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The type specimens of *Bebryce* (Cnidaria, Octocorallia, Plexauridae) re-examined, with emphasis on the sclerites

F.M. BAYER¹ & L.P. VAN OFWEGEN²

¹National Museum of Natural History, Smithsonian Institution, Washington D.C., USA. (deceased) ²Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands. E-mail: leen.vanofwegen@naturalis.nl; ofwegen@yahoo.com

Table of contents

Abstract
Introduction
Genus <i>Bebryce</i> Philippi, 1841
Key to the Atlantic and Mediterranean species of Bebryce (5 species)
Key to the Indo-Pacific species of <i>Bebryce</i> (22 species)
Bebryce asteria n. sp
Bebryce bocki Aurivillius, 1931
Bebryce boninensis Aurivillius, 1931
Bebryce brunnea (Nutting, 1908)
<i>Bebryce cactus</i> Bayer, 1994
Bebryce cinerea Deichmann, 1936
Bebryce cofferi n. sp
Bebryce crucifera (Bayer, 1981)
Bebryce densa Tixier-Durivault, 1972
Bebryce grandicalyx (Kükenthal, 1924)
Bebryce grandis Deichmann, 1936
Bebryce harpy Grasshoff, 1999
Bebryce hicksoni Thomson & Henderson, 1905
"Bebryce hicksoni Thomson & Henderson, 1905"
Bebryce species A
Bebryce species B
Bebryce indica Thomson, 1905
Bebryce inermis Samimi-Namin & Ofwegen, 2010
Bebryce mollis Philippi, 1842
Bebryce nuttingi Stiasny, 1942
Bebryce parastellata Deichmann, 1936
Bebryce philippii Studer, 1889
Bebryce rigida Tixier-Durivault, 1972
Bebryce sirene Grasshoff, 1999
Bebryce studeri Whitelegge, 1897
Bebryce sulfurea Grasshoff, 2000
Bebryce tenuis Thomson & Simpson, 1909
Bebryce thomsoni Nutting, 1910
Species incorrectly attributed to <i>Bebryce</i> :
Discogorgia acanthoides (Thomson & Russell, 1910), n. comb
Discussion
Acknowledgements
References

Abstract

Nineteen species of *Bebryce* are re-described and scanning electron microscopy (SEM) images of sclerites presented. For *B. sulfurea* Grasshoff, 2000, this is the first time SEM images of sclerites are presented. Two new species are described, *Bebryce asteria* **n. sp.** and *B. cofferi* **n. sp.**, and *B. stellata* Hentschel, 1903 is synonymized with *B. studeri* Whitelegge, 1897. *Bebryce acanthoides* Thomson & Russell, 1910 is referred to *Discogorgia* Kükenthal, 1919. The status of the original type material is discussed.

Key words: Bebryce, Discogorgia, re-descriptions, new species, SEM images, Siboga

Introduction

This study is based on an unfinished manuscript of the late Dr. F.M. Bayer (National Museum of Natural History, Smithsonian Institution, Washington D.C.). Sclerites of species of *Bebryce*, often old type material, are redescribed, and depicted using scanning electron microscopy (SEM), and the second author added SEM images and descriptions of the sclerites of *B. bocki*, Aurivillius, 1931, *B. boninensis* Aurivillius, 1931, *B. densa* Tixier-Durivault, 1972, *B. rigida* Tixier-Durivault, 1972, and *B. sulfurea* Grasshoff, 2000 to Bayer's manuscript. The confusing misidentifications of the Siboga species of *Bebryce*, *B. hicksoni* Thomson & Henderson, 1905, and *B. indica* Thomson, 1905, are also re-examined. The only holotype not available was of *B. tenuis* Thomson & Simpson, 1909, stored in the Indian Museum in Kolkata and unavailable for re-examination. We consider that *Bebryce cactus*, Bayer, 1993, *B. harpy* Grasshoff, 1999, *B. sirene* Grasshoff, 1999, and *B. inermis* Samimi-Namin & Ofwegen, 2010 were sufficiently described and are therefore not included in this publication. Two probable new species discovered in the Siboga material are treated as species A and B as we consider the material too old and damaged for formal description. In total 27 species are recognized, including the two described here, *B. asteria* **n. sp.** *Bebryce acanthoides* Thomson and Russell, 1910, cannot be retained in *Bebryce* and is referred to the genus *Discogorgia*. Two keys to the species are provided.

Abbreviations

BMNH	British Museum of Natural History, London, UK					
MNHN	Muséum national d'Histoire naturelle, Paris, France					
NBC	Naturalis Biodiversity Center, Leiden, The Netherlands; previously National Museum of Natural					
	History (NNM); Rijksmuseum van Natuurlijke Historie (RMNH)					
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA					
UUZM	Uppsala University Zoological Museum, Uppsala, Sweden					
ZMA	Zoological museum Amsterdam, The Netherlands					

Genus Bebryce Philippi, 1841

Bebryce Philippi, 1841: 9; 1842: 35, pl. 1, fig. 1; Milne Edwards & Haime, 1857: 187; Kölliker, 1865: 137; Gray, 1869: 246; 1870: 50; von Koch, 1887: 54; Studer [& Wright], 1887: 57; Wright & Studer, 1889: 1v; Studer, 1889: 10; Whitelegge, 1897: 314; Hentschel, 1903: 649; Hickson, 1905: 813; 1940: 282; Thomson & Henderson, 1905: 294; Thomson, 1905: 175; Thomson & Simpson, 1909: 222; Thomson & Russell, 1910: 150; Nutting, 1910: 47; 1912: 87; Kükenthal, 1919: 293, 759, 841; 1924: 208; Aurivillius, 1931: 189; Deichmann, 1936: 124; Bayer, 1956: 203; Grasshoff, 1999: 62; 2000: 101; Fabricius & Alderslade, 2001: 192.

Pseudobebryce Kükenthal, 1919: 841; 1924: 205 (type species *Bebryce philippii* Studer, 1889, by original designation). *Nicaule* Bayer, 1981: 926 (type species, *N. crucifera* Bayer, 1981).

Type species. Bebryce mollis Philippi, 1841, by monotypy.

Diagnosis. Plexaurids with sclerites of coenenchyme in the form of rosettes comprising a continuous outer layer, but which in various species may be indistinctly differentiated and of sparse occurrence, or strongly modified as antler-like forms densely covering the surface; deeper coenenchyme filled with stellate plates having from 3 to

many rays, usually flat and with a central process but sometimes with some of the rays not in the primary plane, sometimes in the form of discoidal bodies with several marginal processes, usually with a central process on the outer surface; spindles of extremely rare occurrence, formed from crosses by suppression of opposite rays; armature of anthocodiae well developed, with eight points consisting of one or more pairs of more or less curved spindles *en chevron* beneath the tentacles above a collaret of several circles of transversely placed bow-shaped spindles, and small, flattened rodlets curved or bent at one end extending along the backs of the tentacles.

Etymology. A Danaid (Philippi, 1841, 1842). According to Barthell (1971: 125), one of the daughters of Danaus was Bryce, but he does not list *Bebryce*.

Remarks. A serious obstacle to the evaluation of species in the genus is the lack of information about morphological variation of colonial form and, especially, of sclerites as most if not all species were described from one or a very few colonies. Fortunately, USNM and NBC collections include several samples from a single locality that are composed of two or more colonies, sometimes even many colonies. These provide information about the extent of skeletal variation that can be expected among colonies of similar form comprising what is interpreted as a single population. Such information will be discussed in the descriptions of those species represented by an adequate number of colonies to permit evaluation.

The sclerites of the outer coenenchyme have been referred to by several ambiguous descriptive expressions including "collarbuttons with beautifully scalloped edges" (Nutting, 1910), "spicules of cotton-reel shape" (Aurivillius, 1931), "spicules [...] resembling the paxillae of starfish" and "Spicula von paxillenähnlicher Form" (Nutting, 1908; Stiasny, 1942), "rosettes" (Bayer, 1956; Bayer, Grasshoff & Verseveldt, 1983), "sclérites en corbeille" (Carpine & Grasshoff, 1975), and (most commonly) "kleine, kelchformige Skleriten" (Kükenthal) and cup-shaped sclerites (Deichmann, 1936). The term "rosette" is used herein, in accordance with terminology adopted by Bayer, Grasshoff & Verseveldt (1983). The flat, stellate to discoidal sclerites of the deeper coenenchyme have often been termed "scales" since Kölliker's (1865) introduction of the term "Schuppen." As these are not "scales" in the sense of the scales of Chrysogorgiidae and Primnoidae, which Kölliker also called "Schuppen," here they will be called discoidal plates or stellate plates, depending upon their shape.

Classification. Kükenthal (1924: 140) separated *Bebryce* Philippi, 1841 from *Pseudobebryce* Kükenthal, 1919 on the basis that the characteristic sclerites have the form of cups ("Kelchform"), whereas those of *Pseudobebryce* are double disks or double spheres (Doppelscheiben oder Doppelkugeln). *Bebryce mollis* Philippi, the type species of *Bebryce*, has characteristic rosettes that are, indeed, shaped rather like miniature cups, as shown by Aurivillius (1931: 192, fig. 37, 3a), Carpine & Grasshoff (1975: 59, fig. 30B), Grasshoff (1977: 60, fig. 60B), and G. von Koch (1887: pl. 1, fig. 1a–c). However, *Bebryce philippii* Studer, 1889, the type species of Kükenthal's genus *Pseudobebryce* (1919: 841), has virtually indistinguishable cup-shaped sclerites rather than the "besonders characteristisch kleine, oberflächlich gelegene, bewarzte Doppelscheiben und Doppelkugeln" cited by Kükenthal (1919: 841; 1924: 205) in the generic diagnosis. Aurivillius (1931: 198) justifiably concluded that the absence of processes in the center of the outer "disk" of the "dumb-bell shaped" sclerites (i.e. the "rosettes" of the outermost cortex) in *B. mollis* is not of generic significance, and correctly regarded *Pseudobebryce* Kükenthal, 1919 as a junior subjective synonym of *Bebryce* Philippi, 1841. Similar cup-shaped sclerites are present in *B. studeri* Whitelegge, 1897, *B. cinerea* Deichmann, 1936, *B. grandis* Deichmann, 1936, and *B. parastellata* Deichmann, 1936. In some cases, the outer part of the sclerite is concave and cup-like, in others more or less convex, and in that case finely sculptured by projecting fascicles of microcrystals of calcite.

Only *B. thomsoni* Nutting, 1910, appears to fit the generic diagnosis of *Pseudobebryce* as originally given by Kükenthal (1919), judged solely from the crude original illustrations resembling double disks and double spheres, but even these were described as "hutpilzartigen Skleriten" by Kükenthal himself (1924: 208), a term not inappropriate for the cup-shaped sclerites found in *Bebryce*.

