota* (Bayer, 1998), new combination |
| | *F. eos* (Bayer, 1998), new combination |
| | *F. aurora* (Bayer, 1998), new combination |
| | *F. mawsoni* (Bayer, 1998), new combination |
| *Fannyella (F.)* ss. Gray, 1872 (= *Ascolepis* Thomson and Rennet, 1931) | **F. rossii* Gray, 1872 |
| | =?*Caligorgia antarctica* Kükenthal, 1909 |
| | = *Ascolepis splendens* Thomson and Rennet, 1931 |
| | *F. kuekenthali* (Molander, 1929) |
| *Fannyella (Scyphogorgia*), new subgenus | **F. liouvillei* (Gravier, 1913) |
| | = *Thouarella abies* Broch, 1965 |
| *Fannyella (Cyathogorgia),* new subgenus | **F. spinosa* (Thomson and Rennet, 1931) |
| | – *F. spinosa* "intermediate form" Bayer, 1998 |
| *Onogorgia,* new genus | **O. nodosa* (Molander, 1929), new combination |
| | = *Primnoella vanhoefeni* sensu Kükenthal, 1912 |
| *Pyrogorgia*, new genus | **P. lemnos* (Bayer, 1998), new combination |
| *Amphilaphis* Studer and Wright in Studer, 1887 | *A. *regularis* Wright and Studer, 1889 |
| | *A. abietina* Studer, 1894 |
| | *A. biserialis* (Nutting, 1908) |
| | *A. plumacea* Thomson and Mackinnon, 1911 |
| | *A. dispersa* (Kükenthal, 1912) |
| | *A. grandiflora* (Kükenthal, 1912) |
| *Mirostenella* Bayer, 1988 | **M. articulata* Bayer, 1988 |
| | ?*M. delicatula* (Thomson and Rennet, 1931), new combination |
| *Acanthoprimnoa* Cairns and Bayer, 2004c | **A. goesi* (Aurivillius, 1931) |
| | *A. cristata* (Kükenthal and Gorzawsky, 1908a) |
| | = *P. carinata* Kinoshita, 1908a |
| | *A. serta typica* (Kükenthal and Gorzawsky, 1908a) |
| | – *A. s. squamosa* (Kükenthal and Gorzawsky, 1908a) |
| | *A. pectinata* Cairns and Bayer, 2004c |

*continued*

**TABLE 4.** (*Continued*)

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| *Plumarella* Gray, 1870 | **P. penna* (Lamarck, 1815) |
| | *P. pourtalesii* (Verrill, 1883) |
| | – *P. p.* forma *robusta* Deichmann, 1936 |
| | – *P. p.* forma *obtusa* Cairns and Bayer, 2004c |
| | *P. delicatissima* Wright and Studer, 1889 |
| | *P. flabellata* Versluys, 1906 |
| | *P. spinosa typica* Kinoshita, 1907 |
| | – *P. s. brevispina* Kükenthal, 1919 |
| | *P. acuminata* Kinoshita, 1908a |
| | *P. alba* Kinoshita, 1908a |
| | *P. dofleini* Kükenthal and Gorzawsky, 1908a |
| | – *P. d.* var. *boninensis* Aurivillius, 1931 |
| | *P. gracilis* Kinoshita, 1908a |
| | *P. lata* Kükenthal and Gorzawsky, 1908a |
| | *P. longispina* Kinoshita, 1908a |
| | *P. rigida* Kükenthal and Gorzawsky, 1908a |
| | *P. dentata* Thomson and Russell, 1910 |
| | *P. laevis* Thomson and Mackinnon, 1911 |
| | *P. adhaerans* Nutting, 1912 |
| | *P. spicata* Nutting, 1912 |
| | *P. aurea* (Deichmann, 1936) |
| | *P. pellucida* Cairns and Bayer, 2004c |
| | *P. laxiramosa* Cairns and Bayer, 2004c |
| | *P. dichotoma* Cairns and Bayer, 2004c |
| | *P. aculeata* Cairns and Bayer, 2004c |
| *Callogorgia* Gray, 1858 (= *Xiphocella* Gray, 1870; = *Callicella* Gray, 1870; = *Caligorgia* sensu Wright and Studer, 1889: spelling variation) | **C. verticillata* (Pallas, 1766) |
| | – *C. v.* var. *grimaldii* (Studer, 1890) |
| | *C. flabellum typica* (Ehrenberg, 1834) |
| | = *Primnoa flabellum* Ehrenberg, 1834 |
| | – *C. f. grandis* Kükenthal and Gorzawsky, 1908a |
| | *C. elegans* (Gray, 1870) |
| | *C. ventilabrum* (Studer, 1878) |
| | *C. modesta* (Studer, 1879) |
| | *C. sertosa* (Wright and Studer, 1889) |
| | *C. gracilis* (Milne Edwards and Haime, 1857) |
| | *C. versluysi* (Thomson, 1905) |
| | *C. dubia* (Thomson and Henderson, 1906) |
| | *C. indica* Versluys, 1906 |
| | *C. robusta* (Versluys, 1906) |
| | *C. joubini* (Versluys, 1906) |
| | *C. pennacea* (Versluys, 1906) |
| | *C. minuta* (Versluys, 1906) |
| | *C. affinis* (Versluys, 1906) |
| | *C. similis* (Versluys, 1906) |
| | *C. formosa* Kükenthal, 1907 |
| | = *Primnoella indica* Kükenthal, 1907 (junior secondary homonym: *P. indica* Verrill, 1906) |
| | *C. gilberti* (Nutting, 1908) |
| | *C. ramosa* (Kükenthal and Gorzawsky, 1908a) |
| | *C. laevis* (Thomson and Mackinnon, 1911) |
| | *C. kinoshitae* Kükenthal, 1913 |
| | *C. cristata* Aurivillius, 1931 |
| | = *C. weltneri* (Versluys, 1906) |
| | *C. chariessa* Bayer, 1982 |
| | *C. linguimaris* Cairns and Bayer, 2003 |
| | *C. americana americana* Cairns and Bayer, 2003 |
| | – *C. a. delta* Cairns and Bayer, 2003 |

*continued*

**TABLE 4.** (_Continued_)

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| _Fanellia_ Gray, 1870 | *_F. compressa_ (Verrill, 1865) |
| | _F. tuberculata_ (Versluys, 1906) |
| | = _Caligorgia aspera_ Kinoshita, 1908a |
| | = _C. pseudoflabellum_ Bayer, 1949 |
| | _F. granulosa_ (Kinoshita, 1907) |
| | _F. fraseri_ (Hickson, 1915) |
| | _F. corymbosa_ Bayer, 1982 |
| | _F. medialis_ Bayer and Stefani, 1989 |
| | _F. euthyeia_ Bayer and Stefani, 1989 |
| | _F. korema_ Bayer and Stefani, 1989 |
| _Paranarella_ Cairns, 2007a | *_P. watlingi_ Cairns, 2007a |
| _Primnoa_ Lamouroux, 1812 | _P. resedaeformis typica_ (Gunnerus, 1763) |
| | = _Gorgonia reseda_ Pallas, 1766 |
| | = *_Gorgonia lepadifera_ Linnaeus, 1767 |
| | _P. pacifica_ Kinoshita, 1907 |
| | – _P. pacifica_ var. _willeyi_ (Hickson, 1915) |
| | Not +_P. costata_ Nielsen, 1913 (Early Paleocene, Denmark) |
| | Not +_P. gracilis_ Nielsen, 1925 (= _Epiphaxum auloporoides_ (Lonsdale, 1850) Early Paleocene, Denmark) |
| | _P. notialis_ Cairns and Bayer, 2005 |
| | _P. wingi_ Cairns and Bayer, 2005 |
| _Australogorgia,_ new genus | *_A. aldersladei_, new species |
| _Narella_ Gray, 1870 (= _Stachyodes_ Wright and Studer in Studer, 1887; not _Stachyodes_ Bargatzky, 1881 (a stromatoporoid); = _Calypterinus_ Wright and Studer in Studer, 1887) | *_N. regularis_ (Duchassaing and Michelotti, 1860) |
| | _N. allmani_ (Wright and Studer, 1889) |
| | _N. ambigua_ (Studer, 1894) |
| | _N. clavata_ (Versluys, 1906) |
| | _N. horrida_ (Versluys, 1906) |
| | _N. obscura_ (Versluys, 1906) |
| | _N. orientalis_ (Versluys, 1906) |
| | _N. parva_ (Versluys, 1906) |
| | _N. dichotoma_ (Versluys, 1906) |
| | = _N. nuttingi_ Bayer, 1997 |
| | _N. studeri_ (Versluys, 1906:94) (nomen novum for _S. regularis_ Wright and Studer, 1889) |
| | _N. grandiflora_ (Kükenthal, 1907) |
| | _N. biannulata_ (Kinoshita, 1907) |
| | _N. irregularis_ (Kinoshita, 1907) |
| | _N. megalepis_ (Kinoshita, 1908a) |
| | _N. compressa_ (Kinoshita, 1908a) |
| | _N. bowersi_ (Nutting, 1908) |
| | _N. versluysi_ (Hickson, 1909) |
| | = ?_N. elegans_ Tixier-Durivault and Lafargue, 1968 |
| | _N. gilchristi_ (Thomson, 1911) |
| | = _S. capensis_ Thomson, 1917 |
| | = _Stachyodes "gilberti"_ Kükenthal, 1919 (misspelling of _gilchristi_) |
| | _N. gaussi_ (Kükenthal, 1912) |
| | _N. bellissima_ (Kükenthal, 1915) |
| | _N. japonensis_ (Aurivillius, 1931) |
| | _N. laxa_ Deichmann, 1936 |
| | _N. pauciflora_ Deichmann, 1936 |
| | _N. leilae_ Bayer, 1951 |
| | _N. ornata_ Bayer, 1995 |
| | _N. spectabilis_ Cairns and Bayer, 2003 |
| | _N. alvinae_ Cairns and Bayer, 2003 |
| | _N. bayeri_ Cairns and Baco, 2007 |

_continued_

**TABLE 4.** (*Continued*)

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| | *N. arbuscula* Cairns and Baco, 2007 |
| | *N. cristata* Cairns and Baco, 2007 |
| | *N. abyssalis* Cairns and Baco, 2007 |
| | *N. alaskensis* Cairns and Baco, 2007 |
| | *N. hawaiinensis* Cairns and Bayer, 2007 [2008] |
| | *N. gigas* Cairns and Bayer, 2007 [2008] |
| | *N. muzikae* Cairns and Bayer, 2007 [2008] |
| | *N. vermifera* Cairns and Bayer, 2007 [2008] |
| | *N. macrocalyx* Cairns and Bayer, 2007 [2008] |
| | *N. alata* Cairns and Bayer, 2007 [2008] |
| *Arthrogorgia* Kükenthal in Kükenthal and Gorzawsky, 1908a | **A. ijimai* (Kinoshita, 1907) |
| | = *A. membranacea* Kükenthal and Gorzawsky, 1908a |
| | *A. kinoshitai* Bayer, 1952 |
| | *A. otsukai* Bayer, 1952 |
| | *A. utinomii* Bayer, 1996c |
| *Paracalyptrophora* Kinoshita, 1908a | **P. kerberti* (Versluys, 1906) |
| | *P. josephinae* (Lindström, 1877) |
| | *P. mariae* (Versluys, 1906) |
| | *P. duplex* Cairns and Bayer, 2004b |
| | *P. simplex* Cairns and Bayer, 2004b |
| | *P. carinata* Cairns and Bayer, 2004b |
| *Calyptrophora* Gray, 1866a | *japonica* complex |
| | "Species group 1" (sensu Bayer, 2001) |
| | **C. japonica* Gray, 1866 |
| | – form A Versluys, 1906 |
| | – form C Versluys, 1906 |
| | *C. clarki* Bayer, 1951 |
| | = *C. japonica* form B Versluys, 1906 |
| | = *C. japonica* of Nutting, 1908 |
| | *C. juliae* Bayer, 1952 |
| | *C. spinosa* Pasternak, 1984 |
| | *C. microdentata* Pasternak, 1985 |
| | = *C. pillsburyae* Bayer, 2001 |
| | *C. gerdae* Bayer, 2001 |
| | *C. antilla* Bayer, 2001 |
| | *C. clinata* Cairns, 2007a |
| | *C. bayeri* Cairns, 2007b |
| | *C. laevispinosa* Cairns, 2007b |
| | "Species group 2" (sensu Bayer, 2001) |
| | *C. trilepis* (Pourtalès, 1868) |
| | *C. angularis* (Nutting, 1908) |
| | *wyvillei* complex |
| | *C. wyvillei* Wright, 1885 |
| | *C. agassizii* Studer, 1894 |
| | = *C. versluysi* Nutting, 1908 |
| *Tokoprymno* Bayer, 1996a | **T. maia* Bayer, 1996a |
| *Parastenella* Versluys, 1906 | **P. doederleini* (Wright and Studer, 1889) |
| | *P. spinosa* (Wright and Studer, 1889) |
| | *P. ramosa* (Studer, 1894) |
| | *P. atlantica* Cairns, 2007a |
| | *P. gymnogaster* Cairns, 2007b |
| | *P. pacifica* Cairns, 2007b |
| *Candidella* Bayer, 1954 (nomen novum for *Stenella* Gray, 1870, not Gray, 1866b) | **C. imbricata* (Johnson, 1862) |
| | *C. johnsoni* (Wright and Studer, 1889) |

*continued*

**TABLE 4.** (*Continued*)

| Genera and subgenera | Species, subspecies, and forms |
|---|---|
| | *C. gigantea* (Wright and Studer, 1889)<br>*C. helminthophora* (Nutting, 1908) |
| *Microprimnoa* Bayer and Stefani, 1989 | **M. diabathra* Bayer and Stefani, 1989 |
| *Pterostenella* Versluys, 1906 | **P. plumatilis* (Milne Edwards, 1857)<br>*P. anatole* Bayer and Stefani, 1989 |
| *Perissogorgia* Bayer and Stefani, 1989 | **P. viridis* Bayer and Stefani, 1989<br>*P. petasus* Bayer and Stefani, 1989<br>*P. colossus* Bayer and Stefani, 1989<br>*P. bythia* Bayer and Stefani, 1989<br>*P. vitrea* Bayer and Stefani, 1989<br>*P. monile* Bayer and Stefani, 1989<br>*P. penna* Bayer and Stefani, 1989 |
| *Dasystenella* Versluys, 1906 | **D. acanthina* (Wright and Studer, 1889) |
| *Pseudoplumarella* Kükenthal, 1915 | **P. thetis* (Thomson and MacKinnon, 1911)<br>*P. corruscans* (Thomson and Mackinnon, 1911)<br>*P. filicoides* (Thomson and Mackinnon, 1911)<br>*P. versluysi* (Thomson and Mackinnon, 1911)<br>*P. echidna* Bayer, 1981a |

keeled). Eight marginals present, the abaxial and lateral marginals pointed, the adaxial marginals smaller and not pointed. Polyps completely covered with eight longitudinal rows of body wall scales, the rows becoming disorganized near base of each calyx. Outer surface of most sclerites smooth. Coenenchymal scales in two layers: outer layer composed of smooth scales (Figure 5m–n); inner layer composed of small irregularly shaped tuberculate spheroids.

DISCUSSION. Kükenthal (1924) inadvertently synonymized this monotypic genus with both *Primnoella* and *Thouarella,* neither of which it appears to be (see Key). Except for the description of another species of *Dicholaphis* from Macquarie Island (Thomson and Rennet, 1931), which is closer to *Mirostenella* than *Dicholaphis*, the genus has not been discussed subsequent to 1924. It is treated herein as a separate genus for the purpose of this revision and the phylogenetic analysis. No specimen of this genus was available for study; thus, this description is from the literature.

DISTRIBUTION. Sagami Bay, Japan, 731 m.

TYPE SPECIES. *D. delicata* Kinoshita, 1907, by monotypy. The type is deposited at the University Museum of the University of Tokyo (G-226).

## 9. *Callozostron* Wright, 1885

FIGURE 5O–X

*Callozostron* Wright, 1885:690–691.—Studer, 1887:48.—Wright and Studer, 1889:48.—Versluys, 1906:124.—Kükenthal, 1912:328–339; 1915:152 [key to genus and species]; 1919:449–450 [key to genus and species]; 1924:306 [key to genus and species].—Bayer, 1961:295 [illustrated key to genus]; 1981b:936 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1996b:151–152 [revision of genus, key to species].

DIAGNOSIS. Colonies unbranched (type species) or sparsely dichotomously branched. Calyces arranged in whorls of up to 14, the bases of adjacent calyces within a whorl often fused, but not as leaves; calyces stand perpendicular to branch or slightly inclined upward. Well-developed operculum present, the operculars having a smooth inner face. Eight marginal scales present, at least four of which have extremely long, smooth apical spines that do not fold over the operculum (Figure 5p, s–t); a second ring of spined submarginals may also be present. Polyp covered with eight longitudinal rows of body wall scales; outer surface of scales smooth. Coenenchymal scales arranged in one layer.

Discussion. Four species are known in this genus (Table 4), all of which are restricted to the Antarctic and subantarctic regions. Bayer (1996b) noted the resemblance of *Callozostron* to *Ainigmaptilon*, particularly with regard to the basal fusion of their calyces; however, whereas some polyps of *Callozostron* are basally united, as is the case of a few other primnoid genera (e.g., *Arntzia, Onogorgia, Ophidiogorgia*), the calyces of *Ainigmaptilon* are supported on distinct, fleshy, leaf-like structures. Furthermore, the marginal scales of *Callozostron* are much larger than those in *Ainigmaptilon* and have prominent apical spines. Finally, *Callozostron* has a typical infolding operculum, whereas the opercular scales of *Ainigmaptilon* bear such long apical spines that they cannot fold over the tentacles as most opercula do. Bayer (1996b:151–152, 200) also compared *Callozostron* to *Convexella* (as *Primnoella magelhaenica*), *Callozostron* differing from that genus in having fused basal calyces and spinose marginal scales that do not fold over the operculum.

Distribution. Antarctic, South Georgia, New Zealand, 1,354–3,876 m.

Type Species. *C. mirabile* Wright and Studer, 1889, by monotypy. The type is deposited at the BM (1889.5.27.33). The type species was recently redescribed and illustrated by Bayer (1996b).

## 10. *Arntzia* López-González, Gili and Orejas, 2002

FIGURE 6A–F

*Primnoella*.—Molander, 1929:63 [in part].—Bayer, 1966:179 [in part: discussion].

*Arntzia* López-González, Gili and Orejas, 2002:385.

Diagnosis. Colonies unbranched (flagelliform). Calyces arranged in whorls of up to 22, the calyces inclined upward or oriented perpendicular to axis and, within each whorl, united at their bases. Brood chamber associated with the fused basal ring in each whorl. Polyps fleshy, a thin layer of tissue covering the calyces and branch, partially obscuring the underlying sclerites; calyces slightly flattened, as in *Primnoella*. Well-developed operculum present, each opercular scale having one or more ridges on its inner surface. Eight marginal scales do not overlap the operculars, the adaxial marginals smaller than the rest. Polyps protected by eight rows of 8–11 thin, smooth, rectangular scales, the adaxial scales smaller and in shorter rows (Figure 6a), resulting in a bare strip on lower adaxial polyp wall. Coenenchymal scales in two layers: outer layer composed of smooth scales; inner layer composed of small irregularly shaped tuberculate spheroids.

Discussion. Although originally placed in *Primnoella*, Bayer (1996b) excluded *P. gracilis* from that genus but did not suggest an alternative. López-González et al. (2002) eventually established a new genus for it. Although the calyces are slightly flattened, *Arntzia* differs from *Primnoella* primarily in having marginal scales that do not overlap or override the bases of the operculars. It also differs in having fused calycular bases, nonappressed calyces, and internally ridged opercular scales. Furthermore, it seems to be unique among the primnoids in having a thin layer of tissue covering its scales.

Distribution. Weddell Sea, Scotia Arc, and Ross Sea, 64–604 m.

Type Species. *Primnoella gracilis* Molander, 1929, by original designation. The holotype is deposited at the Stockholm Museum of Natural History (1140).

## 11. *Thouarella* (*Thouarella*) Gray, 1870

FIGURE 6G–L

*Primnoa*.—Valenciennes, 1846 [in part].

*Thouarella* Gray, 1870:45.—Studer, 1887:50.—Wright and Studer, 1889: xlix, 59–61 [in part].—Versluys, 1906:22–24 [in part: "Isolirte and Antarctic Gruppe"].—Kükenthal, 1908:10–11 [in part]; 1912:292–311 [in part: "*antarctica* and *kollikeri*-Gruppe"].—Bayer, 1961:294 [in part: illustrated key to genus]; 1981b:936 [in part: key to genus].—Williams, 1992:277.

*Primnodendron* Nutting, 1912:70.

*Rhopalonella* Roule, 1908:2–3.

*Thouarella* (*Parathouarella*) Kükenthal, 1915:150 [key to species]; 1919:425–426 [key to species]; 1924:296–297 [key to subgenera and species].

*Thouarella* (*Thouarella*).—Bayer, 1956:F220.—Bayer and Stefani, 1989:455 [key to subgenus].—Cairns, 2006:176.