If there is any morphological justification for a genus closely related to, but distinct from *Bebryce* it must be based upon some character other than "Doppelscheiben" and "Doppelkugeln," which are not morphologically distinct from the cup-shaped rosettes of *B. mollis*. One such feature may be the modification of the larger, inner coenenchymal sclerites as tuberculate disks, in contrast to the stellate plates of *B. mollis* (Grasshoff, 1977: 60, figs. C, C'; Kölliker, 1865: pl. 18, fig. 1; Carpine & Grasshoff, 1975: 58, fig. 30). This type of sclerite is present not only in *B. philippii* but also in several other species of *Bebryce* of the Indo-Pacific.

The stellate coenenchymal plates of *B. mollis* (Figs. 22g, 23f) are so dramatically different from the discoidal plates of *B. philippii* (Fig. 29f) that they justifiably could be recognized as the basis of two distinct genera as

proposed by Kükenthal (1919: 841; 1924: 205, 208). Moreover, no species having discoidal plates as in *B. philippii* has been found in Atlantic waters. However, a survey of species worldwide reveals so many examples of intermediates between the stellate and discoidal sclerite forms that, at least from a pragmatic standpoint, the distinction between *Bebryce* and *Pseudobebryce* becomes ambiguous even though a valid phylogenetic distinction may exist.

Vargas *et al.* (2010) studied the relationship between *Bebryce, Heterogorgia*, and *Lytreia* using the mitochondrial marker mtMutS (= msh1). They found a close phylogenetic relationship between these three genera and provided a morphological characterization of them.

Key to the Atlantic and Mediterranean species of Bebryce (5 species)

1.	Coenenchymal sclerites include discoidal bodies or thick, warty plates
-	Coenenchymal sclerites are stellate plates only
2.	Calycular margins with spindles with blade that often divides into two or more strong spines
-	Calycular margins with spindles with a single blade
3.	Coenenchymal sclerites are 4–5-rayed plates but not multiradiate plates B. parastellata Deichmann, 1936
-	Multiradiate plates also present
4.	No irregular plates present
-	Irregular plates present

Key to the Indo-Pacific species of *Bebryce* (22 species)

1.	Abundant small crosses representing the usual rosettes, together with 6-rayed tuberculate capstans, but no rosettes		
	B. crucifera (Bayer, 1981)		
-	Rosettes present		
2.	Rosettes antler-shaped		
-	Rosettes with bristle-like projections or cup shaped to paxilliform		
3.	Rosettes with bristle-like projections		
-	Rosettes cup-shaped or paxilliform		
4.	Calycular margins without specialized sclerites		
-	Calycular margins with specialized sclerites		
5.	Calycular margins with spindles with blade		
-	Calycular margins with asymmetrical rosettes not strongly modified		
6.	Predominant coenenchymal sclerites are stellate plates		
-	Predominant coenenchymal sclerites are tuberculate disks		
7.	Tuberculate disks up to 0.10 mm long		
-	Tuberculate disks up to 0.15 mm long B. hicksoni Thomson & Henderson, 1905/ B. studeri Whitelegge, 1897		
8.	Coenenchymal sclerites include tuberculate disks with central process		
-	Coenenchymal sclerites are rayed stellate plates		
9.	Calycular margins with spindles with strong blade, rosettes up to 0.10 mm long		
-	Calycular margins with spindles with moderate blade, rosettes up to 0.15 mm long		
10.	Surface sclerites are poorly developed rosettes		
-	Surface sclerites normally developed		
11.	Surface sclerites are rosettes with a few blunt processes		
-	Surface sclerites are rosettes with spiny processes		
12.	Calycular margins with strongly modified, asymmetrical rosettes		
-	Calycular margins without specialized sclerites		
13.	Coenenchymal sclerites up to 0.30 mm long		
-	Coenenchymal sclerites up to 0.20 mm long		
14.	Coenenchymal sclerites predominantly 4-rayed stellate plates B. sirene Grasshoff, 1999		
-	Coenenchymal sclerites 4–6-rayed stellate plates		
15.	Coenenchymal plates with sparse tuberculation		
-	Coenenchymal plates with dense tuberculation		
16.	Rosettes up to 0.25 mm long with long spines		
-	Rosettes up to 0.20 mm long with short spines		
17.	Rosettes few in number		

-	Many rosettes present	
18.	Coenenchyme with small 4-radiates	B. densa Tixier-Durivault, 1972
-	Coenenchyme without small 4-radiates	
19.	Anthocodial sclerites with sparse tuberculation, slender branches	B. sulfurea Grasshoff, 2000
-	Anthocodial sclerites with dense tuberculation, thick branches	B. grandicalyx (Kükenthal, 1924)

Bebryce asteria n. sp.

(Figs. 1-2)

? Bebryce tenella Verrill, in Bayer & Cairns, 2004: pl. 22 fig. 2, pl. 59 fig. 5.

Material examined. USNM 1266063, holotype, Northwest Providence Channel, south of Freeport, Grand Bahama, 26°27'N 78°40'W, 514–586 m, R/V Gerda sta. G-707, 22 July 1965, USNM 56444, paratypes, same data as holotype, 9 colonies and fragments; USNM 56443, paratype, Straits of Florida, south of Cat Cay, Bahamas, 25°20'N 79°15'W, 256–348 m, R/V Gerda sta. G-239, 30 January 1964, 1 colony lacking holdfast; USNM 56471, paratypes, Straits of Florida, south of Cat Cay, Bahamas, 25°25'N 79°18'W, 338–403 m, R/V Gerda sta. G-240, 30 January 1964, 2 incomplete colonies lacking holdfast.

Diagnosis. Unbranched or scantily branched *Bebryce* with large, thorny rosettes in the outer coenenchyme, bifurcate and spinous forms near the summit of the calyces and around the calycular apertures, and 4–6-rayed stellate forms with slender rays in the inner coenenchyme.

Description. Of the 13 colonies comprising the type series, 10 are unbranched, ranging in height from 7 mm to 3.8 cm. The tallest has 15 polyps, the shortest only two not including one situated on its stolon-like holdfast. The stems are 0.4–0.5 mm in diameter, and the calyces are cylindrical, from 0.75 to 0.1 mm in height and up to 1 mm in diameter, more or less tapered to a bluntly rounded apex, irregularly biserial but not always in the same plane. The distance between calyces varies from about 1 mm to as much as 3 mm. Most anthocodiae are retracted within the calyces, the summits of which present a more or less thorny aspect owing to the projecting spiny or bifurcated circumoral sclerites. The surface of both cortex and calyces has a sharply granular appearance owing to the rosette sclerites of the outer coenenchyme.

One small colony mounted entirely for SEM (Fig. 1a) with 6 fully developed calyces provides a good representation of colonial form. The cup-shaped outer portion of the rosettes of the outermost cortex and surface of the calyces is about 0.1 mm in diameter including the marginal spines; in some, the center of the calyx is smooth, but in others spines like those of the rim cover most or all of the surface (Fig. 1b, 2d). These impart a distinctive stellate aspect to the cortex and calyces (Fig. 1c–d). Toward the summit of some but not all calyces, the cup-shaped part of the rosettes surrounding the calycular aperture become asymmetrical by elongation of the rim on one side to form a serrated blade, the teeth of which are conspicuously spine-like in some cases, and not uncommonly the blade divides into two or more strong spines (Fig. 2e). These asymmetrical rosettes are up to 0.30 mm long. The apex of calyces having these strongly developed asymmetrical rosettes is distinctly thorny (Fig. 1d).

The anthocodial armature is a crown and points, rarely preserved exsert. Each of the eight points consists of two or three pairs of bent spindles (Fig. 2a) placed en chevron beneath the tentacles. These spindles are up to 0.45 mm long, with spiny distal end. The collaret consists of about 6 transverse rows of curved spindles (Fig. 2b), up to 0.50 mm long. The tentacles have dragon-wing sclerites (flattened, more or less twisted, boomerang-shaped platelets commonly with the convex edge serrated near the wider end; present in the proximal part of tentacles/see Grasshoff, 1999, 2000) (Fig. 2c), up to 0.20 mm long.

The sclerites of the inner cortex are predominantly 4-rayed crosses, reaching about 0.30 mm in diameter, sometimes with one or more rays subdivided and a central process (Fig. 2f). Forms intermediate between crosses and rosettes, with a stellate base and central cup-like projection are not uncommon.

Etymology. Asterius, adj., from Greek starry, in allusion to the starry pattern produced by the outer layer of sclerites.

Distribution. Bahamas, Straits of Florida.

Comparisons. In the Caribbean this species is unique, with calycular rosettes with a blade dividing into two or more strong spines. In the Indo-Pacific *B. cactus* has similar sclerites, but in that species they occur all over the branches instead of only in the calyces as in *B. asteria*.



FIGURE 1. Bebryce asteria n. sp., holotype, USNM 1266063; a, colony fragment; b, rosettes, view from above; c-d, polyps.



FIGURE 2. *Bebryce asteria* **n. sp.**, holotype, USNM 1266063; a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites; f, 4–6-rayed sclerites of inner coenenchyme. Scale at d only applies to d.

Bebryce bocki Aurivillius, 1931

(Figs. 3–4)

Bebryce brocki Aurivillius, 1931: 194, fig. 38, pl. 4 fig. 4; erroneous original spelling for *bocki*, in honor of Sixten Bock's expedition to the Bonin Islands, Japan. ? Song, 1980: 27, pl. 1 figs. 8–14.

Bebryce bocki; Imahara, 1996: 31.

Material examined. The holotype, UUZM 84, was not available for study as too little remained to be examined (pers. comm., Erica Sjölin, Museum of Evolution, Uppsala University, Sweden). Dr. Asako K. Matsumoto (Chiba Institute of Technology (Chitech), Japan) kindly donated the little fragment she had for SEM images.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Those of calycular margin asymmetrically developed, with strong projecting blade. Coenenchymal sclerites are thick, warty disks.

Description. Aurivillius (1931) described a small, unbranched colony and a fragment of 0.5 cm long. The calyces are dome-shaped, placed biserial or on three sides of the branch.

The anthocodiae are armed with a crown and points consisting of a transverse crown with 3–5 curved, thorny spindles up to about 0.3 mm long (Fig. 3b) and eight points formed by 2–6 bent spindles per point placed en chevron beneath the tentacles (Fig. 3a). The point spindles are 0.15–0.35 mm long, and have a distal spiny end. The tentacles contain flattened, bent rodlets and dragon-wing sclerites, up to 0.15 mm long (Fig. 3c).

The sclerites of the outer surface of coenenchyme and calyces are rosettes 0.05–0.13 mm long with warty, rounded, or bristle-like projections (Fig. 3d). Toward the calycular apertures the rosettes become asymmetrical, with one end becoming much elongated, forming a wide, blade-like process that projects from the surface (Fig. 3e); these sclerites are up to 0.20 mm long.

The deeper layer of coenenchyme contains warty disks with a central process (Fig. 4). These sclerites are 0.04–0.17 mm long. The smallest examples may have as few as 6 rays, which increase in number with increasing length.