Diagnosis. Colonies of most species branch in a bottlebrush fashion, although two species have pinnate branching. Calyces isolated (not in pairs of whorls), arranged in no apparent order on all sides of branches and stand perpendicular or inclined upward (type species) on branch (Figure 6g). Well-developed operculum present. Marginal scales arranged in two circles of four that alternate with one another, the circumference of the distal polyp not being large enough to accommodate eight adjacent marginal scales; distal margins of marginals spinose, folding over lower portion of operculars, forming a circumoperculum. Inner face of operculars and marginals bear ornate keels, each longitudinal keel bearing several smaller ridges oriented at right angles, altogether forming a foliate process (Figure 6i–j); distal edges of same scales finely serrate. Polyps protected by six longitudinal rows of body wall scales, the adaxial face being covered by enlarged inner-lateral scales, resulting in complete coverage of polyp. Outer and inner faces of body wall scales radially ridged distally. Coenenchymal scales in two layers: outer layer composed of irregularly shaped scales with granular outer surface; inner layer composed of small spheroids.

DISCUSSION. Much of the taxonomic history of this subgenus was summarized in Cairns (2006).

An additional specimen of the type species *T. antarctica* is reported herein: *Hero* 715-873, 54°34′S, 65°50′W (Tierra del Fuego), 118 m, USNM 97966.

DISTRIBUTION. Subantarctic, South Africa, off Chile, western Atlantic from Burdwood Bank to northern Florida, Japan, Aleutian Islands, 60–1,005 m.

TYPE SPECIES. *Thouarella*: *Primnoa antarctica* Valenciennes, 1846, by monotypy. Type deposited at the MNHNP.

*Primnodendron*: *P. superbum* Nutting, 1912, by monotypy. The holotype is deposited at the USNM (30691).

*Rhopalonella*: *R. pendulina* Roule, 1908, by monotypy. Type presumably deposited at the MNHNP.

*Parathouarella*: *Primnoa antarctica* Valenciennes, 1846, by virtue of including the type species of the genus in this subgenus. Being the nominate subgenus, it was unnecessary for Kükenthal (1915) to give it another name.

## 12. *Thouarella* (*Euthouarella*) Kükenthal, 1915

FIGURE 6M–S

*?Hookerella* Gray, 1870:45.

*Plumarella*.—Studer, 1878:648 [in part: *P. hilgendorfi*].

*Thouarella*.—Wright and Studer, 1889:59 [in part].—Versluys, 1906:24 [in part: *hilgendorfi*-Gruppe].—Kükenthal, 1912:297–299 [in part: *hilgendorfi*-Gruppe].

*Thouarella* (*Euthouarella*) Kükenthal, 1915:149–150 [in part: not *T. coronata*, key to subgenus and species]; 1919:414–415 [key to subgenus and species]; 1924:292 [key to species].—Bayer, 1956:F220.—Bayer and Stefani, 1989:455 [key to subgenus].—Cairns, 2006:176, 187–188.

DISCUSSION. Differs from the nominate subgenus only in having calyces arranged in pairs or whorls (i.e., not isolated) (Figure 6m) and in having primarily alternately pinnately branched colonies (e.g., type species), although some species are bottlebrush in shape.

DISTRIBUTION. Western Pacific, East Africa, North Atlantic, Indian Ocean, 256–1,644 m.

TYPE SPECIES. *Euthouarella*: *Plumarella hilgendorfi* Studer, 1878, by subsequent designation (Bayer, 1956:F220). The type is presumably deposited at the ZMB; a fragment of the type is deposited at the ZMA (Coel. 3085) (van Soest, 1979:119).

*Hookerella*: *H. pulchella* Gray, 1870, by monotypy. Type not traced.

## 13. *Thouarella* (*Diplocalyptra*) Kinoshita, 1908

FIGURE 7A–H

*Thouarella* (*Diplocalyptra*) Kinoshita, 1908c [15 Nov]:454, 457 [key to subgenus], pl. 17, fig. 2 [in Japanese, English translation at Smithsonian]; 1908d [15 Dec]:517–519 [in Japanese, English translation at Smithsonian]; 1908e [25 Dec]:52 [key to subgenus, in German].

*Thouarella* (*Euthouarella*).—Kükenthal, 1915:151 [in part]; 1924:296 [in part].

DIAGNOSIS. Colony uniplanar and dichotomously branched. Calyces arranged in pairs and whorls of three (Figure 7b), the calyces oriented perpendicular to branch. Operculum small; inner face of operculars keeled. Marginals arranged in two circles of four that alternate with one another, the circumference of distal polyp not being large enough to accommodate the eight marginal scales; distal tips of marginals acutely pointed (almost spinose) and fold over operculars, forming a circumoperculum (Figure 7a, c–d); distal inner face of each marginal and all other body wall scales bear multiple, prominent longitudinal ridges. Polyps protected by six longitudinal rows of almost smooth body wall scales, the adaxial face being covered by enlarged lateral scales, resulting in complete coverage of the polyp; however, the orderly linear arrangement sometimes disrupted on lower half of calyx. Coenenchymal scales in two layers, the inner layer composed of tuberculate spheroids and rods.

DISCUSSION. In the early twentieth century (see synonymy) *Diplocalyptra* was considered to be a subgenus of *Thouarella*, distinguished from other subgenera by its dichotomous mode of branching. It was later essentially synonymized with *Thouarella*, and forgotten, but is once again considered as a separate subgenus on the basis of its dichotomous branching pattern.

DISTRIBUTION. Known only from off Japan, 146 m.

TYPE SPECIES. *Thouarella* (*Diplocalyptra*) *coronata* Kinoshita, 1908c, by monotypy. The holotype is deposited at the University Museum, University of Tokyo (G-223). Part of type is also deposited at the USNM (50118).

## 14. *Thouarella* (*Epithouarella*) Kükenthal, 1915

FIGURE 7I–M

*Thouarella*.—Wright and Studer, 1889:66 [in part]—Versluys, 1906:35 [in part: part of *antarctica* Gruppe]—Kükenthal, 1907:205 [in part: *T. crenelata*]; 1912:301 [in part: *antarctica* Gruppe].

*Thouarella* (*Epithouarella*) Kükenthal, 1915:150–151 [key to subgenus and species]; 1919:435 [key to subgenus and species]; 1924:299 [key to subgenus and species].—Bayer, 1956:F220.

DISCUSSION. This subgenus differs from the nominate subgenus only in having marginal scales that are pointed and deeply serrate (Figure 7k–l), not spinose. All three species have a bottlebrush branching morphology.

Two additional records of the type species, *T. crenelata,* are reported herein: *Eltanin*-1536, 54°29′S, 39°18′W (off South Georgia), 659–686 m, 8 February 1966, many colonies, USNM 84335; and *Hero* 824-26-1, 64°14′18″S, 61°57′36″W (Brabant Island, Antarctic Peninsula), 238–285 m, one colony, USNM 98086.

DISTRIBUTION. Antarctic and subantarctic: Bouvet Island, Tristan de Cunha, South Georgia, Antarctic Peninsula, off southern Chile, 106–686 m.

TYPE SPECIES. *Thouarella crenelata* Kükenthal, 1907, by subsequent designation (Bayer, 1956:F220). Types not traced.

## 15. *Metafannyella,* new genus

FIGURE 7N–U

*Fannyella*.—Bayer, 1998:176–188 [in part: *Fannyella eos, aurora, lepidota, mawsoni*].

DIAGNOSIS. Colonies uniplanar and dichotomously branching, sometimes lyrate. Calyces usually arranged in whorls of up to seven but occasionally arranged in spirals, the appressed calyces facing upward. Well-developed operculum present; inner face of opercular scales longitudinally keeled. Eight marginal scales fold over the operculars, forming a circumoperculum; distal edges of marginals rounded. Polyp protected by eight longitudinal rows of body wall scales, the two adaxial rows short but complete, resulting in a complete coverage of polyp. Outer face of body wall scales smooth except for simple granules or tubercles localized along a curved, transverse, thickened ridge (Figure 7o) that separates exposed part of sclerite from its tuberculate base embedded in the body wall and overlapped by edge of subjacent scale; distal portion of inner face bears prominent radial ridges (Figure 7s). Coenenchymal scales in two layers: outer layer composed of smooth scales (Figure 7r), inner layer composed of small irregularly shaped tuberculate rods (Figure 7p).

DISCUSSION. Bayer (1998) placed these four species (Table 4) in the genus *Fannyella* but implied that more study was necessary to understand the *Fannyella* species complex. These four species differ from *Fannyella* in having "weakly developed" ascus scales, but, in fact, the body wall scales do not form cup-like platforms at all; instead, there is only a thickened transverse ridge across each body wall scale on which there are usually a few granules (Figure 7o). *Metafannyella* also differs from typical *Fannyella* in having prominently keeled opercular scales (Figure 7u) and a complete coverage of the adaxial side of the polyp.

DISTRIBUTION. Antarctic: Auckland Rise, Antarctic Peninsula, Scotia Sea, Ross Sea, Weddell Sea, 265–1,280 m.

ETYMOLOGY. Greek *meta* = near + *Fannyella*, implying a close relationship with the genus *Fannyella*. Gender: feminine.

TYPE SPECIES. *Fannyella lepidota* Bayer, 1998, here designated. The holotype is deposited at the USNM (82961).

## 16. *Fannyella* (*Fannyella*) Gray, 1872

FIGURE 8A–H

*Fannyella* Gray, 1872:744.—Bayer, 1990:774; 1998:164–165 [in part: *F. rossi, F. kuekenthali*].

*Ascolepis* Thomson and Rennet, 1931:20–23.—Bayer, 1981b:936 [in part: not fig. 66, key to genus].—Bayer and Stefani, 1989:454 [key to genus].

DIAGNOSIS. Colonies uniplanar and dichotomously branching (often lyrate). Calyces arranged in whorls of up to 10, the appressed calyces facing upward; brood chamber in base of polyps common. Well-developed operculum present; inner face of operculars bear multiple longitudinal ridges (but not keeled). Eight marginal scales fold over the bases of the opercular scales, forming a circumoperculum; distal edges of marginals pointed or rounded but never spinose. Polyps protected by six longitudinal rows of body wall scales, the two abaxial rows consisting of up to 16 scales, the outer- and inner-lateral rows having fewer scales; adaxial row usually absent, resulting in a naked adaxial face (Figure 8b). Body wall scales distinctively shaped, the outer surface with a dentate or smooth transverse crest that divides the scale into a distal, more or less concave or oblique cup-shaped part, and a proximal, tuberculate base, these chalice-like sclerites termed ascus scales (Figure 8c–d). Distal surface of ascus scales smooth, proximal surface tuberculate, and edge of cup-shaped cavity granular to finely serrate. Coenenchymal scales in two layers: outer layer composed of thick polygonal smooth scales, inner layer composed of irregular tuberculate sclerites and small spindles (Figure 8f).

Discussion. This long-overlooked generic name was resurrected by Bayer (1990), who redescribed and figured its type species, *F. rossii*. He (Bayer, 1998) later placed eight additional species in the genus but was never comfortable with the expanded definition of the genus needed to accommodate those species (Bayer, 1998, personal communication, 2001). Most of the species he placed in *Fannyella* have been reattributed herein to other genera and subgenera to be consistent with Bayer's view of primnoid taxonomy adopted toward the end of his career.

Distribution. Antarctic: Ross Sea, Weddell Sea, South Shetland Islands, Antarctic Peninsula, Coates Land, 46–852 m.

Type Species. *Fannyella*: *F. rossi* Gray, 1872, by monotypy. The neotype (designated by Bayer, 1990) is deposited at the Australian Museum (G-13237).

*Ascolepis*: *A. splendens* Thomson and Rennet, 1931, subsequent designation (Bayer, 1990:774). The lectotype (designated by Bayer, 1990) is deposited at the Australian Museum (G-13237), the same specimen as the neotype of *F. rossi*, making them objective synonyms.

## 17. *Fannyella* (*Scyphogorgia*), new subgenus

FIGURE 8I–P

*Stenella* (*Dasystenella*).—Gravier, 1913:590; 1914:63–69.

*Thouarella* (*Euthouarella*).—Broch, 1965:29 [in part: *T. abies*].

*Thouarella*.—Bayer, 1998:171, 173 [in part: *T. abies*].

Diagnosis. See Table 3 and discussion below.

Discussion. The subgenus is monotypic (Table 4). As noted by Bayer (1998:171, 173), *Thouarella abies* Broch, 1965 (herein synonymized with *Stenella liouvillei*) is remarkably similar to *Ascolepis spinosa* (herein considered to be the type species of the new subgenus *Fannyella* (*Cyathogorgia*)). Indeed, they would seem to be identical except for their branching mode, which is of the bottlebrush type in *F. liouvillei*. On the basis of the high systematic value placed on branching mode as well as personal communications with Bayer after 1998, we propose creating a new subgenus for this species. Otherwise the subgeneric diagnosis of *F.* (*Cyathogorgia*) (see below) may be used for *F.* (*Scyphogorgia*).

Additional records of *F. liouvillei* are posted herein from the Antarctic Peninsula (USNM 81545, 82114, 82980), South Orkney Islands (USNM 58156), and the Ross Sea (USNM 82981).

Distribution. South Orkney Islands, Antarctic Peninsula, Ross Sea, 100–550 m.

Etymology. Greek *skyphos* = cup + *gorgia*, in allusion to the cup-shaped body wall ascus scales

Type Species. *Stenella* (*Dasystenella*) *liouvillei* Gravier, 1913, here designated. The holotype is presumed to be deposited at the MNHNP.

## 18. *Fannyella* (*Cyathogorgia*), new subgenus

FIGURE 9A–G

*Ascolepis*.—Thomson and Rennet, 1931:22–23 [in part: *A. spinosa*].

*Fannyella*.—Bayer, 1998:171–173 [in part: *F. spinosa*].

Diagnosis. Colonies multiflabellate and dichotomously branching, verging on pinnate. Calyces arranged in whorls of up to 10, the appressed calyces facing upward. A small operculum present; inner face of operculars bear multiple longitudinal ridges but not a keel. Eight ascus-type marginal scales (Figure 9b) fold over the operculum, forming a circumoperculum; distal edges of marginals spinose, inner surface bearing a longitudinal keel. Polyps protected by eight longitudinal rows of body wall ascus scales (Figure 9c); the abaxial submarginals are also spinose; those more proximal progressively less exsert. Perimeter of cup-like structure of ascus scales finely serrate. Adaxial row quite short but present, resulting in complete coverage of the polyp. Coenenchymal scales in two layers: outer layer composed of plates with a smooth outer surface (Figure 9f), inner layer composed of tuberculate spindles.

Discussion. *Cyathogorgia* is monotypic (Table 4), differing from the nominate subgenus in having spinose marginal (and submarginal) scales that have a keeled inner surface and in having eight rows of body wall scales, which completely cover the polyp. Although Bayer (1998) placed *A. spinosa* in *Fannyella*, in later unpublished notes and conversations, he implied that this species should represent a different genus. Because the differences are so few, a middle course is taken herein, i.e., the establishment of a subgenus for this species.

Distribution. Antarctic: Ross Sea, South Orkney Island, Balleny Islands, Coats Land, 55–485 m.

Etymology. Greek *kyathos* = cup + *gorgia*, in allusion to the cup-shaped body wall ascus scales

Type Species. *Ascolepis spinosa* Thomson and Rennet, 1931, here designated. The type is purported to be deposited at the National Museum of Victoria, Melbourne.

## 19. ***Onogorgia*, new genus**

FIGURE 9H–M

*Caligorgia*.—Molander, 1929:60 [in part: *C. nodosa*].

*Ascolepis*.—Bayer, 1981b:934 [fig. 66], 936 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].

*Fannyella*.—Bayer, 1998:197–204 [in part: *F. nodosa*].

Diagnosis. Colonies unbranched (flagelliform). Calyces arranged in whorls (Figure 9j) of up to 24, the appressed calyces facing upward; calyces within a whorl are slightly fused basally. Well-developed operculum present; inner face of operculars bear multiple longitudinal ridges but no single keel. Eight marginal scales fold over operculars, forming a circumoperculum; distal edges of marginals elongate and pointed but not spinose. Polyps protected by eight longitudinal rows of body wall scales, the two abaxial rows consisting of up to 14 scales; scales in lateral rows equal in number and size to the abaxials, but adaxial scales much smaller and somewhat randomly arranged (Figure 9i), nonetheless resulting in complete coverage of polyp. Body wall scales are ascus scales (Figure 9k), quite similar to those of *Fannyella*, having a smooth distal surface and tuberculate proximal surface, but unlike *Fannyella*, the perimeter of the cup-like structure is coarsely serrate (Figure 9l). Serrations on distal portion of body wall scales are on the inner side and correspond to radial ridges, whereas serrations on the proximal portion of the scales are on the outer side, such that inner distal ridges of one scale intercalate with proximal serrations of the more distal scale, providing stability and alignment in opening and closing of the calyx. Coenenchymal scales in two layers: outer layer composed of flat or ascus-type scales, inner layer composed of irregular tuberculate sclerites.

Discussion. Bayer (1998) placed the type species in the genus *Fannyella* s.l., noting the close resemblance of the ascus body wall scales between the two genera. *Onogorgia* differs from *Fannyella* (Table 3) in having a flagelliform colony, eight longitudinal rows of body wall scales and, thus, a completely covered polyp, and a coarse serration of the proximal outer edges and a corresponding coarse ridging of the distal inner edges of the body wall scales. The genus is monotypic.

Distribution. Antarctic: Ross Sea, Scotia Sea, South Shetland Islands, South Georgia, Antarctic Peninsula, 22–433 m.

Etymology. Greek *onos* = wine cup or beaker + *gorgia*, in allusion to the cup-shaped body wall ascus scales. Gender: feminine.

Type Species. *Caligorgia nodosa* Molander, 1929, here designated. Types reputedly deposited at the Stockholm Museum of Natural History.

## 20. ***Pyrogorgia*, new genus**

FIGURE 10A–I

Diagnosis. Colonies uniplanar and dichotomously branched (often lyrate). Calyces arranged in whorls of up to seven, the appressed calyces facing upward. Well-developed operculum present; inner face of operculars bear multiple longitudinal ridges (Figure 10g; but not keeled). Eight marginal scales fold over the bases of the operculars, forming a circumoperculum; distal edges of marginals finely serrate. Polyps protected by eight longitudinal rows of body wall scales, those of the adaxial rows somewhat smaller but completely covering polyp; body wall scales often irregularly arranged on lower half of polyp. Outer surface of body wall scales covered with radiating spinose ridges (Figure 10b–c). Coenenchymal scales in two layers: outer layer composed of spinose platelets, inner layer composed of small tuberculate spheroids (Figure 10h–i).

Discussion. Although the type species was originally placed in *Fannyella* by Bayer (1998), the lack of ascus body wall scales would argue for a different generic assignment.

Distribution. Tierra del Fuego, 384–511 m

Etymology. Greek *pyros* = fire + *gorgia*, an allusion to Tierra del Fuego. Gender: feminine.

Type Species. *Fannyella lemnos* Bayer, 1998, here designated. The holotype is deposited at the USNM (58392).

## 21. *Amphilaphis* Studer and Wright in Studer, 1887

FIGURE 10J–Q

*Amphilaphis* Studer and Wright in Studer, 1887:50–51.—Wright and Studer, 1889:xlix, 70–71.—Versluys, 1906:20–22.—Kinoshita, 1908e:49–50 [key to genus].—Thomson and Mackinnon, 1911:680.—Bayer, 1981b:936 [key to genus].

*Thouarella*.—Kükenthal, 1912:307 [in part: "*regularis*-Gruppe"].

*Thouarella* (*Amphilaphis*).—Kükenthal, 1915:149 [key to subgenus and species]; 1919:407–409 [key to subgenus and species]; 1924:288–289 [key to subgenus and species].

Diagnosis. Colonies uniplanar, alternately pinnately branched. Calyces arranged in irregular spirals along branch (Figure 10j) or isolated; calyces inclined upward. Well-developed operculum present; inner face of operculars bears multiple ridges. Marginals arranged in two circles of four that alternate with one another, the circumference of distal polyp not being large enough to accommodate eight marginal scales; eight marginal scales fold over bases of operculars forming a circumoperculum; distal edges of marginals pointed (Figure 10m). Polyps protected by eight longitudinal rows of equal-sized body wall scales that completely cover polyp; body wall scales radially ridged on outer and inner surfaces (Figure 10n–o). Coenenchymal scales in two layers: outer layer composed of irregularly shaped scales with serrate edges, inner layer composed of small spheroids.

Discussion. Originally described as a separate genus, *Amphilaphis* was later considered by Kükenthal (1915) to be a subgenus, but it was finally reestablished as a genus by Bayer (1981b) but curiously ignored by him in later general works (Bayer, 1956; Bayer and Stefani, 1989). *Amphilaphis* differs from *Thouarella* in having eight complete longitudinal rows of equal-sized body wall scales and pinnately branched colonies. The six species currently assigned to the genus are tentatively placed there at best, as the genus is badly in need of revision. The diagnosis above is based on the type species.

Distribution. Tristan de Cunha, Bouvet I., Galápagos, Antarctic, Hawaii, 55–3,182 m.

Type Species. *A. regularis* Wright and Studer, 1889, by subsequent monotypy (Wright and Studer, 1889). Syntypes are deposited at the BM (1889.5.27.60, 1889.7.5.1-15, 1894.11.20.1, 1932.12.8.7); a fragment of the type is also deposited at the ZMA (Coel. 3085) (van Soest, 1979) and as SEM stub B576 (USNM).

## 22. *Mirostenella* Bayer, 1988

FIGURE 10R–A′

*Mirostenella* Bayer, 1988:251–252.—Bayer and Stefani, 1989:454 [key to genus].

Diagnosis. Colonies branch in a regular, planar, dichotomous manner, the calcified axis interrupted by organic nodes at points of bifurcation. Calyces arranged in pairs or whorls of three or four, the calyces inclined slightly upward (Figure 10r); brooding polyps common. Well-developed operculum present, operculars smooth (not keeled or ridged) on distal portion of inner surface (Figure 10w). Eight elongate marginals, each with a prominent spine (Figure 10x–y), form a nonfolding crown around the operculum. Polyps completely covered by eight rows of body wall scales, these scales becoming smaller and somewhat disorganized toward base of calyx. Outer surface of all sclerites except for coenenchymals smooth. Coenenchymals arranged in one layer, their outer surface covered with coarse granules (Figure 10z, a′), as in *Acanthoprimnoa*.

Discussion. An additional specimen from close to the type locality is reported herein, which allows a proper illustration of polyp morphology (Figure 10r–a′) as well as an extension of the depth range: R/V *Prof. Siedlecki* 610-29, 54°32′S, 39°05′W, 201–210 m, 3 December 1986, USNM 84344.

In an unpublished manuscript, Bayer diagnosed a second species of *Mirostenella* from three stations off the Falkland Islands (493–1,647 m), differing from the type species in having alternately pinnately branched colonies, much longer marginal scales, and lack of organic nodes at the branching axils. He thus implied that the peculiar organic nodes of *Mirostenella* may be only of species level value. *Mirostenella* is thus keyed twice in the key to the genera, allowing for both branching morphologies. A third species is also placed in the genus as a new combination, *M. delicatula* (Thomson and Rennet, 1931), from Macquarie Island. The type is deposited at the AM (G13266).

Although similar to the family Isididae in the nature of its jointed axis, the scales of *Mirostenella* have the typical primnoid cruciform extinction pattern. If the unique character of organic nodes is ignored, *Mirostenella* is remarkably similar to *Plumarella*, as noted by Bayer (1988), differing primarily in having calyces arranged in whorls and pairs, not in an alternate biserial manner.

DISTRIBUTION. South Georgia, Falkland Islands, 201–1,647 m; Macquarie Island, 2,742 m.

TYPE SPECIES. *Mirostenella articulata* Bayer, 1988, by original designation. The holotype is deposited at the USNM (79959).

## 23. *Acanthoprimnoa* Cairns and Bayer, 2004

FIGURE 11A–J

"*Acanthoprimnoa*" Bayer and Cairns (Verrill), 2004:pls. 10, 13, 27, 141 [nomen nudum].

*Acanthoprimnoa* Cairns and Bayer, 2004c:470.

DIAGNOSIS. Colonies uniplanar, often plumose, and usually pinnately branched in an alternating manner, although some specimens are dichotomously branched or lyrate. Calyces occur in an alternating biserial arrangement, the calyces inclined upward (not appressed to branch); brood polyps common. Well-developed operculum present, the opercular scales bearing multiple low ridges on their inner distal surface (but not keeled) and smooth (not tuberculate) proximally (Figure 11c). The eight marginal scales do not fold over operculars and usually bear a prominent spine (Figure 11g–h). Lateral edges of opercular and body wall scales (including marginals) have a finely pectinate margin. Polyps protected by eight fully developed longitudinal rows of body wall scales. Outer surfaces of body wall and coenenchymal scales coarsely granular to nodose; inner surfaces smooth (Figure 11j; not tuberculate). Coenenchymal scales in one layer.

DISCUSSION. *Acanthoprimnoa* is morphologically most similar to *Plumarella*, but, following Verrill's lead, Cairns and Bayer (2004c) established the new genus *Acanthoprimnoa*, which differs from *Plumarella* by lacking tubercles on the inner surfaces of its sclerites (however, *Plumarella penna* also lacks tubercles), having pectinate distal and lateral edges of the body wall and opercular scales, and having coarsely granular coenenchymal scales.

DISTRIBUTION. Caribbean, Japan, 45–686 m.

TYPE SPECIES. *Plumarella goesi* Aurivillius, 1931, by original designation. Syntypes are deposited at the Stockholm Museum (#28) and USNM (44192). The type species was redescribed and figured by Cairns and Bayer (2004c).

## 24. *Plumarella* Gray, 1870

FIGURE 11K–S

*Cricogorgia* Milne Edwards, 1857:6, pl. B2, fig. 6 [nomen nudum].

*Plumarella* Gray, 1870:36.—Studer, 1887:51.—Wright and Studer, 1889: xlix, 73–74.—Versluys, 1906:13–14.—Kinoshita, 1908a:6–8.—Kükenthal, 1915:144–145 [key to genus and species]; 1919:340–343 [key to genus and species]; 1924:255 [key to genus and species].—Deichmann, 1936:155 [key to genus].—Bayer, 1956:F220; 1961:293 [illustrated key to genus]; 1981b:936 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].—Cairns and Bayer, 2004c:448–449 [key to western Atlantic species].

DIAGNOSIS. Colonies uniplanar, often plumose, and usually pinnately branched in an alternating manner (e.g., type species); some species dichotomously branched. Calyces occur in an alternating biserial arrangement (e.g., type species) (Figure 11k) or, rarely, in an irregular fashion; calyces inclined upward or closely appressed (type species) to branch. Well-developed operculum present, the opercular scales smooth on their inner distal surface (not keeled) and tuberculate to smooth proximally; the operculars of the type species are uniquely shaped with a broad base and a very slender distal part (Figure 11o–p). The eight marginal scales do not fold over the operculars and have a variety of distal shapes, including serrate (type species), straight, pointed, and prominently spinose. Polyps protected by eight longitudinal rows of body wall scales, those on the adaxial side sometimes fewer in number (type species). Outer surfaces of sclerites smooth or slightly granular; inner surfaces tuberculate in regions where they overlap the outer surface of another sclerite (as in most primnoids). Coenenchymal sclerites in one layer of scales that are externally smooth or slightly granular (Figure 11n; type species).

DISCUSSION. The 20 species in the genus are listed in Table 4. Characters used to distinguish species include shape of the distal edge of the opercular and marginal scales, number of scales in the abaxial body wall row, branching mode, and the sculpture on outer surface of scales. The type species, *P. penna*, differs from most of the species currently placed in the genus in several characters.

Its opercular scales are uniquely shaped (Figure 11o–p) and so slender that they do not form a complete covering of the polyp; they articulate to form a flat operculum over the polyp. The calyces are quite small (only 0.4 mm long and 0.25 mm in diameter) and are closely appressed to the branch, almost adnate, having only very short (two or three scales) adaxial rows of body wall scales. Coenenchymal scales are elongate and have coarse granules on their edges (Figure 11n). Finally, none of the sclerites appear to have tubercles on their inner surface, a character that blurs the distinction between *Plumarella* and *Acanthoprimnoa*.

Distribution. Western Pacific, Patagonia, northwest Atlantic, 10–1,914 m.

Type Species. *Gorgonia penna* Lamarck, 1815, by subsequent designation (Wright and Studer, 1889:73). Type deposited at MNHNP (fide Versluys, 1906:18) and a fragment of the type at the ZMA (Coel. 3085) (van Soest, 1979). The type species is well described and figured by Versluys (1906:18–20) and Fabricius and Alderslade (2001), the latter in color.

## 25. *Callogorgia* Gray, 1858

FIGURE 12A–D

*Callogorgia* Gray, 1858:286.—Bayer, 1956:F220; 1961:294 [illustrated key to genus]; 1981b:938 [key to genus]; 1982:119–123 [in part: key to Indo-Pacific species, genus synonymy].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1998:162–163.—Cairns and Bayer, 2002:841–845 [key to western Atlantic species].

*Calligorgia* Gray, 1870:35 [unjustified emendation].—Studer, 1887:51.

*Callicella* Gray, 1870:37.

*Xiphocella* Gray, 1870:56.

*Caligorgia* Wright and Studer, 1889:75–77 [in part; unjustified emendation].—Versluys 1906:55–58 [in part].—Kinoshita, 1908a:34.—Kükenthal, 1915:146 [key to genus and species]; 1919:362–366 [in part: key to species]; 1924:267–269 [in part: key to species].

Diagnosis. Colonies usually pinnately branched in an alternating manner (e.g., type species), dichotomously branched in one plane, or, rarely, opposite pinnately branched. Calyces arranged in whorls of up to 12, the appressed calyces facing upward (Figure 12a). Well-developed operculum present, the operculars ridged on their inner surface. Eight marginal scales present, which do not fold over operculars. Polyps protected by four to eight longitudinal rows of up to 12 body wall scales, the abaxials occurring in fully developed rows but lateral and adaxial scale rows progressively shorter toward adaxial side; in some species adaxial and even inner-lateral body wall scales absent, resulting in the lower adaxial body wall being naked. Outer surface of body wall scales smooth, granular, or covered with prominent radiating or reticulate ridges (Figure 12b); distal edge of inner surface of body wall scales radially ridged, these ridges sometimes continuous with the ridges of the outer surface. Coenenchymal scales arranged in one layer, outer surface usually granular.

Discussion. Many of the listings in the genus synonymy must be listed as “in part” because species now attributed to *Fanellia* were customarily placed in *Callogorgia*. The 26 valid species known in the genus are listed in Table 4, most of these keyed by either Bayer (1982) or Cairns and Bayer (2002), both of whom extensively discuss the characters used to identify species. Bayer (1982) distinguished two groups of species within the genus based on the sculpturing of the body wall scales (granular versus crested) but did not suggest taxonomic distinction at any level.

Distribution. Indo-Pacific, North Atlantic, 37–2,472 m.

Type Species. *Callogorgia*: *Gorgonia verticillata* Pallas, 1766, by monotypy. Type not traced. The type species was well described and illustrated by Carpine and Grasshoff (1975).

*Callicella*: *C. elegans* Gray, 1870, by monotypy. The dry types are deposited at the BM (1965.12.15.6, 8).

*Xiphocella*: *Gorgonia verticillata* sensu Esper, 1797, by monotypy. Type not traced.

## 26. *Fanellia* Gray, 1870

FIGURE 12E–M

*Fanellia* Gray, 1870:46.—Bayer, 1982:134–135 [key to species].—Bayer and Stefani, 1989:470–471 [key to genus and all species].

Diagnosis. Colonies usually dichotomously branched in one plane (e.g., type species), although some species branch in a pinnate or bushy dichotomous manner. Calyces arranged in whorls (type species) of up to 16 and, in some species, in pairs, the appressed calyces facing upward. Well-developed operculum present; operculars ridged on their inner surface. The eight marginal scales do not fold over operculars. Polyps protected by four to eight longitudinal rows of up to 11 thick body wall scales, the abaxials constituting fully developed rows but lateral and adaxial scale rows progressively shorter toward adaxial side; in some species adaxial and even inner-lateral body wall scales absent, resulting in a naked lower adaxial body wall. When inner-lateral scales absent, usually an adaxial wing-like projection of the outer lateral covers this region. Outer surface of body wall scales, operculars, and coenenchymal scales all covered with prominent tubercles, often arranged in ridges (Figure 12h, j–k). Coenenchymal scales in two layers, including an inner layer of tuberculate spheroids (Figure 12m) that separates the stem canals; coenenchymal scales polygonal and quite thick.

DISCUSSION. As Bayer (1982) discussed, *Fanellia* is morphologically very similar to *Callogorgia*, differing primarily in the nature of the sculpture of the outer sclerite surface, which is tuberculate to nodular for *Fanellia* instead of granular to smooth for *Callogorgia*. Also, species of *Fanellia* are predominantly dichotomous in branching, whereas species of *Callogorgia* are predominantly pinnate, although both genera contain species with the alternately branching mode. The eight *Fanellia* species are listed in Table 4, all of which are keyed by Bayer and Stefani (1989).

DISTRIBUTION. Western and central Pacific Ocean from New Caledonia to Alaska, 92–1,028 m.

TYPE SPECIES. *Primnoa compressa* Verrill, 1865, by monotypy. The type could not be located at the Yale Peabody Museum or Museum of Comparative Zoology and is presumed to be lost. The type species is well described and illustrated by Bayer (1982).

## 27. *Paranarella* Cairns, 2007

FIGURE 13A–G

*Paranarella* Cairns, 2007a:258–259.

DIAGNOSIS. Colonies dichotomously branched in one plane, but with long terminal branches. Calyces arranged in whorls of up to five, appressed to axis, but of unknown orientation. Well-developed operculum present, the operculars prominently keeled on inner surface. Polyps protected by five pairs (Figure 13b) of large abaxial scales, one pair of both inner- and outer-lateral marginal scales, and three or four pairs of vestigial adaxial scales (Figure 13d), leaving the lower adaxial body wall bare. Thus, whereas there are eight marginal scales, there are only two longitudinal rows of large scales. Coenenchymal scales arranged in one layer, prominently keeled (Figure 13c).

DISCUSSION. Only one species is known from this recently described genus (Table 4). It differs from *Narella* in having one pair of both inner- and outer-lateral scales, and in having five pairs (not three or four pairs) of abaxial body wall scales.

DISTRIBUTION. New England Seamounts, 3,855 m.

TYPE SPECIES. *P. watlingi* Cairns, 2007, by original designation. Holotype deposited at the USNM (1096721).

## 28. *Primnoa* Lamouroux, 1812

FIGURE 13H–P

*Primnoa* Lamouroux, 1812:188.—Studer, 1887:49.—Wright and Studer, 1889:xlviii.—Versluys, 1906:84–85.—Kükenthal, 1915:143 [key to genus]; 1919:357–360 [key to genus]; 1924:265–266 [key to genus and species].—Bayer, 1956:F220; 1961:294 [illustrated key to genus]; 1981b:937 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].—Cairns and Bayer, 2005:226–228 [revision and key to species].

*Lithoprimnoa* Grube, 1861:174–175.

DIAGNOSIS. Colonies dichotomously branched and usually bushy, some reaching a height of 2 m. Calyces closely spaced and randomly arranged on all branch surfaces, the appressed calyces facing downward. Well-developed operculum present, the operculars keeled on inner surface. Polyps large and fleshy, each polyp protected by two rows of four or more large abaxial scales, sometimes arranged in an irregular manner, two short inner-lateral rows of two or three smaller scales (including the marginals), and two even shorter rows of two (including the marginals) adaxial scales, resulting in six longitudinal rows, but four of them composed of very small and few scales; adaxial side of body wall predominantly bare (Figure 13i). There is also a crown of eight large, concave marginals, the adaxial marginals usually smaller than other marginals. Coenenchymal scales arranged in one layer. Tentacular rods are often present (Figure 13j).

DISCUSSION. The four Recent species and one variety (Table 4) in this genus were described, illustrated, and keyed by Cairns and Bayer (2005); the two Paleocene fossil species listed in Table 4 from Denmark (Nielsen, 1913, 1925) are highly doubtful identifications, Bayer (1992) synonymizing one of them, *P. gracilis,* with the lithotelestid *Epiphaxum auloporoides* (Lonsdale, 1850). Characters used to distinguish species include the size and shape of the basal scales, size and shape of the polyps, and the shape of the marginal scales. Distribution patterns (Watling and Auster, 2005) and characteristics of the massive axis of this genus have been the subject of many studies, including aspects of growth rate (Andrews et al., 2002), and paleoceanographic isotopic analysis (Heikoop et al., 2002; Sinclair et al., 2005; Sherwood et al., 2005).

DISTRIBUTION. North Pacific, North Atlantic, subantarctic South Pacific, 9–1,020 m.

TYPE SPECIES. *Primnoa*: *Gorgonia lepadifera* Linnaeus, 1767 (= *Gorgonia resedaeformis* Gunnerus, 1763), by monotypy. Type not traced.

*Lithoprimnoa*: *L. arctica* Grube, 1861, by monotypy. Type not traced.

## 29. *Australogorgia,* new genus

FIGURE 13Q–A′

DIAGNOSIS. Colonies dichotomously branched in one plane in a regular manner. Calyces large, with a tendency to be arranged unilinearly on one branch face, the appressed calyces oriented perpendicular to branch to downward against the branch. Well-developed operculum present, the operculars prominently keeled on inner surface; tentacles contain numerous, small, rods (Figure 13t). Polyps protected by two longitudinal rows of three large abaxial body wall scales, one pair of slightly smaller inner-lateral marginals (Figure 13x), and one pair of adaxial marginals (Figure 13v); marginal scales do not fold over operculum. Adaxial side of polyp also covered with small, irregularly arranged, elliptical scales. Thus, there are only six marginal scales (Figure 13s), the wide abaxial marginals occupying space usually covered by outer-lateral marginals, and only two rows of body wall scales. Coenenchymal scales elongate and granular, arranged in one layer.

DISCUSSION. The tendency toward unilinearly arranged calyces and the presence of only six marginal scales in each polyp are unique for this genus. Also, it is unusual for there to be such an abundance of tentacular rods. Otherwise, its marginal scales resemble those of *Primnoa* in shape, and its low, fixed number of abaxial body wall scales resembles that of *Narella* and *Paranarella*, although its abaxial scales do not encircle the polyp as they do in those genera.

DISTRIBUTION. Known only from the type locality off southeastern Tasmania, 987–1,200 m .

ETYMOLOGY. Greek *australis* = southern + *gorgia*, a common octocoral suffix, in allusion to the southern distribution of the genus. Gender: feminine.

TYPE SPECIES. *Australogorgia aldersladei,* new species, here designated. Holotype deposited at the NTM (CO 13054).

### *Australogorgia aldersladei,* new species

DESCRIPTION. General characters given above. The holotype is a fragment of a larger colony, measuring only 4.5 cm tall and 7 cm wide, missing its base. An additional even smaller branch is also present. The axis is golden yellow. In total, there are only 27 calyces, separated from one another by about 2.5 mm. The calyces are quite large, up to 5 mm in height and 3.8 mm in apical diameter. The abaxial marginal scales (Figure 13w) are tall (up to 2.6 mm) and wide (2.3 mm), their distal edges straight to slightly rounded and quite delicate. The remaining two pairs of abaxial body wall scales are somewhat smaller. The inner-lateral marginals (Figure 13x) are almost as large as the abaxial marginals (2.1–2.3 mm long) but are slightly asymmetrical in shape. The adaxial marginals (Figure 13v) are only about 1.5–1.7 mm in length, the remainder of the adaxial side of the polyp covered with a random coverage of small (0.6 mm) elliptical scales (Figure 13q). All body wall scales are slightly convex to follow the curvature of the polyp, and all body wall scales as well as the operculars are covered with a low granulation on their outer surface (Figure 13w), the granules appearing to radiate outward from a low knob near the center of the scales. The opercular scales are large (up to 2.1 mm in length, L:W = 1.5–1.9) and roughly of the same size, the abaxial operculars not much larger than those on the adaxial side. Cylindrical tentacular rods (Figure 13t) are common, measuring up to 0.25 mm in length and having an L:W of 3.3–4.0. Coenenchymal scales (Figure 13u) are elongate, sometimes fusiform, and rather thick, up to 2.1 mm in length, granular above and tuberculate below.

REMARKS. After this manuscript was submitted, additional larger specimens were received from CSIRO (Hobart), one of which measures 20 cm in height and 13 cm in width, having a basal stem diameter of 3.3 mm. It and another are designated as paratypes (see below in Material Examined). They were attached to living specimens of the scleractinian coral *Solenosmilia variabilis*. Calyces on these colonies were arranged randomly on the branches, including unilaterally, in whorls of four, as well as irregularly. Also, many calyces contained two rows of small adaxial body wall scales.

MATERIAL EXAMINED. Holotype: One colony, NTM CO 13054, FRV *Southern Surveyor*, 44°16′S, 147°20′E (Tasman Sea, off southeastern Tasmania), 987 m, 27 January 1997 (type locality). Paratypes: One colony, Tasmania Museum and Art Gallery K3713, SS02/2007, Station 25-036, 44.326°S, 147.114°E, 1,100–1,200 m, 3 April 2007; one colony, USNM 1116407, same station.

Distribution. Same as for the genus.

Etymology. Named in honor of Philip Alderslade, for his many contributions to octocoral taxonomy, especially in the Australian region.

## 30. *Narella* Gray, 1870

FIGURE 14A–G

*Narella* Gray, 1870:49.—Bayer, 1956:F222; 1961:295 [illustrated key to genus]; 1981b:937 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Cairns and Bayer, 2003:618–619.—Cairns and Baco, 2007:392–393.—Williams, 1992:272.—Cairns and Bayer, 2007[2008]:84–86.

Not *Stachyodes* Bargatzky, 1881 [a stromatoporoid].

*Stachyodes* Wright and Studer in Studer, 1887:49 [junior homonym].—Wright and Studer, 1889:54.—Versluys, 1906:86–88.—Kinoshita, 1908a: 45–47.—Kükenthal, 1912:325–328 [in part: not group 4]; 1915:143, 152 [key to genus and species]; 1919:452–456 [key to genus and species]; 1924:308–309 [key to genus and species].

*Calypterinus* Wright and Studer in Studer, 1887:49–50.—Wright and Studer, 1889:53.

Diagnosis. Colonies dichotomously branched in one or more planes, pinnate, or unbranched. Calyces usually arranged in whorls of up to 14, occasionally reduced to only two (i.e., paired), the appressed calyces always facing downward. Well-developed operculum present (Figure 14a), the operculars prominently keeled on inner surface. Polyps protected by three (Figure 14c) or, rarely, four pairs of large abaxial body wall scales (one pair of basals, one or two pairs of medials, and one pair of buccals), one to three pairs of much smaller (vestigial) adaxial buccal (marginal) scales (Figure 14a), and sometimes additional smaller scales scattered on the adaxial surface; adaxial side only partially covered with scales. Large abaxial scales often meet on adaxial side of polyp but do not fuse. Coenenchymal scales arranged in one layer; outer surface often elaborately ridged (Figure 14e) or keeled.