Remarks. The material examined had many broken sclerites, therefore the larger disks are under-represented in the SEM images.

Song (1980) identified two specimens from Beomdo Island, Korea, as this species. Song's description and figures of sclerites are insufficient to confirm that identification.

Distribution. Bonin islands (Japan), ?Korea.

Comparisons. The species differs from all other species of *Bebryce* with rosettes with warty, rounded, or bristle-like projections by those adjacent to the calycular rim having a wide blade-like process.

Bebryce boninensis Aurivillius, 1931

(Figs. 5-6)

Bebryce boninensis Aurivillius, 1931: 200, fig. 39, pl. 4 fig. 3 (Japan, Bonin Islands); Imahara, 1996: 31. Not *Bebryce boninensis*; Iwase & Matsumoto, 2006: 82. (Sagami Bay); Imahara *et al.*, 2014: 249, figs. 161–162 (Sagami Bay).

Material examined. The holotype, UUZM 69, was not available for study as too little remained to be examined (pers. comm., Erica Sjölin, Museum of Evolution, Uppsala University, Sweden). Dr. Asako K. Matsumoto kindly donated the small holotype fragment she had.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Calycular margins without specialized sclerites. Coenenchymal sclerites are thick, warty disks.

Description. Aurivillius (1931) described a small, sparsely branched colony 7 cm tall. The calyces are dome-shaped, placed all around the branches.

The anthocodiae are armed with a crown and points consisting of a transverse crown consisting of 3–5 curved, thorny spindles up to 0.45 mm long (Fig. 5b) and eight points formed by of 2–4 bent spindles per point, up to 0.40 mm long, placed en chevron beneath the tentacles. The collaret and point spindles can have irregular outgrows making them look plate-like (Fig. 5a). The tentacles have dragon-wing sclerites up to 0.17 mm long.

The sclerites of the outer surface of coenenchyme and calyces are rosettes with warty, rounded, or bristle-like projections (Fig. 5c). These rosettes are 0.05–0.10 mm long.



FIGURE 3. *Bebryce bocki* Aurivillius, 1931, holotype, UUZM 84; a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites.



FIGURE 4. Bebryce bocki Aurivillius, 1931, holotype, UUZM 84; disks of inner coenenchyme.

The deeper layer of coenenchyme contains warty disks with a central process (Fig. 6). These sclerites are 0.04–0.20 mm long. The smallest examples may have as few as 6 rays, which increase in number with increasing length. **Remarks.** Tentacular sclerites and the unbranched point spindles described by Aurivillius were not found

during our re-examination. Instead irregularly shaped slerites in the form of plates were found (Fig. 5a).

Imahara (2014) depicted sclerites of a specimen he identified as *B. boninensis* from Sagami Bay, Japan, with calycular sclerites having a large blade. It resembles *B. bocki* Aurivillius, 1931, but the calycular sclerites Imahara shows are more developed than those in *B. bocki*.

Distribution. Bonin islands (Japan).

Comparisons. The species differs from all other species of *Bebryce* by the presence of rosettes with warty, rounded, or bristle-like projections and the lack of specialized calycular sclerites. Aurivillius could not find specialized calycular sclerites and neither could we.



FIGURE 5. Bebryce boninensis Aurivillius, 1931, holotype, UUZM 69; a, irregular polyp sclerites; b, collaret spindles; c, rosettes.



FIGURE 6. *Bebryce boninensis* Aurivillius, 1931, holotype, UUZM 69; a–b, disks of inner coenenchyme with complex tubercles; c, with simple tubercles and fewer rays. Scale at b only applies to b.

Bebryce brunnea (Nutting, 1908)

(Fig. 7)

Echinomuricea brunnea Nutting, 1908: 585, pl. 45 fig. 1, pl. 49 fig. 4; Kükenthal, 1924: 191.

Material examined. The type specimen of *Echinomuricea brunnea* Nutting (USNM 25325) and five additional paratype lots from Hawaiian waters, and eight other lots also from Hawaii.

Diagnosis. *Bebryce* with 3–6 rayed stellate plates and paxilliform rosettes. Calyx rim with rosettes with serrated blade-like process.

Description. The type colony (USNM 25325) consists of four stems arising from a spreading holdfast encrusting a very old, broken, gastropod shell fragment, one of them crooked, about 12 cm tall, producing 6 lateral branches a little more than 1 mm in diameter exclusive of calyces to form a sprawling, irregularly branched colony. The anthocodiae are fully retracted within short, cylindrical calyces about 1 mm tall and 1.5–2 mm wide placed in irregular spirals around the branches.

The anthocodiae are armed with a crown and points consisting of a transverse crown with curved, thorny spindles up to about 0.6 mm long (Fig. 7b) and eight points formed by bent spindles about 0.5 mm long (Fig. 7a) placed en chevron beneath the tentacles. The tentacles contain flattened, dragon-wing sclerites about 0.2 mm long (Fig. 7c).

The coenenchyme has a coarsely granular aspect, and the calyces are increasingly prickly toward their apices owing to the projecting ends of sclerites. The sclerites of the outer surface of coenenchyme and calyces are rosettes consisting of a cup-shaped thorny projection arising from a warty base. Some, about 0.15 mm tall, have a widely flared calyx part about 0.2 mm in greatest diameter with coarsely serrated rim, joined by a smooth, slender stem to a warty base narrower than the calyx (Fig. 7d). Others are proportionally taller, reaching about 0.3 mm tall, with the calyx part consisting of several strong, serrate spines that may be blade-like (Fig. 7e). These were described by Nutting (1908: 585) as "resembling the paxillae of starfish in miniature." Toward the calycular apertures the rosettes become asymmetrical (Fig. 7f), with the margin of the calyx becoming much elongated on one side, forming a serrated, blade-like process that projects from the surface and surrounds the calycular aperture as a prickly barrier.

The deeper layer of coenenchyme contains stellate plates, predominantly 4-rayed forms up to 0.30 mm in the greater diameter, with a strong central process (Fig. 7g), a few with only 3 rays, and some with 5 or 6 rays. Stellate sclerites with a prominent, thorny central process, intermediate in form between the cup-shaped outer forms and the stellate plates of the deeper coenenchyme, are not uncommon (Fig. 7h).

Distribution. Hawaii.

Comparisons. The species mostly resembles *B. cofferi* **n. sp.**, but that species has smaller coenenchymal stellate plates, only up to 0.20 mm long, and no 3–4-rayed plates.

Bebryce cactus Bayer, 1994

Bebryce cactus Bayer, 1994: 547, figs. 1-4.

Material examined. Two colonies, holotype (USNM 93204) and paratype (USNM 93205). Papua-New Guinea: south side of Bagabag Island, 62 km NE of Madang; barrier reef wall at 30–60 feet.

Diagnosis. *Bebryce* with coenenchyme covered by antler-like spiny rosettes, and cruciform to 6-rayed plates in the deeper layers.

Description. See Bayer 1994: 547.

Remarks. This species shows extreme development of the paxilliform rosette sclerites of the outermost layer of coenenchyme.

Distribution. Papua-New Guinea.

Comparisons. This is the only species of *Bebryce* known with the coenenchyme covered by antler-like spiny rosettes.



FIGURE 7. *Bebryce brunnea* (Nutting, 1908), holotype, USNM 25325; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, 3–6-rayed sclerites of inner coenenchyme; h, intermediate form between rosette and internal sclerite.

Bebryce cinerea Deichmann, 1936

(Fig. 8)

Bebryce cinerea Deichmann, 1936: 126, pl. 8 fig. 5, pl. 10 figs. 1–8. (Western Atlantic, off Barbados); Devictor & Morton, 2010: 37, fig. 34.

Material examined. The type (MCZ 4611) and one additional specimen identified by E. Deichmann (USNM 43781), and many additional lots from northern Bahamas, Gulf of Mexico, Greater and Lesser Antilles, and Caribbean Sea southward to Venezuela, 77–549 m (all USNM).

Diagnosis. *Bebryce* with well-separated, cylindrical calyces, cup-shaped rosettes and stellate plates mostly with 5 rays; rosettes of calycular margin asymmetrically developed, with serrated projecting blade.

Description. See Deichmann, 1936: 126.

Remarks. Colonies are abundantly branched, usually in one plane. The stubby, cylindrical calyces are placed roughly biserially along the branches, about 1 mm high and wide, separated by about their own width except near the branch tips where they are somewhat closer. Some of the cup-shaped rosettes are about 0.08 mm high by as much as half as wide, as reported by Deichmann, but many are wider than high (Fig. 8d–e). In spite of Deichmann's statement that the calycular margins have no special armature, the asymmetrical rosettes are concentrated there, and the projecting blades may be as much as 0.16 mm long (Fig. 8f).

Some of the stellate plates are distinctly star-shaped with five tapered rays, some are pentagonal with tuberculate margins, and some are multiradiate with several tuberculate rays (Fig. 8g).

Morphological differences between *B. cinerea* Deichmann and *B. mollis* Philippi are minimal, and it could be one amphi-Atlantic species.

Colonies of *B. cinerea* are prone to infestation by a variety of epizoa, which apparently cause no harm. Some colonies are quite clean, but others are heavily overgrown by ciliates such as *Folliculina*, Foraminifera, hydroids, bryozoans, and polychaete worms. It is interesting that neither Carpine & Grasshoff (1975) nor Grasshoff (1977) mention such fouling on *B. mollis* in Mediterranean waters.

Distribution. South Carolina, Gulf of Mexico, Bahamas, Panama, Venezuela.

Comparisons. Resembles *Bebryce mollis*, but inner coenenchyme with irregular plates, caused by some rays of the plates being bent.

Bebryce cofferi n. sp. (Figs. 9–10)

Material examined. MNHN-IK-2012-13042, HGP-20, holotype, New Caledonia, Chesterfield Bank: 19°40'S 158°27.05'E [?27'30"], 250 m, chalutage no. 2, 18 May 1979, dry specimen; MNHN, HGP-20, paratype, same data as holotype, alcohol specimen.

Diagnosis. *Bebryce* with 5–7-rayed stellate plates and paxilliform rosettes. Calyx rim rosettes with projecting blade-like projection.

Description. Colonies sparsely branched in one plane, openly pinnate or "lateral" (Fig. 9); calyces mostly biserial but with some individuals towards one plane of the colony, 6–8 in 1 cm but main stem with only a few; calyces nearly cylindrical or bluntly conical, about 1 mm tall and 1 mm wide, with a few anthocodiae preserved exert.

The anthocodial armature consists of 2 or 3 pairs of bent spindles (Fig. 10a) en chevron in each of the eight points above a transverse crown of 5 or 6 rows of bow-shaped spindles (Fig. 10b). The tentacles have dragon-wing sclerites up to 0.20 mm long (Fig. 10c).

Sclerites of outermost cortex in the form of cup-shaped rosettes up to 0.2 mm wide and 0.18 mm tall, rim of the cups formed by several strong, laciniated projections (Fig. 10d–e); adjacent rosettes may be inseparably interlocked if not actually fused together. Sclerites near the apex of the calyces becoming strongly asymmetrical, forming strong, blade-like or spatulate projections (Fig. 10f) that produce a bristling barricade around the calycular apertures. These sclerites are up to 0.25 mm long.

Sclerites of the deeper cortex are small, irregularly rounded plates with 5–7 marginal rays and a strong central process (Fig. 10g). Individuals with increasingly strong development of the central process intergrade with the



FIGURE 8. *Bebryce cinerea* Deichmann, 1936, USNM 43781; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, 4–6-rayed sclerites of inner coenenchyme. Scale at e only applies to e.



FIGURE 9. Bebryce cofferi n. sp. MNHN-IK-2012-13042, holotype colony. Scale 1 cm. Photo T.N. Molodtsova.

rosettes of the outer layer by way of forms with a prominent, blunt central projection resembling a dock-side bollard (Fig. 10h).

Etymology. Named after Tim Coffer (National Museum of Natural History, Smithsonian Institution, Washington D.C.).

Remarks. The external parts of the outermost sclerites are especially heavily encrusted with coccoliths. The specimens were on loan to the first author and returned to Paris (correspondence T. Coffer). The MNHN did provide a collection number for the holotype to the second author; the paratype was not located.

Distribution. Chesterfield Bank (New Caledonia).



FIGURE 10. *Bebryce cofferi* **n. sp.** MNHN-IK-2012-13042; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, 5–7-rayed stellate plates of inner coenenchyme; h, intermediates between rosettes and 5–7-rayed stellate plates. Scale at e only applies to e.

Comparisons. At first glance, the strongly projecting blade-like sclerites bristling around the calycular apertures of this species bring to mind Nutting's "*Bebryce hicksoni*" (= *Bebryce* species A), which has calycular sclerites of similar form. However, Nutting's specimens have thick, warty disks in the deeper coenenchyme instead of 5 to 7 rayed plates, and the rosettes of the outer layer are coarse forms most of which have a coarsely granular central projection (the "cup") rather than strong, serrated marginal projections.

The rosettes of this species are similar to those of *B. brunnea* (Nutting) from Hawaiian waters, but the predominant sclerites of the inner coenenchyme of that species are 4-rayed crosses, which are not present in *B. cofferi*.

Bebryce crucifera (Bayer, 1981)

(Fig. 11)

Nicaule crucifera Bayer, 1981: 926, fig. 48. Bebryce crucifera; Bayer, 1994: 547.

Material examined. USNM 59482, the holotype, Palau Islands, south point of Augulpelu Reef, 10 m, coll. Douglas Faulkner, 27 October 1971; RMNH Coel. 40879, PAL-112, Republic of Palau, Koror, Siaies Tunnel, 7°18.686'N 134°13.596'E, 30 m, coll. C.S. McFadden, 21 May 2010; RMNH Coel. 40880, PAL-266, Republic of Palau, Babeldaob, NW Barrier Reef, 7°41.888'N 134°33.833'E, 9 m, coll. C.S. McFadden, 23 May 2010; RMNH Coel. 40881, PAL-330, Republic of Palau, Koror, Turtle Cove, 7°05.078'N 134°15.730'E, 39 m, coll. C.S. McFadden, 24 May 2010; RMNH Coel. 40882, PAL-289, Republic of Palau, Pelelieu, southern wall, 6°58.612'N 134°13.330'E, 24.9 m, coll. C.S. McFadden, 24 May 2010 (dry material).

Diagnosis. *Bebryce* with abundant small crosses representing the usual rosettes, together with 6-rayed tuberculate capstans.

Description. The holotype is about 30 cm tall, irregularly branched in one plane, without anastomosis. The terminal branchlets are up to 60 mm but mostly 30–40 mm long and 3 mm in diameter. Polyps are situated on all sides of the branches, 1.5–3.0 mm apart, retractile into low calyces with 8 marginal lobes. The anthocodiae are occasionally preserved expanded.

The anthocodial armature consists of eight points each composed of 2 bent, tuberculate tapered spindles up to 0.5 mm long (Fig. 11a) above a transverse neck ring 2–3 sclerites deep, composed of curved, bow-shaped spindles up to 0.6 mm long (Fig. 11b); smaller, straight rods extend from the points along the proximal part of the tentacles, followed by dragon-wing sclerites (Fig. 11c).

The predominant sclerites of the coenenchyme are tuberculate crosses and elaborately tuberculate 6-rayed capstans (Fig. 11d), which resemble double wheels, corresponding to the rosettes of other species of *Bebryce*. The largest crosses are about 0.28 mm wide diagonally across the rays, sculptured by complex tubercles, of which 2–4 at the center form a raised process; developmental stages of smaller sizes are less strongly sculptured, the rays of the smallest being almost smooth. Crosses having an especially prominent central process approach the shape of the paxilliform rosettes of some species of *Bebryce* (e.g. *B. indica* Thomson & Henderson, *B. grandicalyx* (Kükenthal) and *B. nuttingi* Stiasny). A few tuberculate spindles are present, up to 0.3 mm long (Fig. 11e), situated chiefly in the calycular margins, corresponding to the asymmetrical rosettes of species such as *B. mollis*.

Five-rayed sclerites are present but uncommon, and 3-rayed forms are rare. The fully developed 6-rayed capstans reach 0.22 mm in greatest diameter and are profusely sculptured by complex tubercles; smaller, developmental stages are not so strongly sculptured and show the 6-radiate symmetry more clearly (Fig. 11f).

The supporting axis is very soft and flexible, with a thin, loculated cortex that collapses on drying owing to the wide, hollow central core.

Photographs of the living specimen made by Mr. Douglas Faulkner (not available for duplication in this manuscript) show that the color in life is dull orange, with polyps orange except for the oral disk and adoral surface of the tentacles, which are white. As is common among species of *Bebryce*, the surface of the coenenchyme is overgrown by attached epizoa supporting a diverse community of small crustaceans.

Remarks. The four specimens from Palau identified by McFadden *et al.* (2014) as *Bebryce* sp. were checked and proved to be this species.

Distribution. Palau Islands.



FIGURE 11. *Bebryce crucifera* (Bayer, 1981), holotype, USNM 59482; a, point spindles; b, collaret spindle; c, tentacle sclerite; d, tuberculate crosses, 6-rayed capstans; e, calyx sclerites; f, 3–6-rayed sclerites of inner coenenchyme. Scale at c only applies to c.



FIGURE 12. *Bebryce densa* Tixier-Durivault, 1972, holotype, MNHN-IK-0000-579; a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites. Scale at b only applies to b.

FIGURE 13. *Bebryce densa* Tixier-Durivault, 1972, holotype, MNHN-IK-0000-579; a, rosettes; b–c, 4–6-rayed sclerites of inner coenenchyme. Scale at c only applies to c.

Comparisons. The small crosses representing the usual rosettes, together with the 6-rayed tuberculate capstans are unique in the genus. *Bebryce indica* Thomson & Henderson, 1905 resembles this species but has poorly developed rosettes. This species has remarkable thick branches, up to 5 mm wide, in common with *B. grandicalyx*.

Bebryce densa Tixier-Durivault, 1972

(Figs. 12–13)

Bebryce densa Tixier-Durivault, 1972: 34, figs. 4-5 (Madagascar).

Material examined. Holotype, MNHN-IK-0000-579, Island Europe, st. P41, nr 5, 40–50 m depth, coll. P. Vasseur 1969, 23 December 1965.

Diagnosis. *Bebryce* with 4–6 rayed stellate plates and paxilliform rosettes. Calycular margins lacking strongly modified sclerites.

Description. The colony is depicted by Tixier-Durivault (Fig. 4).

The anthocodial armature consists of bent spindles up to 0.45 mm long (Fig. 12a) en chevron in each of the eight points above a transverse crown of bow-shaped spindles up to 0.55 mm long (Fig. 12b). The tentacles have straight, flattened rods and dragon-wing sclerites up to 0.15 mm long (Fig. 12c), all with sparse tuberculation.

Sclerites of outermost cortex in the form of paxilliform rosettes up to 0.30 mm tall and 0.20 mm wide, rim of the cups formed by several strong, laciniated projections (Figs. 12d, 13a). Near the apex of the calyces the rosettes become somewhat asymmetrical, forming small, blade-like projections (Fig. 12e).

The coenenchymal sclerites are 4–6 rayed plates (Fig. 13b) up to 0.35 mm long, mostly with sparse, simple tuberculation. The smallest have hardly any tubercles (Fig. 13c).

Distribution. Madagascar.

Comparisons. This species very much resembles *B. grandicalyx* (Kükenthal, 1924), differing in having stellate plates with more simple, sparse tuberculation. Further, the rosettes of *B. densa* seem to have a more spiny appearance, but this difference could be caused by the condition of the *B. grandicalyx* material showing many disintegrated sclerites. *Bebryce densa* also shows small 4-radiates not observed in *B. grandicalyx*.

Bebryce grandicalyx (Kükenthal, 1924)

(Figs. 14–15, 21a)

Heterogorgia verrucosa; Nutting, 1910: 88.
Not Heterogorgia verrucosa Verrill, 1868: 414; 1869: 451, pl. 6 fig. 11, pl. 8 fig. 16.
Heterogorgia grandicalyx Kükenthal, 1924: 230; Soest, 1979: 89, pl. 1 figs. 2–3.
Bebryce verrucosa Stiasny, 1942: 197.
Bebryce indica (part); Nutting, 1910: 48
Not Bebryce indica Thomson, 1905: 175 (Indian Ocean).

Material examined. ZMA 1572, holotype, Pulu Missa, near Flores, de Siso don.; USNM 1013313, part of holotype; ZMA 2258 (partly), Siboga sta. 310, Indonesia, Flores Sea, east end of Sumbawa, 8°30'S 119°07.5'E, 73 m, 12 February 1900.

Diagnosis. Colony with thick branches, calycular margins with asymmetrical rosettes not strongly modified; coenenchymal sclerites are 4–6 rayed plates with rather dense tuberculation.

Remarks. Little can be determined about the sclerites of this grossly misidentified specimen (ZMA 1572) from Nutting's (1910: 89) comments: "All spicules of this species are small; crosses, stars and multiradiate forms predominating. The rays of the stars are strongly tuberculate, and sometimes branched. A few small, curved spindles are seen, but they are probably from the collarets and opercula." As usual, Nutting did not illustrate species that he did not describe as new.

In establishing Nutting's specimen as a new species of *Heterogorgia*, Kükenthal (1924: 230) merely accepted Nutting's account of the sclerites, which bear no resemblance to those of the Panamic *Heterogorgia verrucosa*

Verrill, 1868 ("large, more or less elongated, roughly warted spindles from the verrucae; much smaller, very rough spindles and heads from the surface of the verrucae and coenenchyma; .. " 1869: 451).