Discussion. *Narella*, consisting of 38 valid species (Table 4), is the most species-rich genus within the Primnoidae, each oceanographic region hosting a set of often sympatric species, e.g., Hawaiian Islands (eight species), western Atlantic (seven species), Gulf of Alaska (five species), and Japan (five species). Cairns and Bayer (2007 [2008]) list all species with their approximate geographic ranges. As seen from the generic synonymy, it is a frequently studied and named taxon, and it is likely that there are many more undescribed species in the genus.

Morphological characters used to discriminate species include branching mode, polyp size, number of polyps per whorl, nature of adaxial buccal scales, shape and ornamentation of the body wall scales (especially the nature of the dorsolateral ridge, if present, of the basal scales), and shape and ornamentation of the coenenchymal scales. Molecular sequences have also been published for some species (e.g., France et al., 1996; Berntson et al., 1999, 2001; France and Hoover, 2001, 2002; Cairns and Baco, 2007).

Distribution. Known from all ocean basins from 55 to 4,594 m (Cairns and Bayer, 2007 [2008]).

Type Species. *Narella*: *Primnoa regularis* Duchassaing and Michelotti, 1860, by monotypy. The neotype of *P. regularis*, designated by Cairns and Bayer (2004a), is deposited at the USNM (49385).

*Stachyodes*: *S. regularis* Wright and Studer, 1889 (not *P. regularis* Duchassaing and Michelotti, 1860), = *Stachyodes studeri* Versluys, 1906 (nomen novum), by subsequent monotypy (Wright and Studer, 1889:55). The type (in alcohol) is deposited at the BM (1889.5.27.71), and a fragment is at the ZMA (Coel. 3085) (van Soest, 1979).

*Calypterinus*: *C. allmani* Wright and Studer, 1889, by subsequent monotypy (Wright and Studer, 1889:53). The type is deposited at the BM (1889.5.27.104).

## 31. *Arthrogorgia* Kükenthal, 1908

FIGURE 14H–K

*Arthrogorgia* Kükenthal in Kükenthal and Gorzawsky, 1908a:625.—Kükenthal and Gorzawsky 1908b:28.—Kükenthal, 1915:144, 154 [key to genus]; 1919:476–477; 1924:319–320.—Bayer, 1952:63–64; 1956:F222; 1961:296 [illustrated key to genus]; 1981b:937 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 1996c:605 [key to the species].

*Calyptrophora* (*Arthrogorgia*).—Kinoshita, 1908a:57–58.

Diagnosis. Branching of colonies alternately pinnate (type species) or planar dichotomous. Calyces arranged in whorls of up to nine, the appressed calyces always pointed downward. Well-developed operculum present, the operculars prominently keeled on inner surface. Polyps protected by two pairs of crescent-shaped sclerites, basal (Figure 14k) and buccal (Figure 14i), each pair of which may completely encircle the polyp but are not fused; several pairs of small (vestigial) adaxial body wall sclerites present on most species, but lower adaxial body wall is bare. At least one species (not type species) has additional small infraopercular scales intercalated between opercular and buccal scales, these apparently associated with brooding polyps (Bayer, 1996c). Buccal scales (marginals) have a smooth or spinose distal margin (Figure 14i). Two or more transverse rows of unpaired, crescent-shaped infrabasal scales present, often forming a low conical tube on which calyx sits (Figure 14h). Coenenchymal scales arranged in one layer.

DISCUSSION. *Arthrogorgia* differs from *Paracalyptrophora* primarily in having four or more unpaired infrabasal scales that form a hollow basal tube and in having a pinnate branching pattern. At least one species also has accessory infrabasal scales associated with brood polyps. The four species (Table 4) are keyed and illustrated by Bayer (1996c); characters used to distinguish species include colony branching and spination and ornamentation of the body wall scales.

DISTRIBUTION. North Pacific: Japan to Aleutian Islands, including Bering Sea, 163–1,127 m.

TYPE SPECIES. *Arthrogorgia membranacea* Kükenthal and Gorzawsky, 1908a (= *A. ijimai* (Kinoshita, 1907)), by monotypy. The type is deposited at the Zoological Museum of the Wroclaw University (No. 2, 4) (Wiktor, 1974). Kükenthal and Gorzawsky described *A. membranacea* twice in 1908, the second account (Kükenthal and Gorzawsky, 1908b) being much more detailed and accompanied with illustrations; however, the original account must be the slightly earlier publication of Kükenthal and Gorzawsky (1908a). The type species was also well described and illustrated by Kinoshita (1908a) and Utinomi (1979) as *A. ijimai*.

## 32. *Paracalyptrophora* Kinoshita, 1908

FIGURE 15A–H

*Calyptrophora*.—Versluys, 1906:104 [in part].—Kükenthal, 1919:468 [in part]; 1924:317 [in part: key to genus and species].—Aurivillius, 1931:301 [in part: key to species].

*Calyptrophora* (*Paracalyptrophora*) Kinoshita, 1908a:58.

*Paracalyptrophora* Bayer, 1981b:937, 946.—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 2001:367.—Cairns and Bayer, 2004b:115–116 [revision of genus and key to species].

DIAGNOSIS. Colonies dichotomously branched in one plane (the type species), sometimes in a lyrate pattern and sometimes as two parallel fans (biflabellate). Calyces arranged in whorls up to eight, the appressed calyces always directed downward. Well-developed operculum present, the operculars prominently keeled (Figure 15g) on inner surface. Polyps protected by two pairs of crescent-shaped sclerites, basal and buccal, each pair of which may completely encircle the polyp but are not fused to one another; in only one species, the type species, are there several additional adaxial buccal scales (Figure 15d), but in other species the adaxial region is base. Buccal scales (marginals) have a smooth or spinose distal margin. A pair of crescent-shaped infrabasal scales is present (Figure 15h). Coenenchymal scales elongate, granular and sometimes ridged, arranged in one layer.

DISCUSSION. Most of the species now placed in this genus were originally described in the genus *Calyptrophora*. Kinoshita (1908a) separated them as a subgenus on the basis of their lack of fusion of the body wall scales. Bayer (1981b) eventually elevated the taxon to generic rank, this classification being the current one. Whereas the two pairs of body wall scales of *Paracalyptrophora* may completely encircle the polyp, they never inseparably fuse on the ab- or adaxial side, which is the primary difference from *Calyptrophora*. The genus was recently revised (Cairns and Bayer, 2004b), which includes two keys to the six species. The size, shape, and ornamentation of the basal scales were found to be sufficient to distinguish the species (Cairns and Bayer, 2004b: tbl. 1).

DISTRIBUTION. Southwestern Pacific, Japan, Hawaii, North Atlantic, 150–1,480 m.

TYPE SPECIES. *Calyptrophora kerberti* Versluys, 1906, by subsequent designation (Cairns and Bayer, 2004b:115). The holotype is deposited at the ZMA (Coel. 2294). The type species is well described and illustrated by Utinomi (1979) and Cairns and Bayer (2004b)

## 33. *Calyptrophora* Gray, 1866

FIGURE 15I–N

*Calyptrophora* Gray, 1866a:25, fig. 1.—Wright and Studer, 1889:xlvii, 50.—Versluys, 1906:104–105 [in part].—Kinoshita, 1908a:54–59 [in part].—Kükenthal, 1915:144 [key to genus]; 1919:468–472 [in part: key to genus and species]; 1924:317 [in part: key to genus and species].—Bayer, 1956:F221; 1961:296 [illustrated key to genus]; 1981b:937 [key to genus].—Bayer and Stefani, 1989:455 [key to genus].—Bayer, 2001:367–368.

DIAGNOSIS. Colonies dichotomously branched (uniplanar and lyrate), the type species being uniplanar dichotomous, or unbranched (flagelliform). Calyces arranged in whorls of up to seven (usually four), the appressed calyces usually facing upward (Figure 15i–j) but in two species facing downward. Well-developed operculum present; operculars prominently keeled on inner surface. Polyps protected by two pairs of crescent-shaped sclerites (each sclerite with its separate center of calcification), basal (Figure 15m) and buccal, each pair formed by the inseparable fusion of two sclerites both ab- and adaxially, resulting in solid rings; no additional adaxial sclerites present, and adaxial symphysis is narrow, resulting in a relatively bare adaxial face. Buccal scales (Figure 15k–l) often, but not always, bear distal spines. A pair of crescent-shaped infrabasal scales usually present. Coenenchymal scales (Figure 15i) elongate and flat, arranged in one layer.

Discussion. Bayer (2001) divided the species in this genus into two species complexes: the "*japonica* complex," which includes the type species and consists of species with calyces facing upward, and the smaller "*wyvillei* complex," consisting of two species with calyces facing downward (Table 4). Thus far, this division has not been used as a subgeneric character. Bayer (2001) further subdivided the *japonica* complex into two species groups: one having marginal spines on the buccal scales and a second group of two species that lack basal spines (Table 4). Species within this genus usually can be distinguished based on branching pattern, orientation of calyces, and body scale spination (number of spines, length, and whether smooth or covered with serrate ridges; see Kükenthal, 1924; Cairns, 2007a, 2007b).

Distribution. Pacific Ocean, western Atlantic, 229–3,107 m.

Type Species. *Calyptrophora japonica* Gray, 1866a, by monotypy. The type (dry) is deposited at the BM (1866.1.8.2). The type species was nicely described and illustrated by Utinomi (1979).

## 34. *Tokoprymno* Bayer, 1996

FIGURE 15O–U

*Tokoprymno* Bayer, 1996a:511.

Diagnosis. Colonies bushy and irregularly dichotomous in branching. Calyces arranged biserially, projecting perpendicularly from opposite edges of each branch; brood polyps common. Well-developed operculum present (Figure 15o) unless the brood polyp has released its planulae, in which case operculars are lost (Figure 15q); operculars keeled (Figure 15u) on inner surface. Eight marginal scales have straight to rounded distal edges that do not fold over operculum. Polyp completely protected by eight rows of body wall scales. Most scales bear short, radiating ridges (Figure 15s–t) on their outer surface. Coenenchymal scales arranged in one layer.

Discussion. The genus is monotypic (Table 4) and known from only one locality.

Distribution. The type locality, an unnamed seamount in the subantarctic South Pacific seamount (549 m), is a deepwater coral bank formed by the scleractinian *Solenosmilia variabilis* and is known to host a large diversity of invertebrate fauna (Cairns, 1982a, 1982b).

Type Species. *T. maia* Bayer 1996, by original designation. The holotype is deposited at the USNM (81535).

## 35. *Parastenella* Versluys, 1906

FIGURE 16A–G

Not *Stenella* Gray, 1866b:213 [a cetacean].

*Stenella*.—Wright and Studer, 1889:56 [in part: *S. doederleini, S. spinosa*].—Kükenthal, 1915:151–152 [in part]; 1919:443–445 [in part: key to species]; 1924:303 [in part: key to species].—Aurivillius, 1931:289 [in part].

*Stenella* (*Parastenella*) Versluys, 1906:39, 45.

*Candidella* (*Parastenella*).—Bayer, 1956: F222.

*Parastenella* Bayer, 1961:295 [illustrated key to genus]; 1981b:936 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].—Cairns, 2007a:245–247; 2007b:518, tbl. 2 [generic revision, tabular key to species].

Diagnosis. Colonies of most species planar dichotomous, occasionally slightly bushy. Calyces arranged in whorls (type species) of up to four, pairs or isolated, calyces standing perpendicular to the branch. Well-developed operculum present, the operculars prominently keeled (Figure 16f) on inner surface. Eight marginal scales present, alternating in position (offset; Figure 16a) from operculars. Most operculars bear an elongate, distal, concave to tubular extension (a flute; Figure 16a–b, d), although in some species these are missing from adaxial marginals. Abaxial body wall scales may also have distal flutes (Figure 16g). Each calyx completely covered with five to eight longitudinal rows of body wall scales (five in type species), their outer surfaces covered with small granules. Coenenchymal scales arranged in one layer. Tentacular rods are often present (Figure 16g).

Discussion. Originally proposed by Versluys (1906) as one of four subgenera of *Stenella* sensu Gray, 1870, the subgenus was raised to generic status by Bayer

(1981b), who considered the alternation of marginal and opercular scales to be of generic significance. The genus was partially revised by Cairns (2007a), who provided a tabular key to the six species (Table 4). Characters used to distinguish species include colony shape, arrangement of calyces, size and presence of marginal flutes, and number of body wall scale rows.

Distribution. Known from all ocean basins except the eastern Atlantic and off continental Antarctica, 567–3,470 m.

Type Species. *Stenella doederleini* Wright and Studer, 1889, by subsequent designation (Bayer, 1956: F222). The type is deposited at the BM (1889.5.27.37), and a fragment of the type is deposited at the ZMA (Coel. 3085) (van Soest, 1979).

## 36. *Candidella* Bayer, 1954

FIGURE 16H–N

Not *Stenella* Gray, 1866b:213 [a cetacean].

*Stenella* Gray, 1870:48 [junior primary homonym of *Stenella* Gray, 1866b, a cetacean].—Studer, 1887:50.—Wright and Studer, 1889:56 [in part: *S. johnsoni* and *S. gigantean*].—Kükenthal, 1915:151–152 [in part: key to genus and species]; 1919:443–445 [in part: key to genus and species]; 1924:303 [in part: key to genus and species].—Aurivillius, 1931:289–290 [in part].

*Stenella* (*Stenella*) Versluys, 1906:38–39.

*Candidella* Bayer, 1954:296 (nomen novum); 1961:295 [illustrated key to genus]; 1981b:937 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].—Cairns and Bayer, 2004c:476–477.—Cairns, 2007a:250–251.

*Candidella* (*Candidella*) Bayer, 1956:F222.

Diagnosis. Colonies dichotomously branched in one plane (type species) or unbranched (flagelliform). Calyces arranged in whorls (type species) of up to four or in pairs, calyces standing perpendicular to branch. Well-developed operculum present, the opercular scales keeled (Figure 16k) on their inner surface. Four marginal scales present, the two on the adaxial side much wider than those on adaxial side (Figure 16h, l); thus, marginals cannot have a 1:1 correspondence with the operculars. Polyp completely protected by body wall scales, but scales not arranged in longitudinal rows: three or four circles of sclerites surround each polyp, each circle differing in number (e.g., four marginals, two to four medials, and four to eight basal scales). Outer surface of all scales finely granular. Coenenchymal scales arranged in one layer.

Discussion. Originally considered by Versluys (1906) to be one of four (and the nominate) subgenera of *Stenella* sensu Gray, 1870, the subgenus was raised to genus level and given a separate name by Bayer (1954), as the name *Stenella* was preoccupied by *Stenella* Gray, 1866b, the name of a cetacean. Four species are known in this genus (Table 4). They vary in branching mode, arrangement and size of calyces, and the number of circles of body wall scales. Although *C. imbricata* is often collected and reported, the other three species are in need of revision.

Distribution. Amphi-Atlantic, Fiji, Hawaiian Islands, 378–2,165 m.

Type Species. *Primnoa imbricata* Johnson, 1862, by monotypy. The holotype (dry) is deposited at the BM (1863.1.31.1), and a fragment of that type is deposited at the ZMA (Coel. 3085) (van Soest, 1979). The type species was recently described and illustrated by Cairns and Bayer (2004c).

## 37. *Microprimnoa* Bayer and Stefani, 1989

FIGURE 17A–G

*Microprimnoa* Bayer and Stefani, 1989:454, 458 [key to genus].

Diagnosis. Colonies uniplanar, sparsely dichotomously branched. Calyces arranged in pairs (Figure 17a), oriented perpendicular to branch and thus pointing directly away from each other. Well-developed operculum present, but only four or five opercular scales visible when calyx is contracted (Figure 17b); distal inner side of operculars smooth (no keel), whereas proximal distal portion consists of a well-delineated, elliptical depression from which a pad of tubercles rises (Figure 17c–d). Calyces cylindrical and completely covered with scales on all sides, but scales not arranged in rows (Figure 17a). Four marginal scales present and approximately an equal number occur submarginally and sometimes a third tier. Body wall and coenenchymal scales do not overlap one another, instead their edges abut each other; the polygonal scales are extremely thick (plate-like; Figure 17e–g), their outer surface covered with low spinose ridges; no distinctive inner layer of coenenchymal sclerites.

Discussion. This monotypic genus and species are known from only one locality. It is unique among the primnoids in its nonaligned, mosaic-like, nonimbricating coenenchymal and body wall scales, the concealment of three of its opercular scales in the closed calyx position, the raised patch of opercular tubercles on the lower inner surface, and its extraordinarily thick sclerites. Although all sclerites are quite thick (plate-like, not scale-like), on the thinnest of the opercular scales, one can discern the distinctive cruciform extinction pattern characteristic of the radial crystal growth of primnoids. The original description reports the polyps to be arranged in whorls of two, but this is another way of saying in pairs, as is coded as such in the phylogenetic analysis.

DISTRIBUTION. New Caledonia, 415 m.

TYPE SPECIES. *M. diabathra* Bayer and Stefani, 1989, by original designation. Holotype deposited at the MNHN (OCT.A 1987.3 and 23), and a paratype is also at the USNM (79977).

## 38. *Pterostenella* Versluys, 1906

FIGURE 17H–O

*Stenella* (*Pterostenella*) Versluys, 1906:39.

*Pseudoplumarella* Kükenthal, 1915:146 [in part]; 1919:356 [in part]; 1924:265 [in part].

*Pterostenella* Bayer, 1961:294 [illustrated key to genus]; 1981a:622–624 [comments]; 1981b:937.—Bayer and Stefani, 1989:454, 456 [key to genus].

DIAGNOSIS. Colonies uniplanar (plumose), pinnately branched in an alternating manner. Calyces small, arranged in pairs and whorls of three or four, the calyces inclined upward (type species) or standing perpendicular to branch (Figure 17j). Well-developed operculum present, the operculars keeled on their inner surface (Figure 17n). Five marginal scales present (Figure 17i), those on abaxial side often pointed. Polyp completely protected by six rows of body wall scales (no adaxial bare region): two rows of abaxial, two rows of lateral, and two rows of small adaxials. Inner faces of body wall scales bear prominent radial ridges (Figure 17i, l, o) as in *Callogorgia*, whereas outer surface is granular; coenenchymal scales occur in one layer and bear reticulate ridges (Figure 17k).

DISCUSSION. Originally described as one of four subgenera of *Stenella* by Versluys (1906), *Pterostenella* was raised to generic rank by Bayer (1961, 1981b), who considered the unique character of having five marginal scales to be of generic significance. Only two species are known in this genus (Table 4), the subspecies *P. p. anatole* being raised to the species rank by Grasshoff (1999).

DISTRIBUTION. Reunion (type locality), Philippines, New Caledonia, 60–75 m.

TYPE SPECIES. *Primnoa plumatilis* Milne Edwards, 1857, by monotypy. The type is deposited at the MNHNP, and a fragment is at the ZMA (Coel. 3085) (van Soest, 1979). The type species is best described and illustrated by Versluys (1906).

## 39. *Perissogorgia* Bayer and Stefani, 1989

FIGURE 18A–H

*Perissogorgia* Bayer and Stefani, 1989:459–461 [key to genus and species].

DIAGNOSIS. Colonies unbranched (e.g., flagelliform, as in type species) or dichotomously branched in a lyrate or alternate pinnate manner. Calyces arranged in whorls of up to eight, the appressed calyces facing upward. Well-developed operculum present, the operculars keeled on inner surface. Polyps protected by one abaxial row of three to five (usually three in type species; Figure 18a–b) large, unpaired scales, termed buccal, basal, and a variable number of medials. Basal scale (Figure 18e) robust and curved in order to support upper calyx. A pair of smaller lateral buccals (inner lateral) (Figure 18d) and an even smaller pair of adaxial buccal scales present, resulting in five buccal scales (marginal scales) of very different sizes. Lateral and adaxial buccal scales not part of a longitudinal row, although there may be a pair of scales in the lateral position adjacent to the basal scales. Most of adaxial body wall naked. Brood polyps have been observed. Coenenchymal scales arranged in one layer.

DISCUSSION. Species of this genus have not been reported subsequent to its original description. It is unique among the subfamily in having only one longitudinal row of body wall scales, those on the abaxial side. The seven species are distinguished by their branching mode, polyp size, and shape of the distal margin of their buccal scales (Bayer and Stefani, 1989).

DISTRIBUTION. Known only from off New Caledonia, 55–750 m.

TYPE SPECIES. *P. viridis* Bayer and Stefani, 1989, by original designation. The holotype and three paratypes are deposited at the MNHN (OCT.A. 1987.4.24); paratypes are also deposited at the USNM (79976, 80043).

## 40. *Dasystenella* Versluys, 1906

FIGURE 18I–P

*Stenella*.—Wright and Studer, 1889:59 [in part: *S. acanthina*].

*Stenella* (*Dasystenella*) Versluys, 1906:39, 48.

*Thouarella*.—Kükenthal, 1915:151 [in part]; 1919:441 [in part]; 1924:302 [in part].

*Dasystenella* Bayer, 1981b:934, 937, 946 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].—Cairns, 2006:188–189.

Diagnosis. Branching of colonies in a bottlebrush arrangement. Calyces arranged in whorls of up to five, the calyces inclined upward (Figure18i). Well-developed operculum present, the operculars prominently keeled (Figure 18n) on their inner surface. Five marginal scales (Figure 18j) present, all bearing apical spines, but abaxial and two lateral marginals bear extremely long spines. Marginal spines bear longitudinal serrate ridges. Polyps completely covered by five longitudinal rows of body wall scales (one abaxial row, two lateral rows, and two adaxial rows, the adaxial scales much smaller than the others). Inner surface of body wall scales tuberculate (Figure 18m), outer surface finely granular (Figure 18l). Coenenchymal scales elliptical, arranged in one layer.