All sclerites from the dry USNM specimen show evidence of damage by acidity, maybe atmospheric because the specimen has been dried from the time it was acquired during the expedition. The coenenchymal sclerites are 4–6-rayed plates with a more or less prominent tuberculate projection at the center, usually on one side, but occasionally a weaker projection is present on the opposite side (Fig. 15d). The large 4-rayed plates are up to about 0.26 mm in diameter across the longest opposite arms; the 6-rayed forms tend to be somewhat smaller, fully developed individuals being about 0.2 mm in diameter. Rosettes are derived from the radiate plates by a stronger development of the central process, and are poorly differentiated in size from the large plates, with which they imperceptibly intergrade (Fig. 15c). The digitate central process, which corresponds to the outer, cup-shaped part of *mollis*-type rosettes, is about 0.1 mm high, projecting from a multiradiate base that varies in size. To judge by the shape of the anthocodial sclerites, the polyps are armed with a conventional crown and points consisting of the usual bow-shaped sclerites about 0.32 mm in length (Fig. 15a). So far as can be determined from a gross examination of the calyces of the long-dried type specimen, no specially modified forms are developed around the calycular margins.

FIGURE 14. Bebryce grandicalyx (Kükenthal, 1924), ZMA 1572, holotype colony. Scale 1 cm.

FIGURE 15. *Bebryce grandicalyx* (Kükenthal, 1924), holotype, ZMA 1572; a, point spindles; b, collaret spindles; c, rosettes; d, 4–6-rayed sclerites of inner coenenchyme.

The specimen is infested by an encrusting sponge.

The USNM database mentions syntype status of their specimen. However, Nutting described only one specimen, therefore the USNM material must be part of this specimen, the holotype. Indeed the specimen now present in the NBC (Fig. 14) is 25 cm high and 26 cm wide while Nutting mentioned 25.5 cm high and 29.5 cm

wide, presumably a piece from one side was removed. Soest (1979) mentioned three syntypes, only one specimen was found in the NBC collection and Nutting also only described one specimen.

One specimen of ZMA 2258 (Fig. 21a), identified by Nutting as *Bebryce indica* proved to be this species. It clearly was dried out once and put back in alcohol later on.

The microscope slides of *Bebryce grandicalyx* present in the NBC also show disintegrated sclerites, alike to the USNM specimen, but contrary to the above findings these show a few not strongly modified asymmetrical rosettes around the calycular margins, similar in shape to those depicted for *B. densa*.

Distribution. Flores Sea (Indonesia).

Comparisons. This species is very similar to *B. densa*; for differences see comparative remarks associated with that species. It even more resembles *B. sulfurea* Grasshoff, 2000, the only difference observed is the more tuberculate anthocodial sclerites in *B. grandicalyx*. We consider them as different species as *B. grandicalyx* seems to have thick branches (up to 5 mm wide) while *B. sulfurea* has slender branches (Grasshoff, 2000, fig. 186; up to 3 mm wide). Moreover, a preliminary examination of Indonesian species of *Bebryce* showed many specimens referable to *B. grandicalyx* having live colonies orange colored while *B. sulfurea* colonies are yellow (Grasshoff, 2000, figs. 183–185).

Bebryce grandis Deichmann, 1936

(Fig. 16)

Bebryce grandis Deichmann, 1936: 125, pl. 8 fig. 3, pl. 10 figs. 9-21 (Western Atlantic, off Montserrat).

Material examined. One specimen identified by E. Deichmann (MCZ 4607, the holotype); and several additional lots from Bahamas, Gulf of Mexico, Greater and Lesser Antilles, and the Caribbean Sea southward to Panama, 49–520 m (all USNM).

Diagnosis. Stout *Bebryce* with bluntly conical calyces mostly biserially aligned; cup-shaped rosettes up to about 0.09 mm in height and diameter, stellate plates with three to six rays, commonly four, up to about 0.32 mm in maximal diameter; sclerites of calycular margins up to 0.22 mm long, with a tuberculate base and an obliquely placed serrated blade, projecting around calycular apertures.

Description. See Deichmann, 1936: 125.

Remarks. Deichmann (1936: 126) considered this species to be "very distinct" on the basis of the stouter aspect of the colonies together with the preponderant 4-rayed stellate plates, which differentiate it from both *B. cinerea* and *B. parastellata.* However, the one lot of four more or less complete colonies present in the National Museum of Natural History identified by Dr. Deichmann herself (USNM 10287, 49470) reveals characters neither mentioned nor illustrated in her original description of the species. Deichmann (1936: 125) reported that in the holotype specimen, the cup-shaped sclerites of the outer layer are 0.09 mm high, and the stellate plates ("stars") of the deeper layer are 0.25 mm in diameter. New measurements of the same specimen record cup-shaped sclerites 0.08 mm high and "stars" 0.32 mm in diameter are in reasonable agreement with Deichmann's measurements. However, bow-shaped sclerites of the crown ("collaret") are found to be as much as 0.6 mm long in contrast to Deichmann's measurement of 0.24 mm, which is slightly less than the size of the "stars." This is unusually small for crown sclerites, which in *Bebryce* are typically larger than the stellate plates, as shown even by Deichmann's report of 0.5 mm for the "collaret" sclerites of *B. cinerea*. Consequently, the measurement of 0.24 mm for the length of the crown sclerites of *B. grandis* must be regarded as an error.

In the original description of *B. grandis*, Deichmann (1936: 125) described the sclerites of the inner layer as "stout, thick crosses or stars with heavy warts or spines." She also mentioned "spinous rods, sometimes with one end flattened and disk-shaped," but these are from the calycular margins, not the inner coenenchyme. She did not mention the thick, warty plates with little or no remnant of stellate symmetry that are present in all specimens examined in the present study. However, the diagnostic statement in the key to species (1936: 125) "Among spicules large four-armed crosses" clearly does not eliminate other forms that were not considered to be taxonomically significant.

The anthocodial armature consists of eight points composed of 3–4 pairs of converging, bent spindles over a transverse crown of bow-shaped spindles about 6 deep. The backs of the tentacles contain the usual flattened, bent rods with conspicuously scalloped convex margin.

FIGURE 16. *Bebryce grandis* Deichmann, 1936, USNM 2149; a, point spindles; b, collaret spindle; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, 3–4-rayed sclerites of inner coenenchyme; h, thick, warty plates of inner coenenchyme. Scale at d only applies to d.

Variation. As the species originally was represented by only two specimens, the type from Montserrat (MCZ 4607) and a small colony only 30 mm tall, from Barbados (MCZ 4608), no information was available regarding variation. Some lots in the present collection are comprised of multiple specimens, and one, USNM 2149, includes 75 colonies from a single haul made off Yucatan. All are of similar aspect, more or less overgrown by various epizoa, chiefly hydroids and bryozoans; in some cases, the colonies are heavily overgrown. Sclerites of three colonies from this lot were prepared for SEM and are illustrated in Fig. 16.

Distribution. Western Atlantic.

Comparisons. The discoidal bodies of *B. grandis* are unique for the Atlantic species of *Bebryce*.

Bebryce harpy Grasshoff, 1999

Bebryce harpy Grasshoff, 1999: 66, figs. 112-113 (New Caledonia).

Material examined. None.

Diagnosis. *Bebryce* with paxilliform rosettes and predominantly irregular sclerites in inner coenenchyme. Calycular margins with asymmetrical rosettes not strongly modified.

Description. See Grashoff, 1999: 66.

Remarks. Grasshoff provided SEM images of the sclerites (1999: fig. 113).

Distribution. New Caledonia.

Comparisons. The rosettes with a few blunt processes are unique for species of *Bebryce*.

Bebryce hicksoni Thomson & Henderson, 1905

(Fig. 17)

Bebryce hicksoni Thomson & Henderson, 1905: 294, pl. 3 fig. 1, pl. 6 fig. 9 (Ceylon).

Not *Bebryce hicksoni*; Nutting, 1910: 47 (= *B. studeri* (part), *Bebryce* sp. A (part), and *Bebryce* sp. B (part)); Tixier-Durivault, 1972: 35, fig. 6 (Madagascar); Stiasny, 1940:156 (= *B. inermis*); Stiasny, 1959: 51, fig. B, pl. 3 fig. 11. (= *B. inermis*). *Pseudobebryce hicksoni*; Kükenthal, 1924: 207.

Material examined. The type, BMNH 1933.03.13.069.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Calycular margins with asymmetrical rosettes not strongly modified. Predominant coenenchymal sclerites are tuberculate disks.

Description. See Thomson & Henderson, 1905: 294.

Remarks. Owing to the limitations of material, it is not possible to provide a detailed description and illustrations of the anthocodial sclerites (Fig. 17a). The rosettes (Fig. 17b) are cup-shaped collar-buttons reaching 0.09 mm in width and 0.09 mm in height, with the cup-shaped part composed of crowded tufts of calcite microcrystals similar to but somewhat larger than those of *B. studeri* Whitelegge, which are up to 0.06 mm in diameter. As nearly as can be determined, the sclerites of the calycular margins are asymmetrical rosettes not strongly modified as antlers or spinous forms (Fig. 17c). The coenenchymal plates are tuberculate disks up to about 0.15 mm in diameter, with a central process or "handle" on one surface; the marginal tubercles of small examples and of some of the large ones are well separated, but of others are complex and closely crowded (Fig. 17d).

As usual in species of *Bebryce*, the superficial rosettes have numerous coccoliths cemented to the distal part of the stem and among the fascicles of crystals in the cup-shaped part.

Distribution. Sri Lanka.

Comparisons. Considering the data known the species cannot be separated from *B. studeri*. Because of the limited material available, we prefer to discuss possible synonymy after once new material from Sri Lanka becomes available for comparison.

FIGURE 17. *Bebryce hicksoni* Thomson & Henderson, 1905, holotype, BMNH 1933.03.13.069; a, collaret spindle; b, rosettes; c, calyx sclerites; d, tuberculate disks of inner coenenchyme. Scale at b only applies to b.

"Bebryce hicksoni Thomson & Henderson, 1905"

Bebryce hicksoni; Nutting, 1910: 47.

Material examined. USNM 43161, Siboga sta. 289, Timor, 9°0.3'S 125°24.5'E, 112 m deep, trawl, mud, sand and shells, 20 January 1900, retained by Nutting and now in the National Museum of Natural History; ZMA 2253, Siboga sta. 289; ZMA 2254, Siboga sta. 305, 10°27.9'S 123°28.7'E, Solor Strait, off Menanga kampong, 113 m, stony bottom, Blake dredge, 8 February 1900, three specimens; ZMA 2255a, Siboga sta. 154, 0°7.2'N 130°25.5'E (near Batanta island), 83 m, grey muddy sand, shells and *Lithothamnion*, dredge, depth decreased till 59 m during this haul, 14 August 1899; ZMA 2255b, Siboga sta. 257, 5°26.6'S 132°32.5'E, till 52 m, coral, Blake dredge, in Duroa Strait, Kei islands, 11 December, 1899; ZMA 2255c, Siboga sta 310, 8°30'S 119°07.5'E, Flores Sea, east end of Sumbawa, 73 m, 12 February 1900.

Remarks. USNM 43161 includes three distinct species of *Bebryce*, none of them *B. hicksoni* Thomson & Henderson, 1905, as well as two other unrelated species belonging to two different genera. It is impossible to determine from Nutting's ambiguous remarks which of the three species of *Bebryce* he considered to be *B. hicksoni* as he wrote that the sclerites "are of the typical *Bebryce* form being round disks with an elevated central portion. In shape they greatly resemble a collar-button with a very short broad connection between the expanded portions. There are also stars and multiradiate forms based on the typical forms just described; and a few small spindles, oval disks, etc." It is likely that he had examined all three of the species in this lot, but did not consider the differences taxonomically significant.

One of these three species we consider to be *B. studeri* (Fig. 33); ZMA 2254, 2255a–b also proved to be this species. The other two species of *Bebryce* we could not relate to any named species. As the material is fragmentary, we prefer to wait with a formal description until more material is available. We treat them here as species A and B.

Bebryce species A

(Fig. 18)

Bebryce hicksoni (part); Nutting, 1910: 47 (Indonesia). Not *Bebryce hicksoni* Thomson & Henderson, 1905: 294, pl. 3 fig. 1, pl. 6 fig. 9 (Ceylon).

FIGURE 18. *Bebryce* species A, USNM 43161; a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites; f, tuberculate disks of inner coenenchyme.

Material examined. USNM 43161, ZMA 2253, Siboga sta. 289, 9°0.3'S 125° 24.5'E (Timor), 112 m deep, trawl, mud, sand and shells, 20 January 1900; ZMA 2255c, Siboga sta 310, 8°30'S, 119°07.5'E, Flores Sea, east end of Sumbawa, 73 m, 12 February 1900.

Diagnosis. Calycular margins with asymmetrical rosettes strongly modified to a blade. Coenenchyme with tuberculate disks.

Description. The anthocodial armature consists of transversely placed, bow-shaped spindles up to 0.50 mm long (Fig. 18b) arranged in a crown beneath the base of the tentacles, with curved, bluntly thorny spindles (Fig. 18a) converging on each tentacle base; these spindles are up to 0.45 mm long. Dragon-wing sclerites up to 0.15 mm long, with the convex edge strongly spinose (Fig. 18c) extend along the backs of the tentacles.

The rosettes are of the usual cup-shaped type, reaching about 0.10 mm in diameter across the outer part, with the tuberculate base somewhat narrower, and up to about 0.10 in height (Fig. 18d).

At the margin of the calyces, the rosettes become asymmetrically modified as projecting, blade-like forms up to 0.25 mm in length (Fig. 18e).

The plates of the inner coenenchyme are thick tuberculate disks up to about 0.15 mm in diameter with tuberculate rim and central process on one surface (Fig. 18f); the margin of the smaller developmental forms is more conspicuously scalloped.

Remarks. ZMA 2253, Siboga station 289 is a piece of branch of 2 cm long, about 1 mm wide with prominent calyces. ZMA 2255c, a colony fragment of 5 cm long, has much thicker branches than ZMA 2253, up to 3 mm wide, but is also more infested by a sponge than ZMA 2253 is.

Distribution. Flores Sea (Indonesia).

Comparisons. The species resembles *B. thomsoni* but *B*. species A has smaller rosettes, many only 0.10 mm in diameter, and the calycular rosettes have a stronger developed blade.

Bebryce species B

(Fig. 19)

Bebryce hicksoni (part); Nutting, 1910: 47.

Not Bebryce hicksoni Thomson & Henderson, 1905: 294, pl. 3 fig. 1, pl. 6 fig. 9 (Ceylon).

Material examined. USNM 43161, Siboga sta. 289, Timor, 9°0.3'S 125°24.5'E, 112 m deep, trawl, mud, sand and shells, 20 January 1900.

Diagnosis. Calyx rim without specialized sclerites. Coenenchyme with paxilliform rosettes, and small 4–6-rayed plates.

Description. The anthocodial armature consists of bent spindles up to 0.35 mm long (Fig. 19a) en chevron in each of the eight points above a transverse crown of bow-shaped spindles up to 0.40 mm long (Fig. 19b). The tentacles have dragon-wing sclerites up to 0.15 mm long (Fig. 19c).

Sclerites of outermost cortex in the form of paxilliform rosettes up to 0.20 mm tall and wide, rim of the cups formed by several strong, laciniated projections (Fig. 19d–e). Near the apex of the calyces no specialized sclerites were observed.

The coenenchymal sclerites are 4–6-rayed plates (Fig. 19f), up to 0.20 mm long, mostly with sparse, simple tuberculation.

Distribution. Timor (Indonesia).

Comparisons. The species resembles *B. rigida* but has smaller coenenchymal plates, up to 0.20 mm in diameter, while those in *B. rigida* are up to 0.30 mm in diameter. *Bebryce rigida* also has more spiny, longer rosettes, up to 0.25 mm tall.

Bebryce indica Thomson, 1905 (Fig. 20)

Bebryce indica Thomson, 1905: 175, supplementary plate, fig. 3 (Indian Ocean, west of Periya Paar, Gulf of Manaar). Not *Bebryce indica*; Nutting, 1910: 48; Song, 1980: 26, pl. 1 figs. 1–7 (Korea). *Pseudobebryce indica*; Kükenthal, 1924: 207.

FIGURE 19. *Bebryce* species B, USNM 43161; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, 4–6 rayed plates of inner coenenchyme. Scale at c only applies to c, scale at e only applies to e.

FIGURE 20. *Bebryce indica* Thomson, 1905, BMNH 1908.02.18.025; a-b, rosettes; c-d, 4-6-rayed plates of inner coenenchyme. Scale at a applies to a, c.

Material examined. Type material, BMNH 1908.02.18.025, 1933.03.13.070.

Diagnosis. Calyx rim without specialized sclerites. Coenenchyme with paxilliform rosettes and predominantly 4-rayed plates.

Description. According to Thomson (1905) the largest colony was 18 cm tall, and all but one of the original type lot were irregularly branched in one plane. The calyces were described as prominent, truncated cones 1.5 mm high and wide, separated by intervals of 1.5–2 mm, usually distributed all around the branches but sometimes "almost restricted to the sides in the plane of branching."

Examination of the type specimen shows that the polyps are armed with eight points each consisting of a pair of strong, bent spindles, above a collaret consisting of two rings of curved spindles; sizes given by Thomson are 0.5–0.6 mm in length. All together it is not a complete account of the sclerites, it is clear rosettes are represented, the forms that Thomson referred to as tuberculate "capstans" and "double-club" types with the part to one side of the waist much smaller than the other (Fig. 20a–b). In many cases the outwardly directed part of the sclerite, corresponding to the cup-shaped part of the *mollis*-type rosettes, is developed as several more or less prominent

serrated spines. The rosettes are up to 0.10 mm tall and wide. The quadriradiates (Fig. 20c–d) are essentially less described by Thomson, but in the sample examined, the largest individuals are not quite as large as reported, up to 0.25 mm in diameter. Although Thomson mentioned "a coherent mosaic of interlocked tuberculated disks," he did not include tuberculate disks in his description of the types of sclerites present, and disks are not present among the sclerites in the preparation now examined. The 3–6 rayed plates, predominantly quadriradiates, are up to 0.30 mm long, with rather dense tuberculation.

Remarks. Nutting identified Siboga expedition specimens from Indonesia as this species. These identifications were checked and proved to be a mixture of no less than three different species of *Bebryce: B. nuttingi*, ZMA 2258 (partly, Siboga sta. 310); ZMA 2259 (Siboga station 310); ZMA 2261 (Siboga sta. 305); *B. grandicalyx* ZMA 2258 (partly); *B. thomsoni* ZMA 2258 (partly). Two others of Nutting's identifications proved to be *Annella reticulata* (Ellis & Solander, 1786): ZMA 2256 (Siboga station 50) and ZMA 2257 (Siboga station 310). The colonies of the mixture of species of *Bebryce* from ZMA 2258 are shown in Figure 21.

Song (1980) identified two specimens from Mundo Island, Korea as *B. indica*. She depicted strongly modified calycular sclerites not present in this species.

The type material is overgrown by a sponge.

Distribution. Gulf of Manaar.

Comparisons. Bebryce crucifera (Bayer, 1981) resembles B. indica but differs in lacking rosettes.

Bebryce inermis Samimi-Namin & Ofwegen, 2010

Pseudobebryce thomsoni; Stiasny, 1940: 168. Bebryce hicksoni; Stiasny, 1940:156; Stiasny, 1959: 51, fig. B, pl. 3 fig. 11. Bebryce inermis Samimi-Namin & Ofwegen, 2010: 480, figs 1, 2A, B, 3–7 (Oman).

Material examined. *Bebryce hicksoni*, RMNH Coel. 6033, Gulf of Suez, coll. R. Ph. Dollfus, 28 December 1928 (dry material); RMNH Coel. 6039, same data (alcohol material); RMNH Coel. 6053 Gulf of Suez, Ashrafi, 40 fms (= 73 m), Agassiz Trawl, bottom coral and shells, coll. Crossland, 30 April 1936 (dry material); RMNH Coel. 6052, Gulf of Suez, Ghardaqa, coll. Crossland (alcohol material); *Bebryce thomsoni*, RMNH Coel. 6100, Red Sea, Mabahith expedition, 28 December, 1934.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Those of calycular margin slightly asymmetrically developed. Coenenchymal sclerites are stellate plates.

Remarks. Grasshoff (2000) included RMNH Coel. 6053 and RMNH Coel. 6033 in his paratype series of *B. sulfurea*. The shape of live colonies of *B. inermis* (Samimi-Namin & Ofwegen, 2010: Fig. 3) and *B. sulfurea* (Grasshoff 2000 Fig. 183) indeed are alike. Also the preserved colonies of these two species (Samimi-Namin & Ofwegen, 2010: Fig. 2A–B; Grasshoff 2000: Fig. 186) are very similar. Probably Grasshoff assumed only one species was present in the Red Sea, his *B. sulfurea*, and did not check the sclerites of the RMNH material. Here the sclerites of the RMNH material have been checked and they are completely different from *B. sulfurea*, which has no rosettes with bristle-like projections. Apparently Grasshoff only checked the dry collection of the RMNH as he did not include the alcohol preserved RMNH Coel. 6039 and RMNH Coel. 6052 in his type series.

The above mentioned finding enlarges the distributional range of *B. inermis*, next to Oman now also including the Red Sea.

RMNH Coel. 6100 *Bebryce thomsoni* is missing in the Naturalis collection, only three microscope slides remained showing disintegrated sclerites. As some of these sclerites could be recognized as rosettes with bristle-like projections we consider it to be *B. inermis*.

Distribution. Oman, Red Sea.

Comparisons. Resembles B. hicksoni and B. studeri but those species have more warty disks.