Discussion. Originally considered by Versluys (1906) to be one of four subgenera of *Stenella* sensu Gray, 1870, *Dasystenella* was raised to generic rank by Bayer (1981b), who distinguished it as having only five marginal scales and bottlebrush-branched colonies. It is a monotypic genus restricted to the subantarctic region.

Distribution. Argentina, Scotia Ridge to South Shetland Islands, abyssal plain west of Tierra del Fuego, 300–5,087 m.

Type Species. *Stenella acanthina* Wright and Studer, 1889, by monotypy. Syntypes are deposited at the BM (1889.05.27.48), and uncataloged syntype SEM stubs B276 and C1185-1186 are deposited at the NMNH. The type species was recently redescribed and figured by Cairns (2006).

## 41. *Pseudoplumarella* Kükenthal, 1915

FIGURE 19A–J

*Plumarella*.—Thomson and Mackinnon, 1911:682 [in part: not *P. laevis*].

*Pseudoplumarella* Kükenthal, 1915:143, 145 [in part: not *P. plumatilis,* key to genus and species]; 1919:353–354 [in part: not *P. plumatilis*, key to genus and species]; 1924:263 [key to genus and species].—Bayer, 1956:F220; 1981a:622–625; 1981b:937 [key to genus].—Bayer and Stefani, 1989:454 [key to genus].

Diagnosis. Colonies uniplanar, branching in an alternate pinnate manner. Calyces small, arranged in an alternate biserial manner on distal branches, becoming random (Figure 19a) on larger branches; calyces face upward and are adnate to branch, such that there is essentially no adnate body wall. Well-developed, tall, conical operculum present, operculars bearing a prominent longitudinal keel (Figure 19d–e). Lower, inner edge of each abaxial and outer-lateral operculars bear two irregularly shaped mounds, one on either side of the midline, each of which articulates with the mound on the adjacent opercular (Figure 19c–e), producing a strong interlocking of adjacent operculars (sometimes joined even after the cleaning treatment). Inner-lateral operculars have only one mound on the abaxial side, and adaxial operculars do not have articulating mounds at all. Usually, five marginal scales present, those on the abaxial may be spinose, but in most species (e.g., the type species) not. Polyp protected by three longitudinal rows of body wall scales: a single row of smooth, large, crescent-shaped abaxial body wall scales (Figure 19h–i) and two outer-lateral rows of about four scales each; inner-lateral and adaxial positions usually limited only to marginal scales (i.e., no rows). Coenenchymal scales in two layers: outer layer composed of smooth scales, inner layer composed of small irregularly shaped tuberculate rods.

Discussion. Characters used to distinguish the five species (Table 4) include number of scales in the abaxial body wall rows, serration or lack thereof on distal margin of abaxial scales, spination of marginal scales, and arrangement of calyces on branch.

The outer-lateral row of the type species consists of a medium-sized marginal scale, two small scales hidden by their adjacent abaxial scales, and a massive basal scale that partially overlaps the basalmost abaxial scale. The opercular locking mechanism appears to be unique among the primnoids.

Distribution. Off New South Wales and Queensland, Australia, 55–115 m.

Type Species. *Plumarella thetis* Thomson and Mackinnon, 1911, by original designation. Syntypes are deposited at the AM, the specimen from *Thetis* station 40 numbered G12137.

# FIGURES 3–19

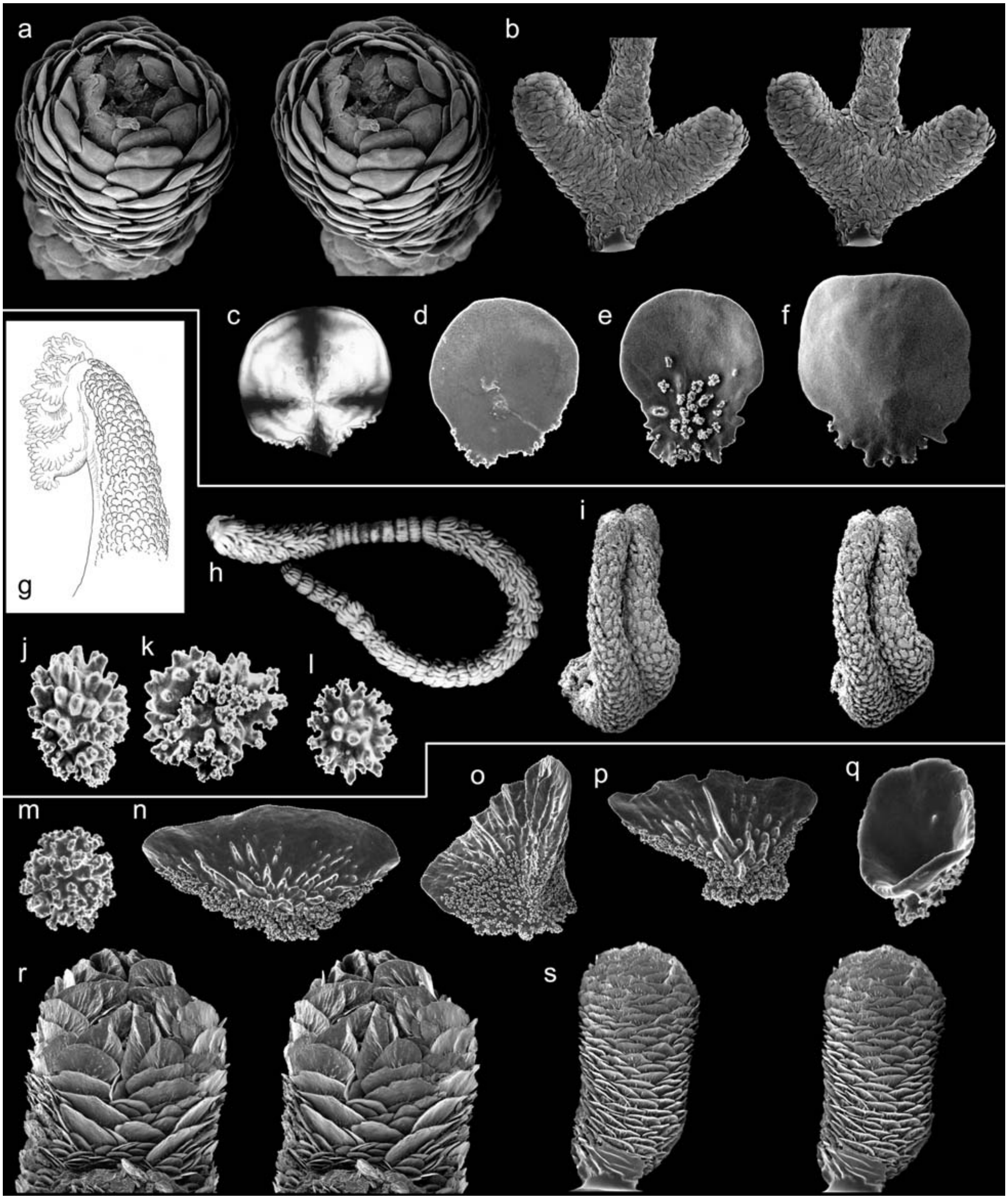

**FIGURE 3.** *Primnoeides sertularoides* (a–b, e–f, holotype, BM 89.5.27.62; c–d, Gilchrist 70, USNM 58601): (a.) stereo view of calyx tip, ×50; (b.) stereo view of a pair of calyces, ×16; (c.) body wall scale showing cruciform extinction pattern under polarized light, ×150; (d.) opercular scale, ×400; (e.) inner and (f.) outer surfaces of body wall scales, ×150. *Ophidiogorgia paradoxa* (g–l, holotype, USNM 58165): (g.) drawing of lateral view of distal part of polyp (from Bayer, 1980), ×24; (h.) holotype colony, ×12; (i.) stereo view of two polyps fused at base, ×50; (j–l.), abaxial body wall sclerites, ×175. *Aglaoprimnoa stefanii* (m–q, s, holotype, USNM 81289; r, *Eltanin*-1594, USNM 81288): (m.) sclerite from inner coenenchyme, ×180; (n.) outer surface of an abaxial body wall sclerite, ×50; (o.) inner surface of an opercular, ×60; (p.) outer surface of a proximal body wall sclerite, ×60; (q.) outer surface of a sclerite from outer coenenchyme, ×180; (r.) stereo view of adaxial face of a calyx, ×21; (s.) stereo of a calyx, ×13.

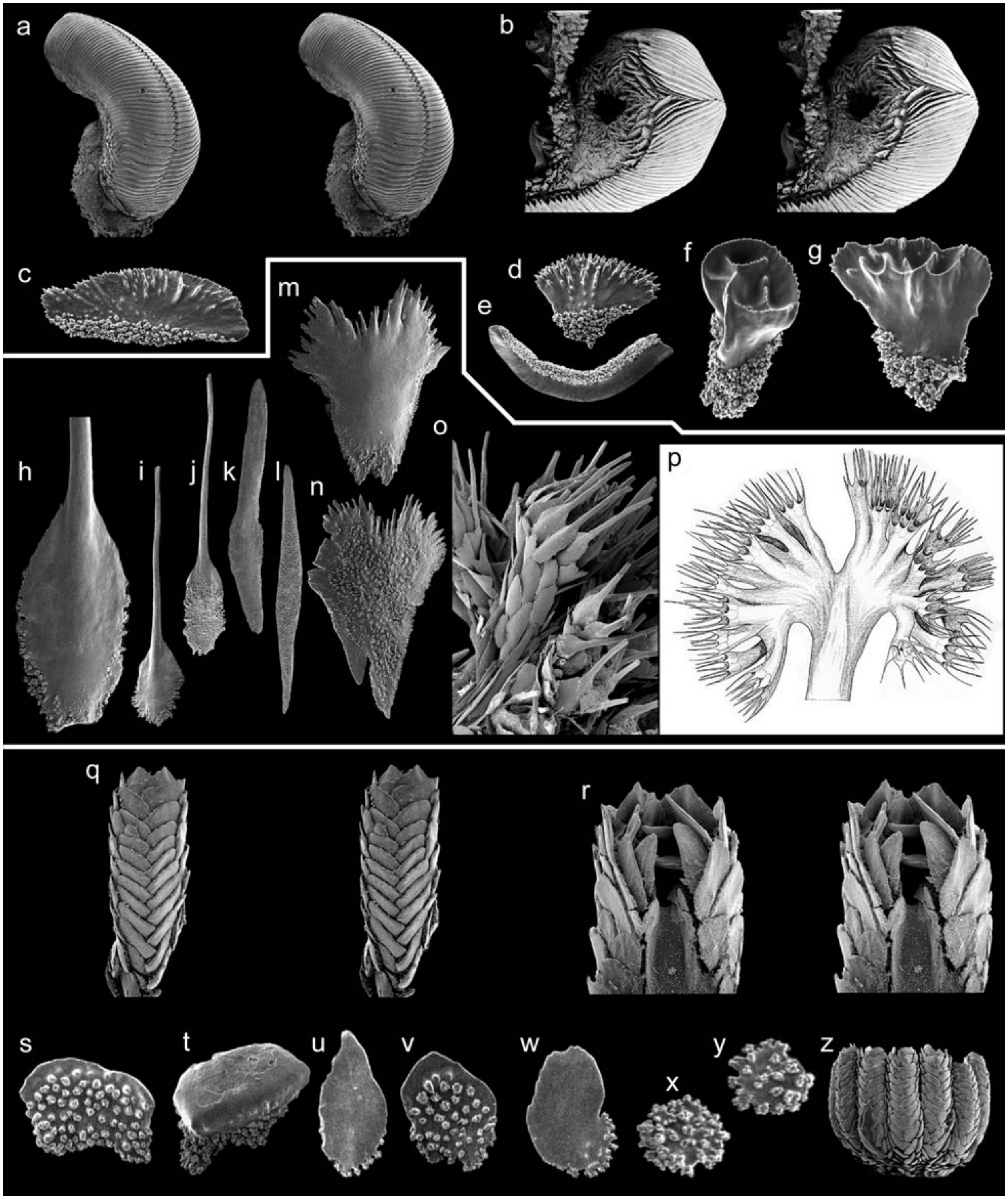

**FIGURE 4.** *Armadillogorgia cyathella* (a, *Eltanin*-1536, USNM 79591; b–g, holotype, USNM 58166): (a.) stereo pair of abaxial side of a calyx, ×7.5; (b.) stereo view of oral region of a calyx, ×15; (c–d.) circumoral (adaxial) sclerites, ×20, ×40, respectively; (e.) an abaxial sclerite, ×14; (f–g.) coenenchymal sclerites, ×105. *Ainigmaptilon edisto* (h–o, *Islas Orchadas*-123, USNM 77140; p, holotype, USNM 49580): (h.) base of an opercular scale, ×77; (i.) outer and (j.) inner surfaces of opercular scales, ×30; (k.) outer and (l.) inner surfaces of coenenchymal scales, ×40; (m.) outer and (n.) inner surfaces of body wall scales; (o.) a cluster of calyces, ×1.7; (p.) drawing of a polyp leaf (from Bayer, 1950), ×7.5. *Primnoella australasiae* (q–z, syntype, BM 1983.3.2.13): (q.) abaxial side of a calyx, ×37; (r.) adaxial side of a calyx showing bare strip, ×71; (s.) inner and (t.) outer surfaces of body wall scales, ×95; (u.) circumoral scale, ×95; (v.) inner and (w.) outer surface of outer coenenchymal sclerites, ×95; (x–y.) inner coenenchymal spheroids on canal walls, ×125; (z.) whorl of calyces, ×13.

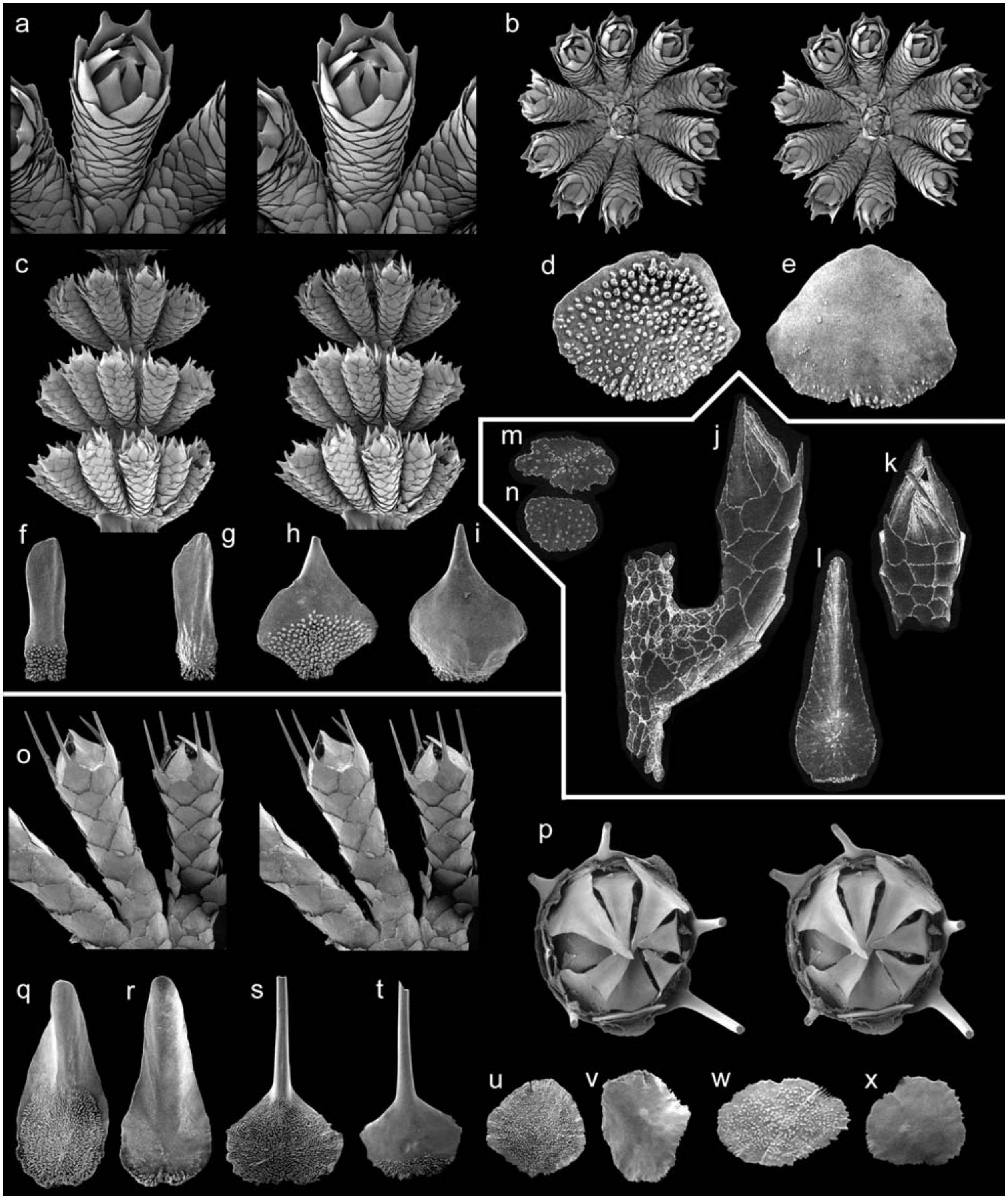

**FIGURE 5.** *Convexella magelhaenica* (a–c, *Hero* 450, USNM 85306; d–e, *Eltanin*-740, USNM 58442; f–g, *Eltanin*-283, USNM 82856; h–i, *Eltanin*-969, USNM 58441): (a.) stereo view of apical end of calyx, ×26; (b.) stereo adaxial view of a whorl of 10 calyces, ×11; (c.) stereo lateral view of three whorls, ×9; (d.) inner and (e.) outer surfaces of body wall scales, ×75; (f.) inner and (g.) outer surfaces of opercular scales, ×31; (h.) inner and (i.) outer surfaces of circumopercular (= marginal) scales, ×38. *Dicholaphis delicata* (j–n, holotype from Kinoshita 1908a): (j.) lateral view of calyx, ×25; (k.) adaxial side of calyx, ×25; (l.) opercular scales, ×50; (m.) outer and (n.) inner surfaces of coenenchymal scales, ×100. *Callozostron mirabile* (o–p, s–x, *Eltanin*-545, USNM 85294; q–r, type, BM 1889.5.27.33): (o.) stereo lateral view of several calyces, ×13; (p.) stereo opercular view, ×25; (q.) inner and (r.) outer surfaces of opercular scales, ×31; (s.) inner and (t.) outer surfaces of marginals scales, ×24; (u.) inner and (v.) outer surfaces of body wall scales, ×24; (w.) inner and (x.) outer surfaces of coenenchymal scales, ×43.

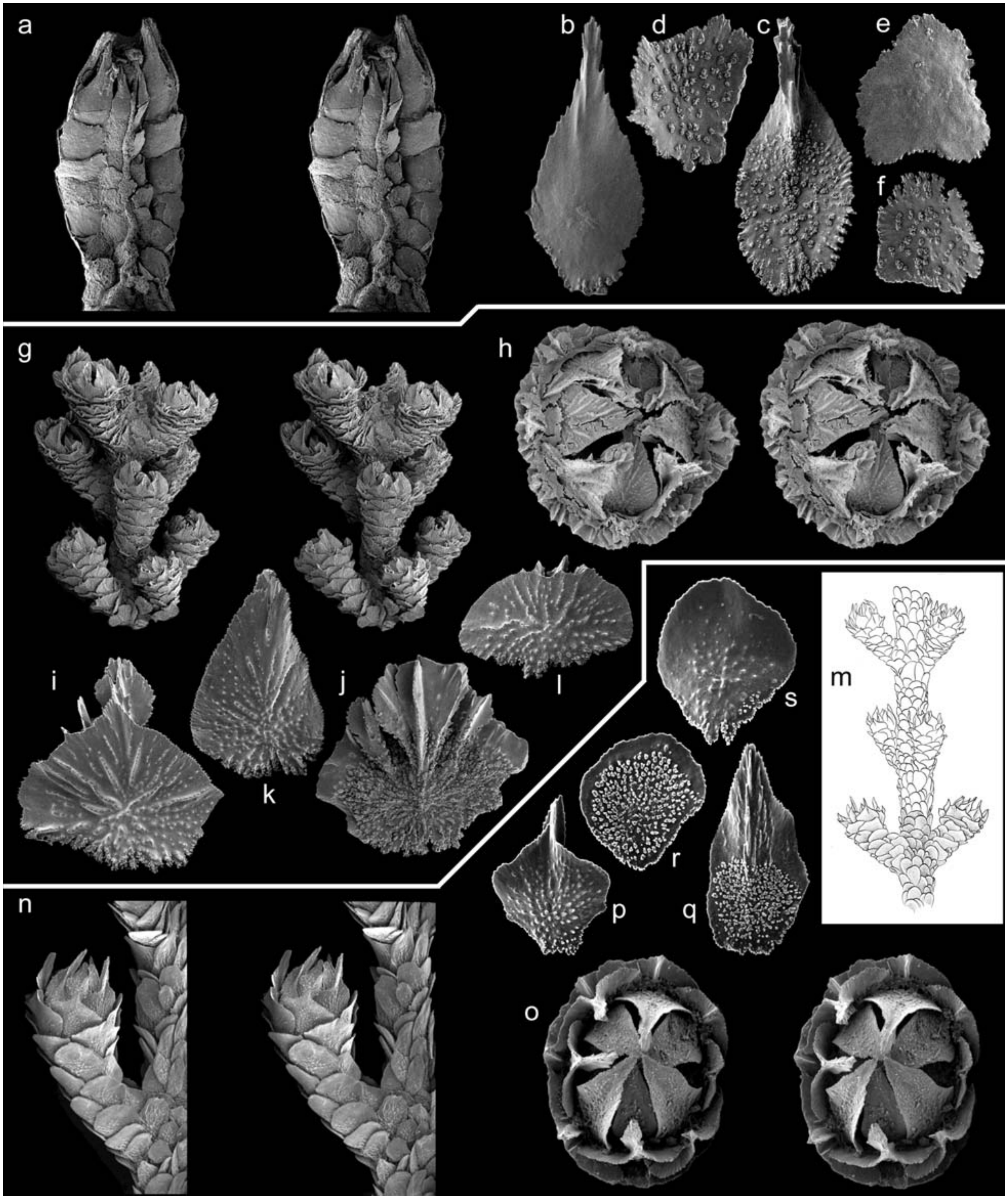

**FIGURE 6.** *Arntzia gracilis* (a–f, *Islas Orchadas*-109, USNM 78666): (a.) stereo view of adaxial side of a calyx, ×33; (b.) outer and (c.) inner surfaces of opercular scales, ×90; (d–f.) outer and inner surfaces of body wall scales, ×90. *Thouarella* (*T.*) *antarctica* (g–l, *Hero* 715-873, USNM 97966): (g.) stereo view of clustered calyces, ×9; (h.) stereo opercular view showing eight opercular and eight marginal scales, ×29; (i.) outer and (j.) inner surfaces of marginal scales showing ornate ridging on inner surface, ×53; (k.) outer surface of an opercular scale, ×53; (l.) outer surface of a body wall scale, ×53. *Thouarella* (*Euthouarella*) *hilgendorfi* (m, *Challenger*-192, BM 89.5.27.40; n–s, *Siboga*-251): (m.) partially stippled drawing of a branch fragment, ×13; (n.) stereo lateral view of a calyx, ×33; (o.) stereo opercular view, ×44; (p.) outer surface of a marginal scale, ×80; (q.) inner surface of an opercular scale, ×120; (r.) inner and (s.) outer surfaces of body wall scales, ×120.