Bebryce mollis Philippi, 1842

(Figs. 22–23)

Bebryce mollis Philippi, 1842: 35, pl. 1 fig. 1-3; Aurivillius, 1931: 190; Carpine & Grasshoff, 1975: 55, figs. 28-31; Grasshoff,

1977: 59, figs. 58-60. (Eastern Atlantic, Mediterranean); Brito & Ocaña, 2004: 240, pl. 29-30.

Not *Bebryce mollis*; Thomson & Simpson: 225, pl. 9 figs. 14–15 (Australia); Thomson & Russell, 1910: 150 (Amirante, Providence); Hickson, 1940: 285 (Maldives, Somalia, Red Sea).

Bebryce stellata; Thomson, 1927: 47, pl. 3 fig. 26, pl. 4 fig. 15 (Mediterranean); Tixier-Durivault & d'Hondt, 1975: 1396 (Atlantic).

Not Bebryce stellata Hentschel 1903: 649.

Material examined. Fragments from specimens from North Africa (USNM 93233) and the Eastern Atlantic (USNM 93234) sent to the first author by M. Grasshoff (honorary scientist Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany).

Diagnosis. Calycular margin with well-developed sclerites derived from the rosette type, with serrated projecting blade. Coenenchyme with multiradiate plates.

Description. See Carpine & Grasshoff, 1975: 55; Grasshoff, 1977: 59; Brito & Ocaña, 2004: 240.

Distribution. Western Mediterranean, eastern Atlantic Ocean.

Comparisons. Mostly resembles *B. cinerea* but that species also has irregular multiradiate plates in the coenenchyme (Fig. 8 last two images), which are not present in *B. mollis*.

FIGURE 21. Colonies of ZMA 2258; a, *Bebryce grandicalyx* (Kükenthal, 1924); b-c, *Bebryce thomsoni* Nutting, 1910; d-e, *Bebryce nuttingi* Stiasny, 1942. Scale 1 cm.

FIGURE 22. *Bebryce mollis* Philippi, 1842; sclerites of a specimen from N Africa; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites, g, 4–6 rayed plates of inner coenenchyme. Scale at d only applies to d.

Bebryce nuttingi Stiasny, 1942

(Figs. 21d-e, 24-26)

Bebryce indica (partly); Nutting, 1910: 48. Not *Bebryce indica* Thomson, 1905:175, supplementary plate, fig. 3. *Bebryce nuttingi* Stiasny, 1942: 195. *Placogorgia dendritica* (partly, one specimen Siboga sta. 117) Nutting, 1910: 79.

Material examined. ZMA 2261, Siboga sta. 305, Indonesia, mid-channel in Solor Strait between Solor and Adonara, off Kampong Menanga, 113 m, stony bottom, 8 February 1900, type; *Bebryce indica*: ZMA 2258 (partly), Siboga sta. 310, Indonesia, Flores Sea, east end of Sumbawa, 8°30'S 119°07.5'E, 73 m, 12 February 1900; ZMA 2259, Siboga station 310; ZMA 3046, Siboga station 117, co-type *Placogorgia dendritica* Nutting, 1910, Indonesia, Sulawesi, Kwandang Bay entrance, 1°0.5'N 122°56'E, 80 m depth, sand and coral, trawl, 12 July 1899.

Diagnosis. *Bebryce* with 3–6 rayed stellate plates and paxilliform rosettes. Calycular margins without specialized sclerites.

Description. Polyps are closely placed on three sides of the branches, leaving one side mostly free. The calyces are contiguous, low, hemispherical, about 1.5 mm in diameter and 0.75 mm high. Save for apertures of the calyces, the surface of the colony bristles with clusters of radiating spicules of an encrusting sponge, which cover the normal surface of the calyces and coenenchyme and obscure the shape of the calyces.

The anthocodiae have a strong crown and points composed of stout, bent spindles about 0.4 mm long converging in pairs to form eight points (Fig. 24a), and the usual bow-shaped spindles about 0.65 mm long forming the transverse crown (Fig. 24b). The tentacles have dragon-wing sclerites, up to 0.15 mm long (Fig. 24c).

Paxilliform rosettes (Fig. 24d–e) about 0.1 mm tall and 0.09 mm across the base intergrade in size with 3–6-rayed plates (Fig. 24g) up to 0.25 mm across the rays, some with a strong central projection, some with the center scarcely raised. Asymmetrical rosettes in the vicinity of calycular margins are only weakly developed (Fig. 24f).

Remarks. In the preliminary account of his revision of the Muriceidae of the Siboga Expedition, Stiasny (1942: 195) established the new species *Bebryce nuttingi* with the following words: "Eines der von Nutting als *Bebryce indica* Thoms. bestimmten Exemplare erwies sich als spec. nova. Hauptmerkmal: Grosse, massive Spicula von paxillenahnlicher Form."

The SEM images of the first author (ZMA 2261, Fig. 24) were difficult to relate to the material present in Naturalis, ZMA 2258 (Fig. 25) and ZMA 2261 (Fig. 26). The larger polyp sclerites were missing in the Naturalis material, in ZMA 2261 even tentacle sclerites were not found, and those of ZMA 2258 looked much more spiny. One character all material had in common, both calyx rim sclerites and rosettes were not very common among the sclerites. The ZMA 2258 fragments are shown in Figure 21d–e.

Noteworthy is the presence of many sponge spicules, acanthostyles, on the rosettes, some even remained after preparing SEM stubs (Fig. 26d).

One of the syntypes of *Placogorgia dendritica* Nutting, 1911 (largest specimen of ZMA 3046, Siboga station 117) is also this species of *Bebryce*.

Distribution. Flores Sea (Indonesia).

Comparisons. This species resembles *B. densa* and *B. grandicalyx*, but has only a few rosettes, which are very common in the other two species.

Bebryce parastellata Deichmann, 1936

(Figs. 27–28)

Bebryce parastellata Deichmann, 1936: 127, pl. 8 fig. 4; pl. 10 figs. 22–28 (Western Atlantic, off Barbados; Cuba); Cairns *et al.*, 2002: 33; Devictor & Morton, 2010: 37, fig. 35.

Material examined. USNM 56463, the type from Barbados, MCZ 4609, Caribbean Sea, north of Paria Penisula, Venezuela, 11°21'N 62°21'W, 79 m, R/V Pillsbury sta. P-707, 19 July 1968, 1 colony lacking holdfast, one small colony on piece of mollusk shell, and one fragment; USNM 56471, Bahama Islands, off Cat Cay, 25°25'N 79°18'W, 403–338 m, R/V Gerda sta. G-240, 30 January 1964, 1 specimen; USNM 56472, Bahama Islands,

THE TYPE SPECIMENS OF BEBRYCE

FIGURE 23. *Bebryce mollis* Philippi, 1842; sclerites of a specimen from the Atlantic Meteor expedition; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites, g, 4–6 rayed plates of inner coenenchyme. Scale at e only applies to e.

FIGURE 24. *Bebryce nuttingi* Stiasny, 1942, ZMA 2261; a, point spindles; b, collaret spindle; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, 3–6-rayed plates of inner coenenchyme. Scale at d only applies to d.

FIGURE 25. *Bebryce nuttingi* Stiasny, 1942, ZMA 2258; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerite; g–j, 3–6-rayed plates of inner coenenchyme. Scale at c also applies to d, f, g, i.

FIGURE 26. *Bebryce nuttingi* Stiasny, 1942, ZMA 2261; a, point spindles; b, collaret spindle; c, calyx sclerite; d–e, rosettes; f–g, 3–6-rayed plates of inner coenenchyme. Scale at c also applies to d, f.

FIGURE 27. *Bebryce parastellata* Deichmann, 1936, USNM 56471; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–f, rosettes; g, top view rosette; h, calyx sclerites; i, 4–5-rayed plates of inner coenenchyme. Scale at e applies to e, g, that at f only to f.

FIGURE 28. *Bebryce parastellata* Deichmann, 1936, USNM 56472; a, point spindles; b, collaret spindles; c, club-like point sclerite; d, tentacle sclerites; e, rosettes; f, calyx sclerites; g, 4–5-rayed plates of inner coenenchyme. Scale at e only applies to e.

Northwest Providence Channel, 26°27'N 78°43'W, 522–487 m, R/V/ Gerda sta. G-706, 22 July 1965, 1 specimen; USNM 56467, Lesser Antilles, off St. Vincent, 13°10.2'N 61°01.5'W, 108–183 m, R/V Pillsbury sta. P-875, 6 July 1969, 1 specimen; USNM 56442, North Carolina, off Cape Lookout, 34°35'N 75°55'W, 46–53 m, M/V Silver Bay sta. 2819, 1 March 1961, 1 specimen; USNM, four additional lots, from off Cape Lookout, North Carolina, and Barbados, 46–586 m.

Diagnosis. Slender, unbranched or scantily branched *Bebryce* with well-separated, cylindrical calyces, cupshaped rosettes up to 0.14 mm in diameter, and stellate plates most with 4 rays, reaching 0.25 mm in diameter; calycular margin with well-developed sclerites derived from the rosette type, with serrated projecting blade.

Description. See Deichmann, 1936: 127.

Remarks. Colonies of this species are more delicate and less abundantly branched than those of *B. cinerea*. Deichmann (1936: 128) reported that the "spicules are almost identical with those characteristic of *B. grandis*." However, the thick, very elaborately tuberculate plates present in all the specimens of *B. grandis* appear never to be present in *B. parastellata*. Such ornate plates were illustrated by Verrill (Bayer & Cairns, 2004) for two of the seven species of *Bebryce* that he recognized in his unpublished Blake report; one of these he intended to call *B. grandis* and doubtless is the species to which Deichmann applied that name. Whether the other was a distinct species or a synonym of *B. grandis* is impossible to determine at this late remove date, owing to the absence of Verrill's text.

Deichmann noted that the rosettes of this species are larger than those of *B. cinerea* and *B. grandis*. Measurements from the types recorded cups about 0.08–0.085 mm high and 0.1–0.14 mm wide for *B. parastellata* (Figs. 27d–g, 28e), 0.05–0.08 mm high and 0.07–0.085 mm wide for *B. cinerea*, and 0.07–0.08 mm high and 0.065–0.08 mm wide in *B. grandis*. Calycular margin has well-developed sclerites derived from the rosette type, with serrated projecting blade (Figs. 27h, 28f). In the inner coenenchyme 4-rayed crosses predominate (Figs. 27i, 28g), but 3-rayed forms are not uncommon; 5- and 6-rayed stars are present but uncommon. Unlike all other species of *Bebryce* known until now, flattened spindles are present in the coenenchyme, although in small numbers; these may be derived from 4-rayed crosses by suppression of 2 rays, as the triradiates probably are derived from crosses with one ray suppressed. The anthocodial armature is arranged as a crown and points as in all species of *Bebryce*, with eight points each composed of 2–3 pairs of bent spindles up to about 0.35 mm long (Figs. 27a, 28a) beneath the tentacles and a strong collaret of curved, bow-shaped spindles about 0.4 mm long in 3 or 4 transverse rings beneath the points (Figs. 27b, 28b). The distal ends of the spindles of the points are more strongly thorny than the proximal ends, and the smaller, bent spindles that extend toward the tentacle base resemble thorny clubs (Fig. 28c). The tentacles contain dragon-wing sclerites (Figs. 27c, 28d).