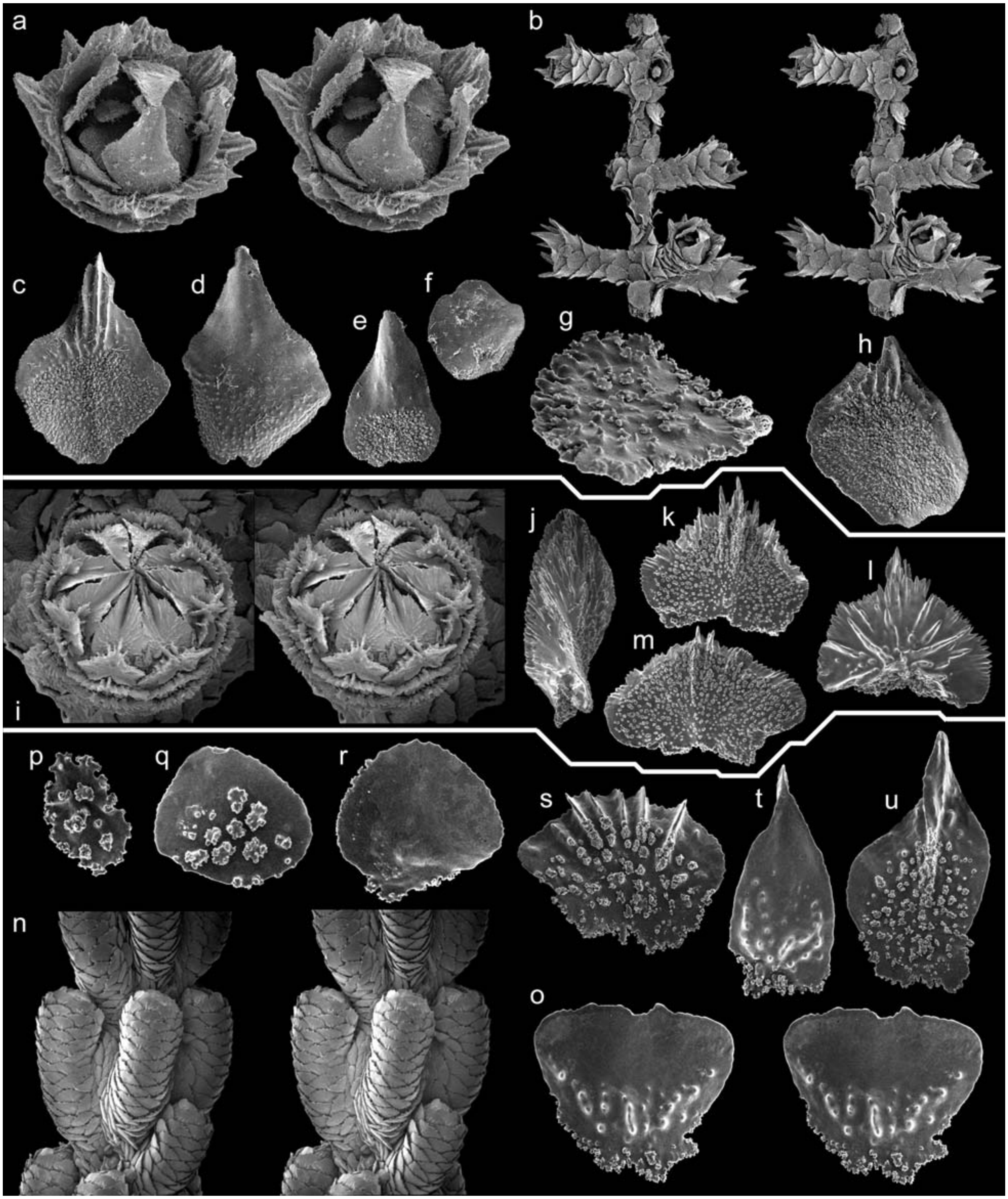

**FIGURE 7.** *Thouarella* (*Diplocalyptra*) *coronata* (a–h, holotype, USNM 50118): (a.) stereo view of opercular region showing eight opercular and eight marginal scales, ×50; (b.) stereo view of several calyces, ×13; (c.) inner and (d.) outer surfaces of marginal scales, ×80; (e.) inner surface of an opercular scale, ×80; (f.) outer and (g.) inner surfaces of coenenchymal scales, ×80, ×360, respectively; (h.) inner surface of a body wall scale, ×80. *Thouarella* (*Epithouarella*) *crenelata* (i–m, *Eltanin*-1536, USNM 84335): (i.) stereo opercular view showing eight opercular and eight marginal scales, ×31; (j.) side view of an opercular scale, ×62; (k.) inner and (l.) outer surfaces of marginal scales, ×62; (m.) inner surface of a body wall scale, ×62. *Metafannyella lepidota* (n, *Eltanin*-1002, USNM 83044; o–u, holotype, *Eltanin*-2002, USNM 82961): (n.) stereo view of a whorl, ×20; (o.) stereo view of the outer surface of a body wall "ascus" scale showing the weak transverse ridge, ×125; (p.) inner coenenchymal sclerite, ×160; (q.) inner and (r.) outer surfaces of surface coenenchymal scales, ×175; (s.) inner surface of a body wall scale, ×115; (t.) outer and (u.) inner surfaces of opercular scales, ×115.

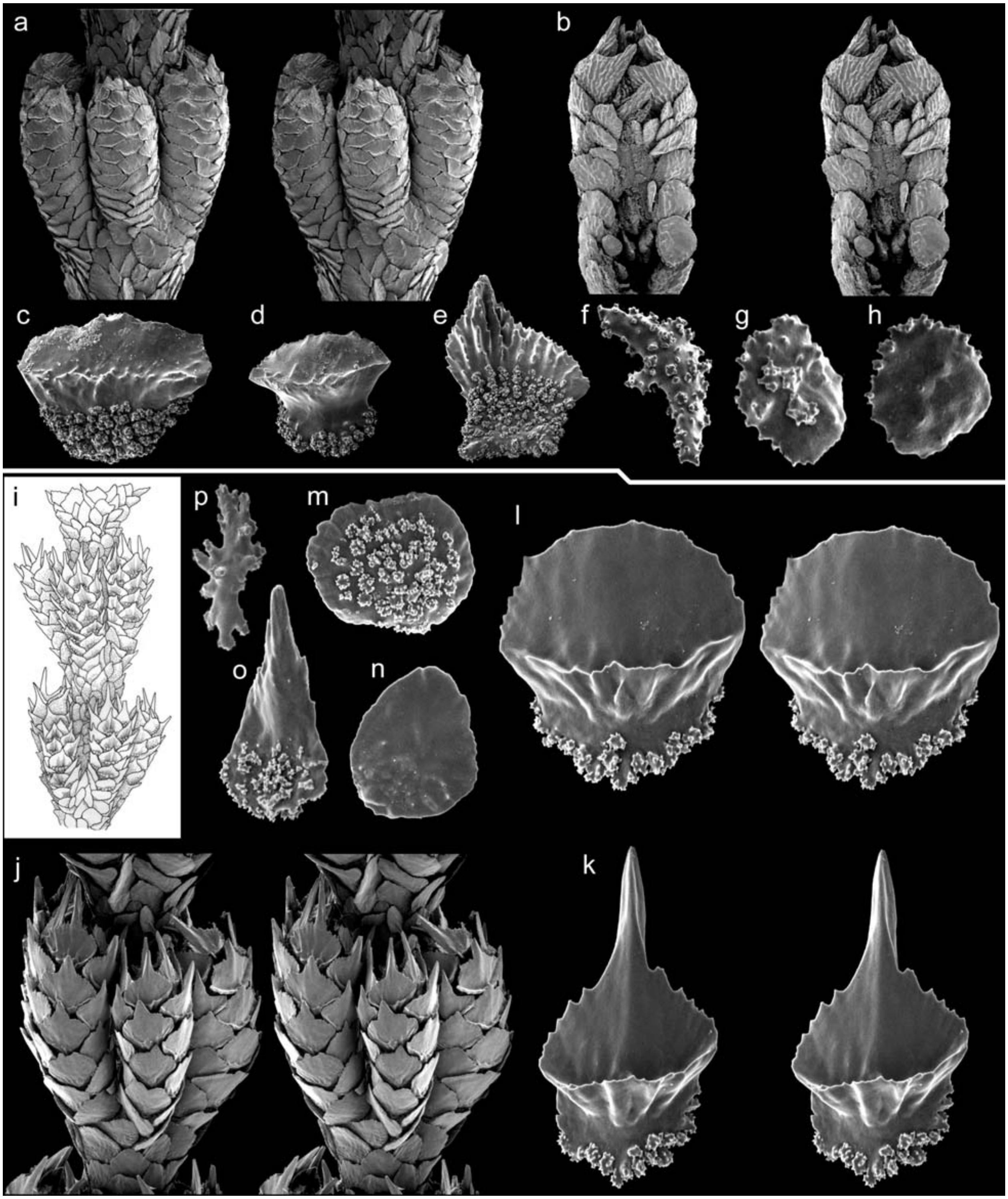

**FIGURE 8.** *Fannyella* (*F.*) *rossi* (a–h, neotype, AM G13237): (a.) stereo view of a whorl of calyces, ×25; (b.) stereo view of adaxial side of a calyx showing bare region, ×40; (c–d.) side views of body wall ascus-type scales, ×100; (e.) inner surface of an opercular scale, ×100; (f.) tuberculate sclerites of inner coenenchyme, ×150; (g.) inner and (h.) outer surfaces of surface coenenchymal scales, ×250. *Fannyella* (*Scyphogorgia*) *liouvillei* (i, *Eltanin*-499-5, USNM 58156; j–o, *Eltanin*-2095, USNM 82981; p, *Eltanin*-418, USNM 82980): (i.) drawing of two whorls of calyces, ×14; (j.) stereo view of one whorl, ×35; (k.) stereo lateral view of an ascus-type marginal scale, ×92; (l.) stereo lateral view of an ascus-type body wall scale, ×100; (m.) inner and (n.) outer surfaces of coenenchymal scales, ×120; (o.) inner surface of an opercular scale, ×155; (p.) tuberculate sclerite from inner coenenchyme, ×155.

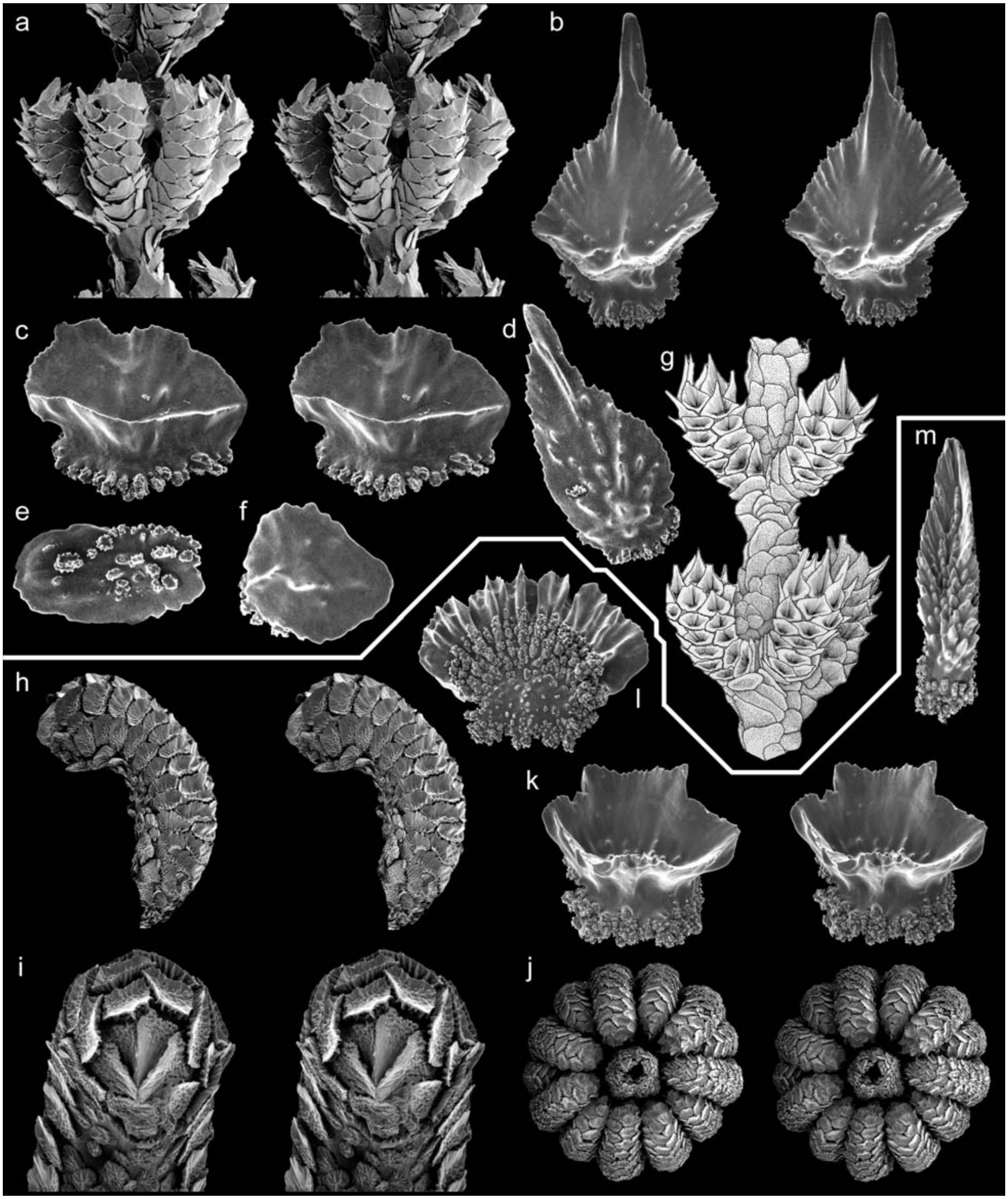

**FIGURE 9.** *Fannyella* (*Cyathogorgia*) *spinosa* (a–g, *Eltanin*-499, USNM 58152): (a.) stereo view of a whorl of calyces, ×21; (b.) lateral stereo view of an ascus-type marginal scale, ×110; (c.) lateral stereo view of an ascus-type body wall scale, ×110; (d.) outer surface of an opercular scale, ×110; (e.) inner and (f.) outer surfaces of coenenchymal scales, ×180; (g.) drawing of two whorls of calyces, ×23. *Onogorgia nodosa* (h, j, *Siedlecki*-76, USNM 82945; i, k–m, *Siedlecki*-47, USNM 82944): (h.) stereo view of lateral face of a calyx, ×22; (i.) stereo view of adaxial side of a calyx, ×44; (j.) stereo view of a whorl from above, ×9; (k.) stereo lateral view of an ascus-type body wall scale, ×100; (l.) inner surface of a body wall scale, ×100; (m.) outer surface of an opercular, ×100.

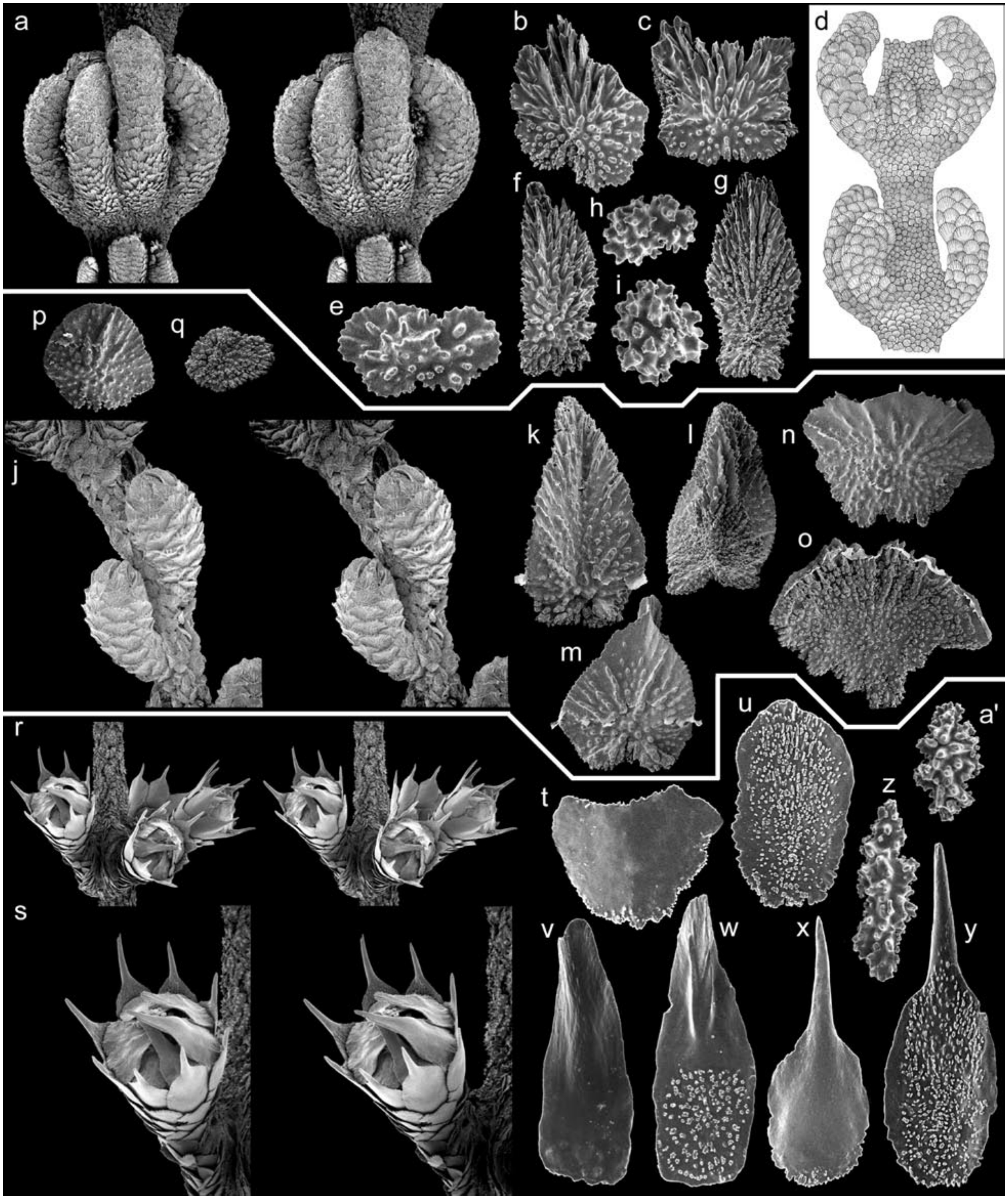

**FIGURE 10.** *Pyrogorgia lemnos* (a–i, holotype, *Eltanin*-740, USNM 58392): (a.) stereo view of a whorl of polyps, ×13; (b–c.) outer surface of body wall scales, ×90; (d.) drawing of two whorls and branch, ×10; (e.) outer surface of coenenchymal scale, ×180; (f.) outer and (g.) inner surfaces of opercular scales, ×90; (h–i.) inner coenenchymal tuberculate sclerites, ×180. *Amphilaphis regularis* (j–q, syntype, BM 1889.5.27.60): (j.) stereo view of several calyces, ×20; (k.) outer and (l.) inner surfaces of opercular scales, ×90; (m.) outer surface of marginal scale, ×90; (n.) outer and (o.) inner surfaces of body wall scales, ×90; (p.) outer and (q.) inner surfaces of coenenchymal scales, ×90. *Mirostenella articulata* (r–s, *Siedlecki*-601-29, USNM 84344; t–a′, holotype, *Eltanin*-1536, USNM 79959): (r.) stereo view of a whorl of calyces, ×18; (s.) stereo opercular view of a calyx, ×36; (t.) outer and (u.) inner surfaces of body wall scales, ×85; (v.) outer and (w.) inner surfaces of opercular scales, ×120; (x.) outer and (y.) inner surfaces of marginal scales, ×73; (z–a′.) outer surface of coarsely granular coenenchymal sclerites, ×85.

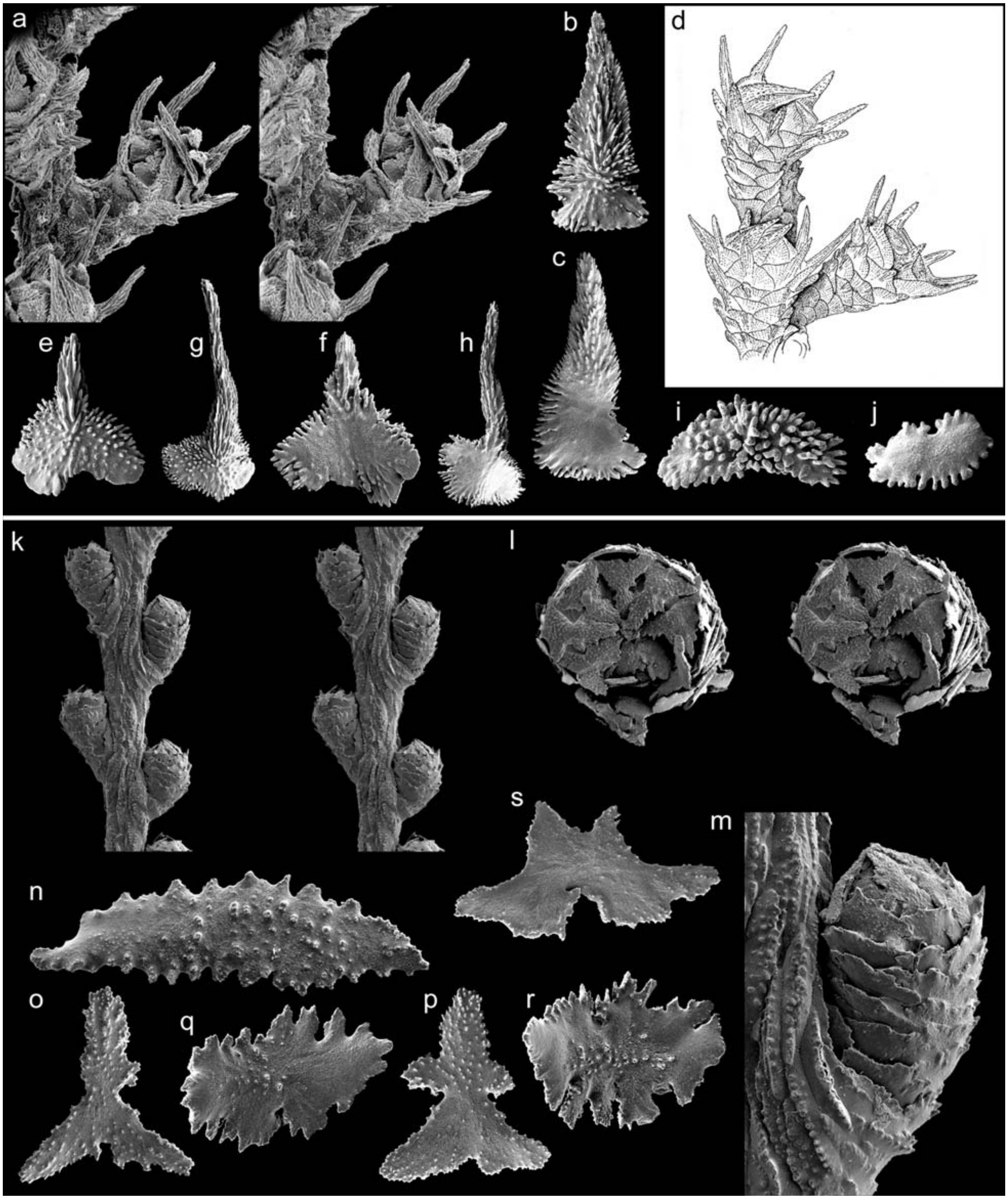

**FIGURE 11.** *Acanthoprimnoa goesi* (a–c, e–j, *Gerda*-633, USNM 52973; d, *Gerda*-242, USNM 52968): (a.) stereo view of apical end of a calyx, ×34; (b.) outer and (c.) inner surfaces of opercular scales, ×85; (d.) drawing of three calyces, ×28; (e.) outer and (f.) inner surfaces of body wall scales, ×85; (g.) outer and (h.) inner surfaces of marginal scales, ×55; (i.) outer (j.) and inner surfaces of coenenchymal scales, ×125. *Plumarella penna* (k–s, Darwin Harbor, USNM 1107503): (k.) stereo view of alternating calyces, ×37; (l.) stereo opercular view, ×120; (m.) lateral view of calyx, ×150; (n.) outer surface of a coenenchymal scale, ×325; (o–p.) outer surface of opercular scales, ×350; (q–r.) inner surface of body wall scales, ×235; (s.) outer surface of a marginal scale, ×325.

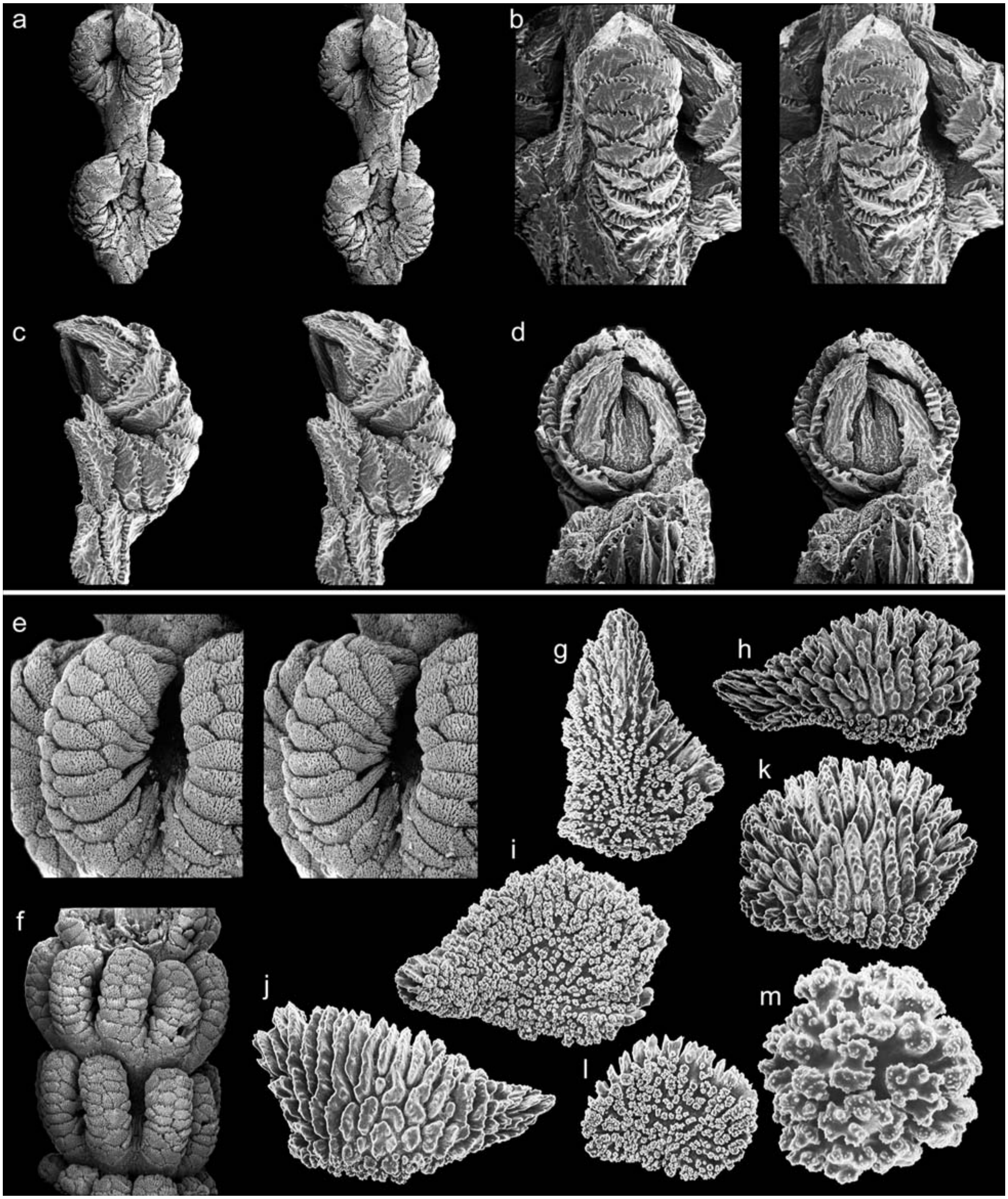

**FIGURE 12.** *Callogorgia verticillata* (a–d, *Meteor*-9148, USNM 59107): (a.) stereo view of two whorls of calyces, ×13; (b.) stereo view of abaxial side of a calyx, ×34; (c.) stereo view of lateral side of a calyx, ×34; (d.) stereo view of adaxial side of a calyx, ×50. *Fanellia compressa* (e, *Albatross*-4781, USNM 57543; f, *Albatross*-3599, USNM 57542; g–m, *Dorothy* C45, Albatross Bank, Alaska, USNM 51284): (e.) stereo lateral view of a calyx, ×27; (f.) two whorls of polyps, ×11; (g.) inner surface of an opercular scale, ×105; (h–j.) outer and inner surfaces of outer-lateral scales, all ×105; (k.) outer and (l.) inner surfaces of body wall scales, ×105; (m.) tuberculate spheroid of inner coenenchyme, ×350.

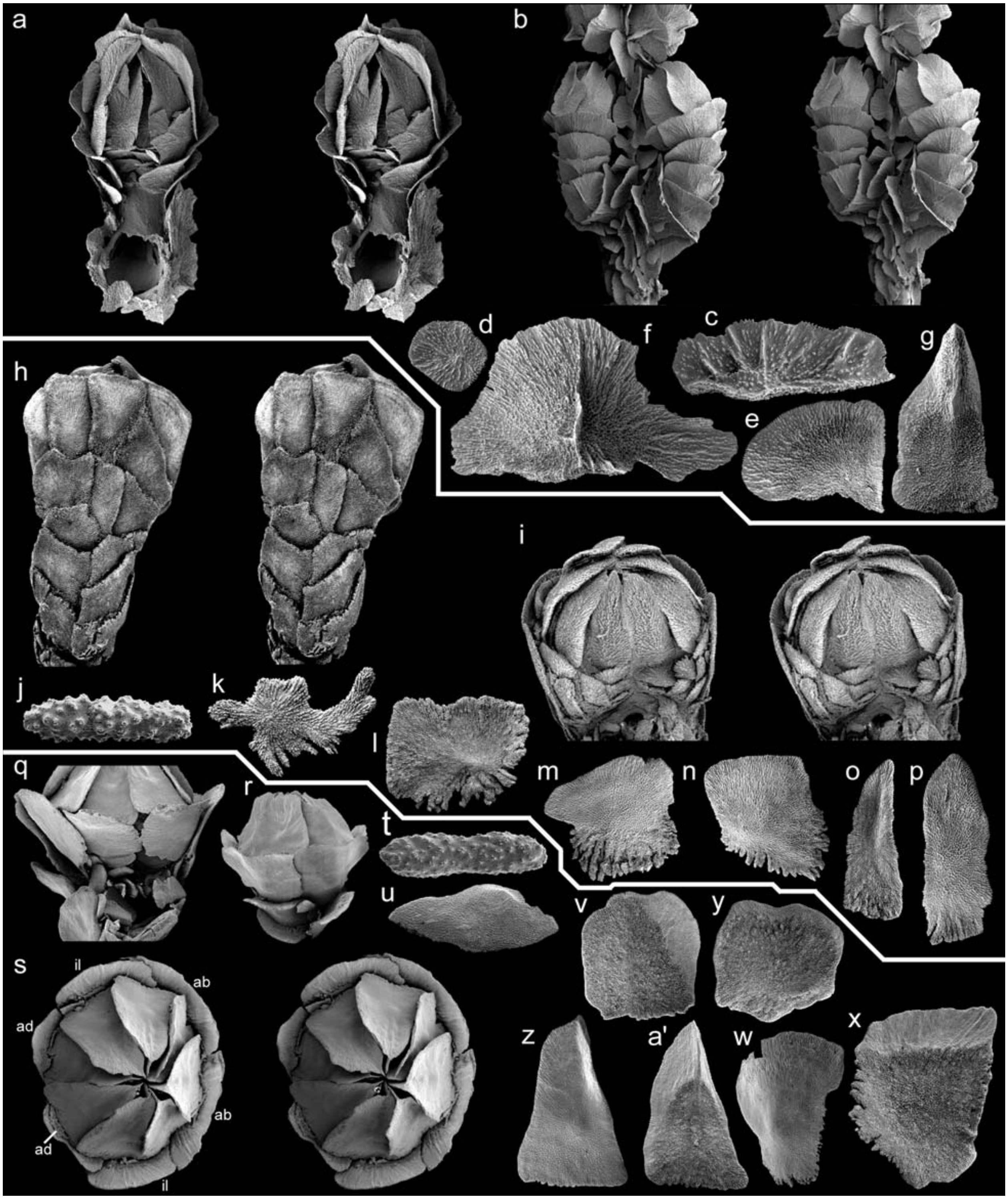

**FIGURE 13.** *Paranarella watlingi* (a–g, holotype, *RB*05-03, USNM 1096721): (a.) stereo view of adaxial side of a calyx, ×21; (b.) stereo view of two calyces, ×11; (c.) ridged coenenchymal scale, ×62; (d.) outer surface of an adaxial body wall scale, ×30; (e.) inner surface of an abaxial body wall scale, ×30; (f.) outer surface of a basal scale, ×30; (g.) inner surface of an opercular scale, ×30. *Primnoa resedaeformis* (h–i, *Albatross*-2068, USNM 16946; j–p, *Albatross*-2527, USNM 12262): (h.) stereo view of abaxial side of a calyx, ×11; (i.) stereo opercular view of adaxial side of a calyx, ×17; (j.) a tentacular rod, ×165; (k.) outer surface of a coenenchymal scale, ×28; (l.) outer surface of a basal scale, ×14; (m.) outer surface of a marginal scale, ×14; (n.) outer surface of an abaxial body wall scale, ×14; (o.) inner and (p.) outer surfaces of opercular scales, ×17. *Australogorgia aldersladei* (q–a′, holotype, NTM CO 13054): (q.) adaxial side of a calyx, ×9; (r.) abaxial side of a calyx, ×7; (s.) stereo view of operculum (marginal scales labeled: ab, abaxial; il, inner lateral; ad, adaxial), ×11; (t.) tentacular rod, ×135; (u.) outer surface of a coenenchymal scale, ×15; (v.) adaxial, (w.) abaxial, and (x.) inner lateral marginal scales, ×15, ×12, ×15, respectively; (y.) abaxial body wall scale, ×15; (z.) outer and (a′.) inner surfaces of opercular scales, ×15.

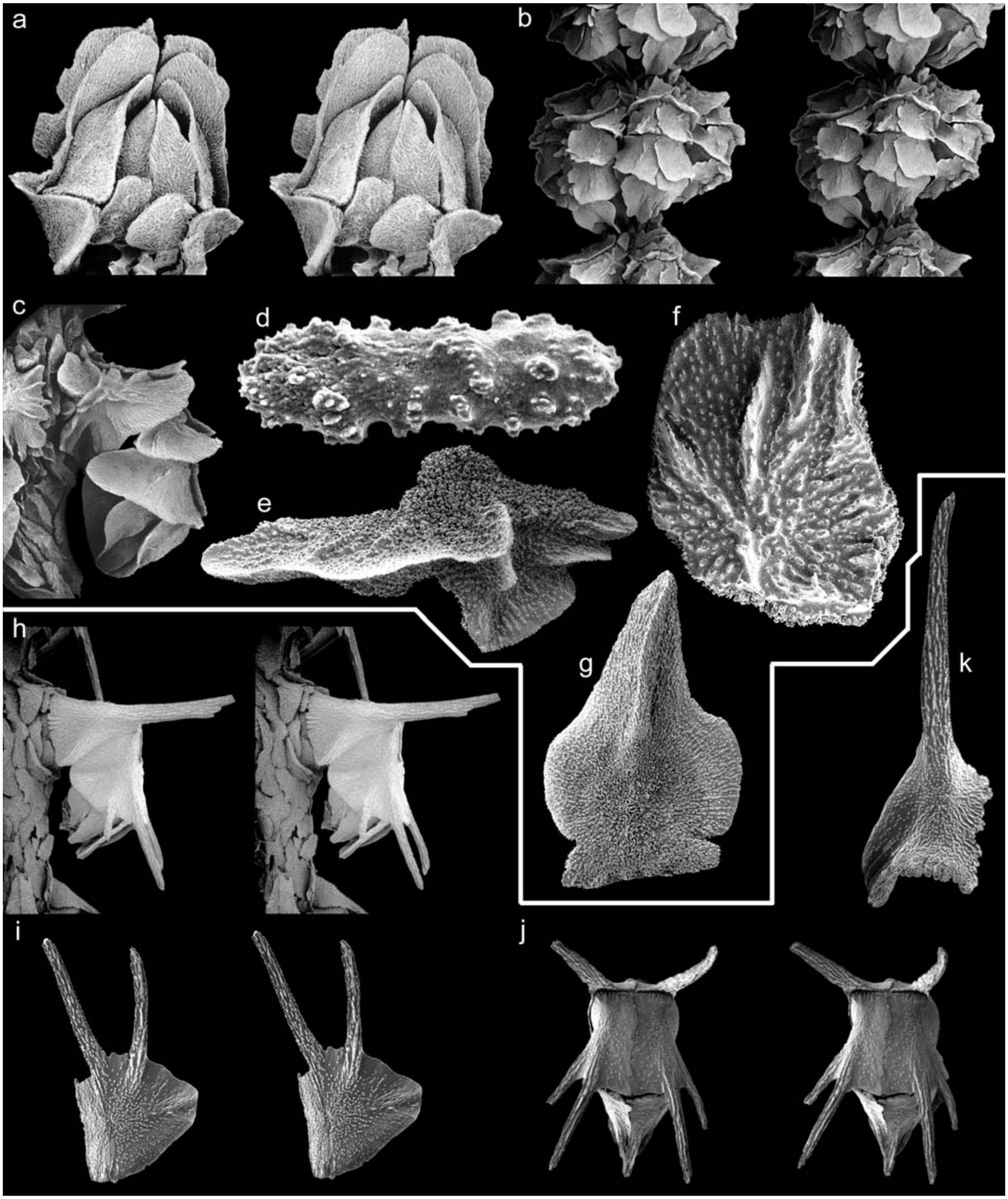

**FIGURE 14.** *Narella regularis* (a–g, neotype, *Albatross*-2752, USNM 49385): (a.) stereo view of adaxial tip of a calyx, ×34; (b.) stereo view of a whorl of calyces, ×11; (c.) lateral view of a calyx, ×20; (d.) tentacular rod, ×1010; (e.) outer surface of a ridged coenenchymal scale, ×150; (f.) outer surface of an adaxial body wall scale, ×150; (g.) inner surface of an opercular scale, ×55. *Arthrogorgia ijimai* (h–i, k, *Albatross*-5087, USNM 30028; j, *Albatross*-5080, USNM 30074): (h.) stereo lateral view of a calyx, ×18; (i.) stereo view of a buccal sclerite, ×25; (j.) stereo view of abaxial side of a calyx, ×21; (k.) basal sclerite with elongate spine, ×29.

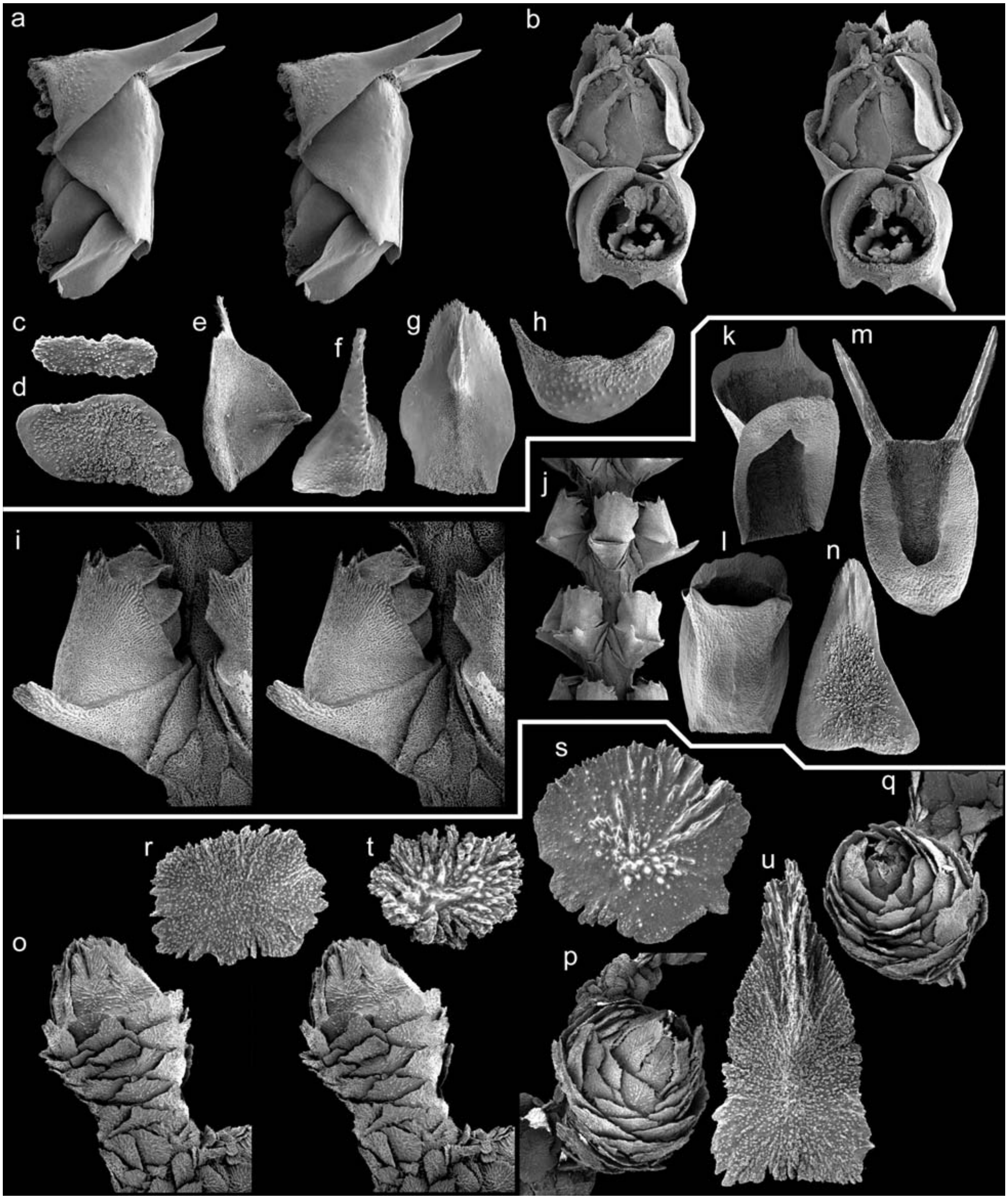

**FIGURE 15.** *Paracalyptrophora kerberti* (a–h, *Albatross*-5093, USNM 30145): (a.) stereo lateral view of a calyx, ×22; (b.) stereo view of adaxial face of a calyx, ×22; (c.) tentacular rod, ×325; (d.) inner surface of an adaxial buccal scale, ×72; (e.) inner surface of a buccal sclerite, ×19; (f.) outer surface of a basal sclerite, ×19; (g.) inner surface of an opercular, ×32; (h.) outer surface of an infrabasal scale, ×32. *Calyptrophora japonica* (i–j, *Albatross*-4924, USNM 30027): (i.) stereo lateral view of a calyx, ×34; (j.) two whorls of calyces, ×11. *Calyptrophora clinata* (k–n, holotype, *RB05*-03-5, USNM 1096714): (k.) inner and (l.) outer surfaces of buccal sclerites, ×25; (m.) inner surface of a pair of fused basal sclerites, ×25; (n.) inner surface of an opercular scale, ×75. *Tokoprymno maia* (o–u, holotype, *Eltanin*-1346, USNM 81535): (o.) stereo lateral view of a vegetative calyx, ×13; (p–q.) opercular views of two brooding calyces, one with intact operculars and the other without, ×13, ×10, respectively; (r.) inner and (s.) outer surfaces of body wall scales, ×40; (t.) outer surface of a coenenchymal scale, ×40; (u.) inner surface of an opercular scale, ×40.

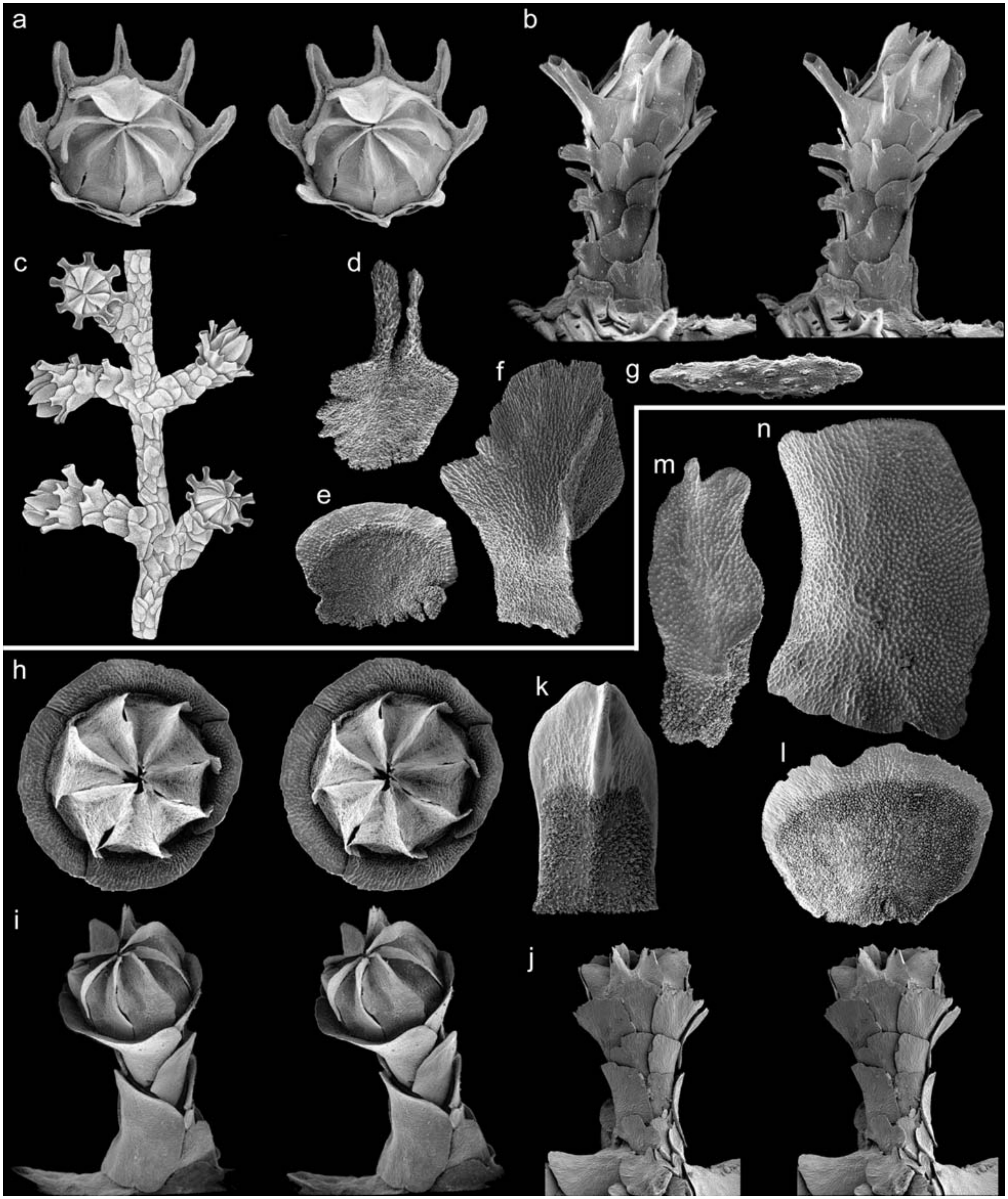

**FIGURE 16.** *Parastenella doederleini* (a–b, Sagami Bay, depth unknown, USNM 50121): (a.) stereo view of operculum and marginal scale flutes, ×27; (b.) stereo lateral view of a calyx showing body wall flutes, ×22. *Parastenella spinosa* (c, *Eltanin*-1416, USNM 98039): (c.) drawing of several calyces, ×7. *Parastenella ramosa* (d–g, *Tiburon*-874-A6, USNM 1102456): (d.) inner surface of a fluted marginal scale, ×40; (e.) inner surface of an abaxial body wall scale, ×40; (f.) outer, lateral view of an opercular scale, ×40; (g.) tentacular rod, ×280. *Candidella imbricata* (h, *Atlantis*-280-9, USNM 57552; i–n, *Eastward*-26031, USNM 57553): (h.) stereo view of operculum and marginal scales, ×25; (i.) stereo lateral view of a calyx, ×25; (j.) stereo lateral view of adaxial side of a calyx, ×21; (k.) inner surface of an opercular scale, ×68; (l.) inner surface of an abaxial marginal scale, ×95; (m.) outer surface of a coenenchymal scale, ×55; (n.) outer surface of a "basal" body wall scale, ×55.

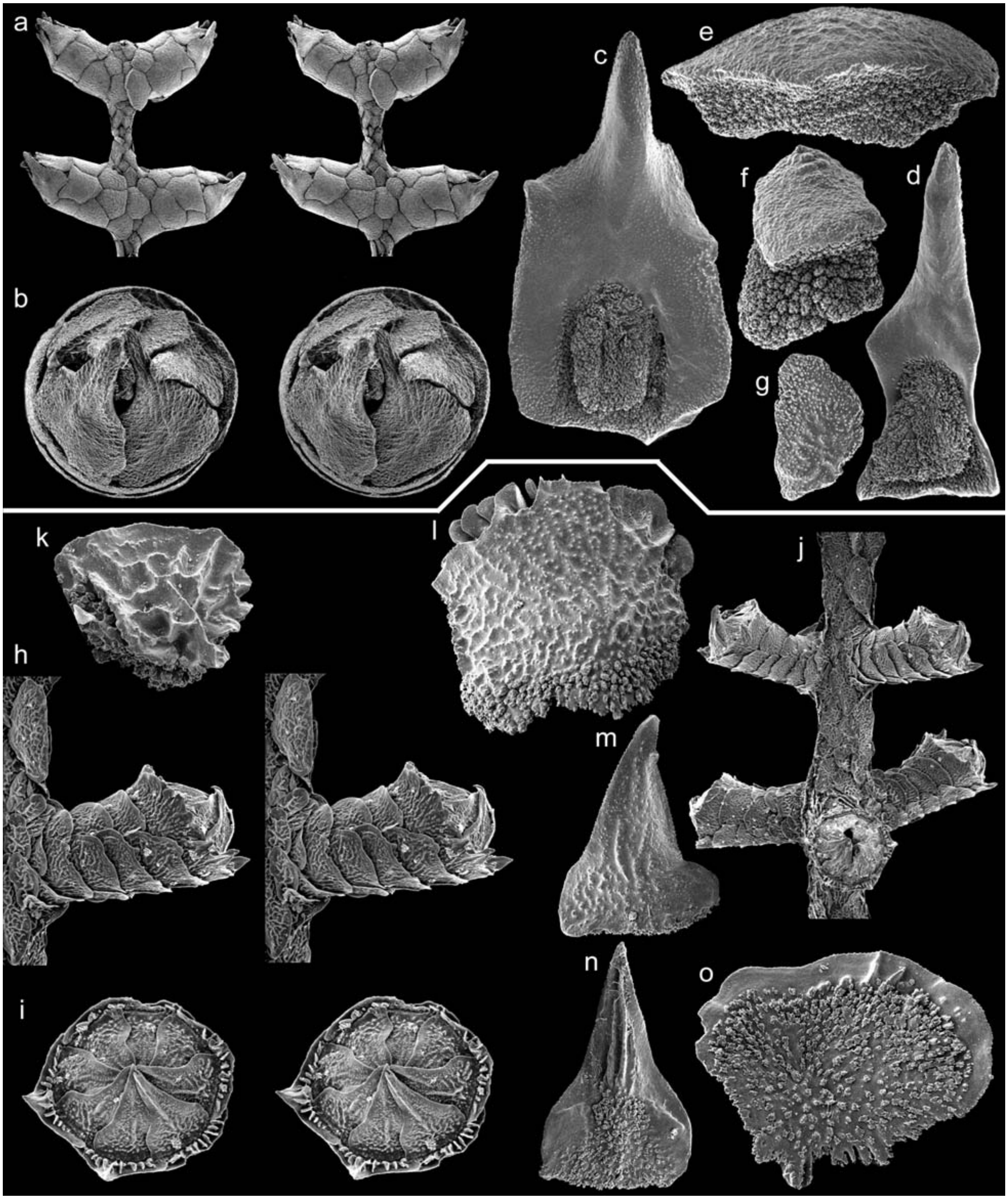

**FIGURE 17.** *Microprimnoa diabathra* (a–g, paratype, *MUSORSTOM* 5-306, USNM 79977): (a.) stereo view of two pairs of calyces, ×10; (b.) stereo opercular view, ×35; (c–d.) inner surface of opercular scales showing discrete patch of tubercles, ×70; (e–f.) lateral view of two thick body wall sclerites, ×70; (g.) outer surface of a coenenchymal scale, ×70. *Pterostenella plumatilis* (h–o, *Albatross*-5414, USNM 76964): (h.) stereo lateral view of a calyx, ×52; (i.) stereo view of operculum and marginals of a calyx, ×60; (j.) two whorls of calyces, ×25; (k.) outer surface of a coenenchymal scale, ×190; (l.) outer view of a marginal scale, ×130; (m.) outer and (n.) inner surface of opercular scales, ×130; (o.) inner surface of a body wall scale, ×165.

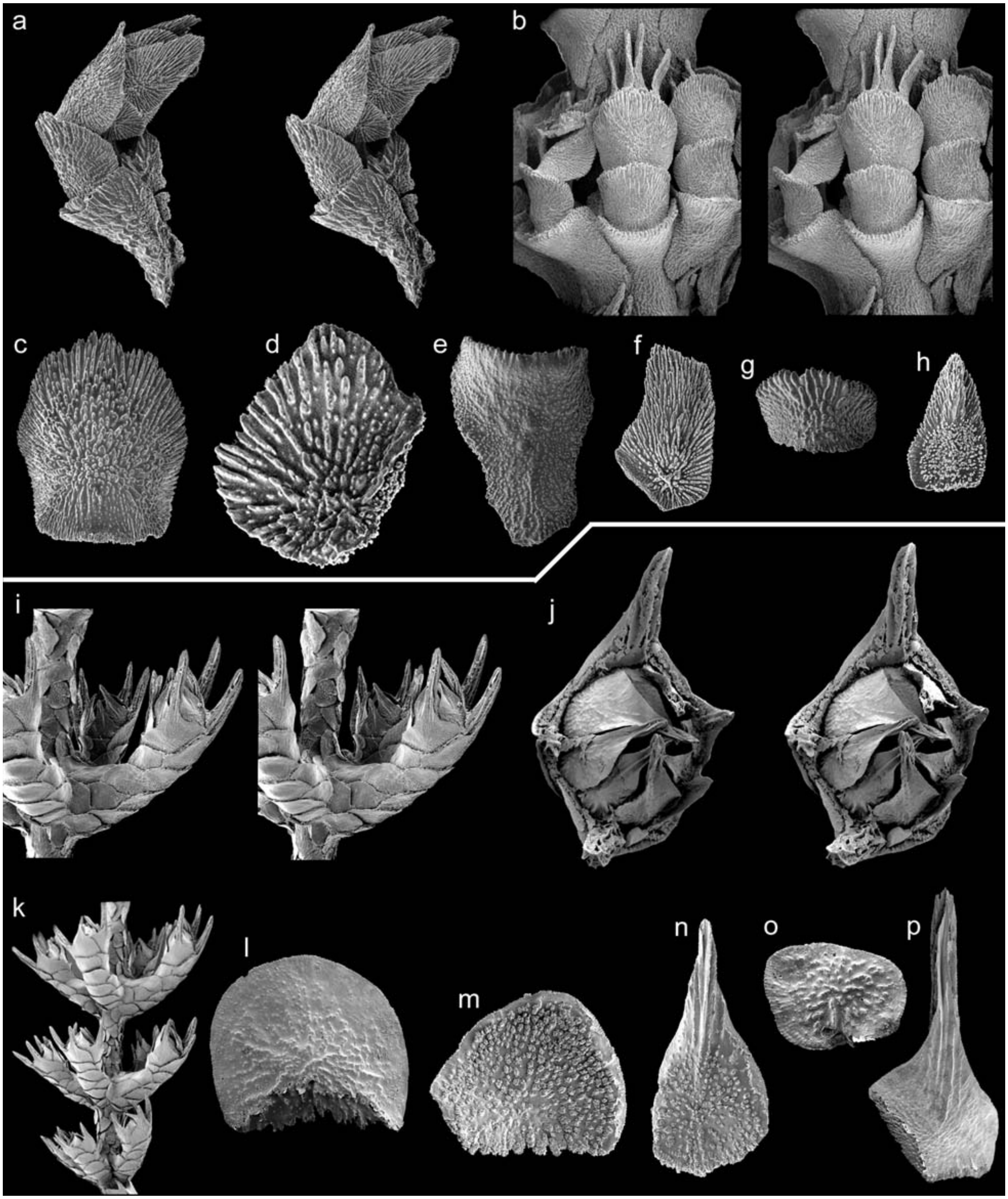

**FIGURE 18.** *Perissogorgia viridis* (a–h, paratype, HG193, USNM 80043): (a.) stereo lateral view of a calyx, ×37; (b.) stereo view of a whorl of calyces, ×24; (c.) outer surface of buccal body wall scale, ×52; (d.) outer surface of lateral buccal scale, ×140; (e.) outer surface of abaxial basal scale, ×43; (f.) outer and (h.) inner surfaces of opercular scales, ×55, ×75, respectively; (g.) outer surface of abaxial medial scale, ×75. *Dasystenella acanthina* (i–p, syntype, *Challenger*-320, ex BM 1889.05.27.48): (i.) stereo lateral view of several calyces, ×14; (j.) stereo opercular view showing eight operculars and the five marginals, ×35; (k.) lateral view of three whorls, ×8; (l.) outer and (m.) inner surfaces of body wall scales, ×55; (n.) inner surface of an opercular scale, ×55; (o.) outer surface of a coenenchymal scale, ×65; (p.) outer surface of a lateral marginal scale, showing ridged distal spine, ×35.

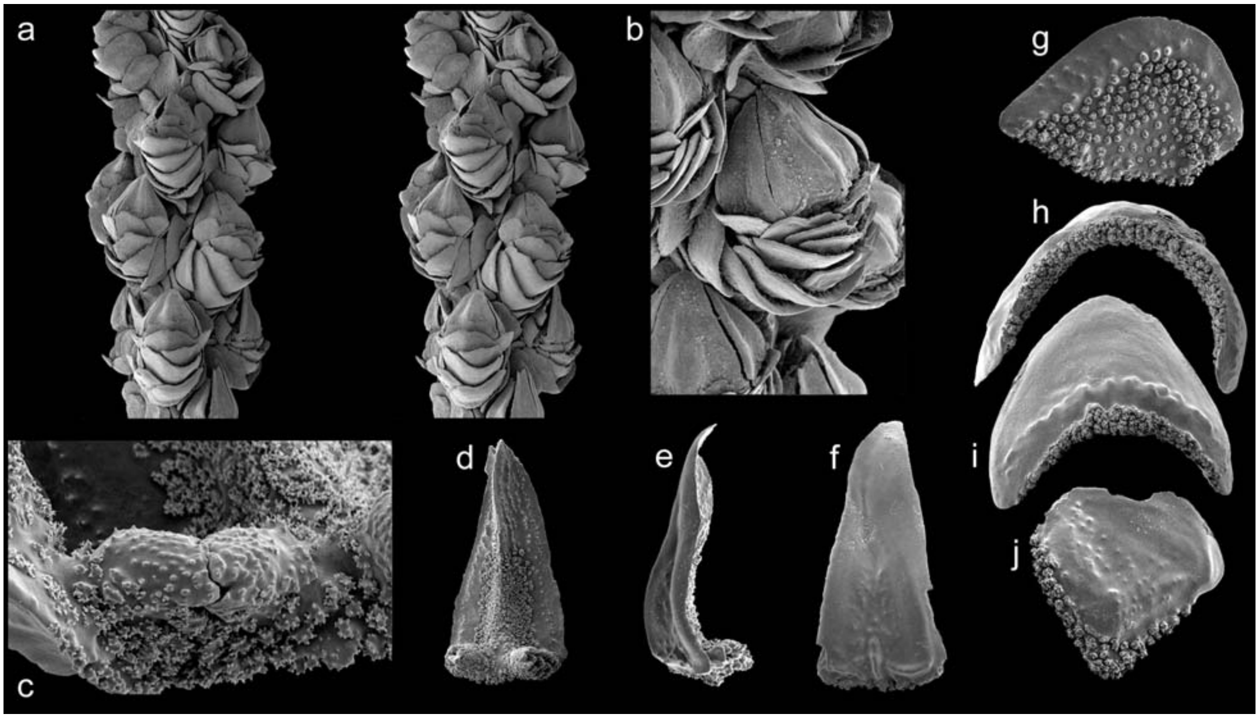

**FIGURE 19.** *Pseudoplumarella thetis* (a–j, syntype *Thetis*-40, AM G12137): (a.) lateral stereo view of calyces on a branch, ×19; (b.) lateral view of a calyx, ×40; (c.) locking apparatus between two adjacent opercular scales, ×320; (d.) inner, (e.) lateral, and (f.) outer surfaces of opercular scales, showing interlocking mounds, ×80; (g.) inner and (j.) outer surfaces of coenenchymal scales, ×80; (h.) edge and (i.) outer views of body wall scales, showing great curvature of scales, ×80.

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