This species seems not to be so prone to fouling by epizoa as is the case with *B. cinerea*, but some epizoans are usually present.

Distribution. N Carolina, Gulf of Mexico, Bahamas, Cuba, Barbados.

Comparisons. Unique in the Caribbean species of *Bebryce* with calycular rim rosettes with a blade by having 4–5 rayed sclerites in the inner coenenchyme, but no multiradiate plates.

Bebryce philippii Studer, 1889

(Fig. 29)

Bebryce philippii Studer, 1889: 10, pl. 3 figs. 3a, 3b, pl. 5 fig. 7 (Arafura Sea, 92 m). *Pseudobebryce philippii*; Kükenthal, 1924: 207.

Material examined. The type BMNH 1890.04.11.47.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Those of calycular margin asymmetrically developed, with strong projecting blade. Coenenchymal sclerites are small, warty disks.

Description. See Studer, 1889; Kükenthal, 1924.

Remarks. The anthocodial armature consists of transversely placed, bow-shaped spindles up to 0.35 mm long (Fig. 29b) arranged in a crown beneath the base of the tentacles, with a pair of curved, bluntly thorny spindles (Fig. 29a) converging on each tentacle base. Dragon-wing sclerites up to 0.12 mm long, with the convex edge strongly spinose (Fig. 29c) extend along the backs of the tentacles.

FIGURE 29. *Bebryce philippii* Studer, 1889, BMNH 1890.04.11.47, the holotype; a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites; f, tuberculate disks of inner coenenchyme. Scale at a applies to a-b, that at d only to d.

The rosettes (Fig. 29d) are of the usual cup-shaped type, reaching about 0.075 mm in diameter across the outer part, with the tuberculate base somewhat narrower, and up to about 0.07 in height. Rosettes consisting of a tuberculate base reaching about 0.1 mm in diameter with a prominent central process about 0.04 mm tall having a rounded top composed of numerous fascicles of calcite microcrystals are present; forms transitional to the cup-

shaped rosettes are not uncommon. At the margin of the calyces, the rosettes become asymmetrically modified as projecting, blade-like forms up to 0.22 mm in length (Fig. 29e).

The plates of the inner coenenchyme are thick tuberculate disks up to about 0.1 mm in diameter with tuberculate rim and central process on one surface (Fig. 29f); the margin of the smaller developmental forms is more conspicuously scalloped.

Distribution. Arafura Sea (Indonesia).

Comparisons. The species resembles *B. studeri* very much. However, it has smaller tuberculate disks, up to 0.10 mm long versus up to 0.15 mm for *B. studeri*. Considering the limited material examined one could predict longer ones could be found when more material is studied. For the moment we consider it a separate species.

Bebryce rigida Tixier-Durivault, 1972

(Figs. 30–31)

Bebryce rigida Tixier-Durivault, 1972: 35, figs. 7-8 (Europe island, Madagscar).

Material examined. holotype, MNHN-IK-0000-578, Island Europe, st. P9, nr 20, coll. P. Vasseur, 1969.

Diagnosis. *Bebryce* with 4–6 rayed stellate plates and paxilliform rosettes. Calycular margins without specialized sclerites.

Description. The colony is depicted by Tixier-Durivault (Fig. 7).

The anthocodial armature consists of bent spindles up to 0.45 mm long (Fig. 30a) en chevron in each of the eight points above a transverse crown of bow-shaped spindles up to 0.45 mm long (Fig. 30b). The tentacles have dragon-wing sclerites up to 0.20 mm long (Fig. 30c).

Sclerites of outermost cortex in the form of paxilliform rosettes up to 0.25 mm tall and wide, rim of the cups formed by several strong, laciniated projections (Fig. 30d, 31a). Near the apex of the calyces the rosettes become asymmetrical, forming small, blade-like projections (Fig. 30e). These sclerites are up to 0.18 mm long.

The coenenchymal sclerites are 4–6 rayed plates (Fig. 31b), up to 0.30 mm long. mostly with sparse, simple tuberculation. The smallest with hardly any tubercles (Fig. 31c).

Distribution. Madagascar.

Comparisons. This species resembles *Bebryce* species B but has longer, more spiny rosettes.

Bebryce sirene Grasshoff, 1999

Bebryce sirene Grasshoff, 1999: 64, figs. 109-111 (New Caledonia).

Material examined. None.

Diagnosis. *Bebryce* with paxilliform rosettes and coenenchyme with predominantly four-rayed sclerites. Calycular margins with asymmetrical rosettes not strongly modified.

Description. See Grasshoff, 1999: 64.

Remarks. Grasshoff provided SEM images of the sclerites (Grasshoff, 1999: fig. 110).

Distribution. New Caledonia.

Comparisons. *Bebryce sirene* is the only species of *Bebryce* with coenenchymal 4-rayed stellate plates but lacking strongly modified calycular rosettes.

Bebryce studeri Whitelegge, 1897

(Figs. 32-33)

Bebryce studeri Whitelegge, 1897: 314, pl. 17 figs. 21–25. (Funafuti); Grasshoff, 1999: 63, figs. 106–108 (New Caledonia); Samimi-Namin & Ofwegen, 2010: figs. 8–9.

Pseudobebryce studeri; Kükenthal, 1924: 206.

Bebryce hicksoni (part); Nutting, 1910: 47 (Indonesia).

FIGURE 30. *Bebryce rigida* Tixier-Durivault, 1972, holotype, MNHN-IK-0000-578 a, point spindles; b, collaret spindles; c, tentacle sclerites; d, rosettes; e, calyx sclerites. Scale at a applies to a, b.

FIGURE 31. *Bebryce rigida* Tixier-Durivault, 1972, holotype, MNHN-IK-0000-578 a, rosettes; b, 4–6-rayed plates of inner coenenchyme, c, smaller coenenchymal plates; d, sponge spicules. Scale at c only applies to c, that at d only to d.

FIGURE 32. *Bebryce studeri* Whitelegge, 1897, type, Australian museum; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, tuberculate disks of inner coenenchyme. Scale at d only applies to d, that at e only to e.

Not *Bebryce hicksoni* Thomson & Henderson, 1905: 294, pl. 3, fig. 1; pl. 6, fig. 9. (Ceylon). *Bebryce stellata* Hentschel, 1903: 649, pl. 53 figs 22–25 (Amboina); Samimi-Namin & Ofwegen, 2010: 490, figs 1, 2C, D, 10, 11.

Material examined. The type, Australian Museum, and specimens from the Philippines, USNM; ORSTOM HG 200, New Caledonia, S lagon, Ilot Canard, stn 136, 23 m depth; material stored in the MNHN (under MNHN-Oct.0000-0569); *B. hicksoni*: USNM 43161, Siboga sta. 289, 9°0.3'S 125°24.5'E (Timor), 112 m deep, trawl, mud, sand and shells, 20 January 1900; ZMA 2254, Siboga Sta. 305, 10°27.9'S 123°28.7'E, Solor Strait, off Menanga kampong, 113 m, stony bottom, Blake dredge, 8 February 1900; ZMA 2255a, Siboga sta. 154, 0°7.2'N 130°25.5'E (near Batanta island), 83 m, grey muddy sand, shells and *Lithothamnion*, dredge, depth decreased till 59 m during this haul, 14 August 1899; ZMA 2255b, Siboga sta 257, 5°.26.6'S 132°32.5'E, till 52 m, coral, Blake dredge, in Duroa Strait, Kei islands, 11 December 1899.

FIGURE 33. *Bebryce studeri* Whitelegge, 1897, USNM 43161; a, point spindles; b, collaret spindle; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, tuberculate disks of inner coenenchyme. Scale at d only applies to d, that at e only to e.

Diagnosis. Rosettes with warty, rounded, or bristle-like projections. Those of calycular margin asymmetrically developed, with projecting blade. Coenenchymal sclerites are warty disks.

Description. The anthocodial armature consists of bent spindles up to 0.35 mm long (Fig. 32a) en chevron in each of the eight points above a transverse crown of bow-shaped spindles up to 0.30 mm long (Fig. 32b). The tentacles have dragon-wing sclerites up to 0.20 mm long (Fig. 32c).

The rosettes of this species are small, cup-shaped forms with a low outer disk (the "cup") up to 0.06 mm in diameter and closely covered with projecting fascicles of microcrystals, joined by a short, smooth stalk 0.04 mm or less in thickness to a discoidal, warty base about 0.05 mm across (Fig. 32d–e). Asymmetrical rosettes near the calycular margins are not strongly developed (Fig. 32f).

The predominant coenenchymal sclerites are thick, warty disks up to about 0.15 mm in diameter, with a conspicuous central process consisting of two to several tubercles (Fig. 32g). The smallest examples of this form may have as few as 6 rays, which increase in number with increasing length. A few of the large plates are angular in outline rather than circular.

Remarks. Part of USNM 43161 (identified by Nutting as B. hicksoni) has sclerites similar to B. studeri (Fig.

33), and is here identified as such. ZMA 2254, ZMA 2255a and ZMA 2255b, identified by Nutting (1910) as *B. hicksoni*, also represent this species. Considering the small differences between *B. stellata* (re-description in Samimi-Namin & Ofwegen, 2010) and the type of *B. studeri*, we here synonymize the two species.

Distribution. Funafuti, New Caledonia, Indonesia, Philippines.

Comparison. Similar to *B. hicksoni*, see comparative remarks associated with that species.

FIGURE 34. *Bebryce sulfurea* Grasshoff, 2000, ZMTAU 9664, holotype; a, point spindle; b, collaret spindles; c, calyx sclerite; d–e, rosettes; f, 4–6-rayed plates of inner coenenchyme. Scale at c applies to c–d.

Bebryce sulfurea Grasshoff, 2000

(Fig. 34)

Bebryce sulfurea Grasshoff, 2000: 101, figs 183-189 (Red Sea).

Material examined. The holotype ZMTAU 9664.

Diagnosis. *Bebryce* with paxilliform rosettes and coenenchyme with 4–6-rayed sclerites. Calycular margins with asymmetrical rosettes not strongly modified.

Description. See Grasshoff, 2000: 101.

Remarks. Grasshoff did not provide SEM images of the sclerites, we present them here (Fig. 34). The sclerites show evidence of damage by acidity.

Distribution. Red Sea.

Comparisons. It resembles *B. grandicalyx* very much, see comparative remarks associated with that species.

Bebryce tenuis Thomson & Simpson, 1909

Bebryce tenuis Thomson & Simpson, 1909: 228, pl. 6 figs. 4–5 (India) *Pseudobebryce tenuis*; Kükenthal, 1924: 206.

Material examined. None.

Remarks. The description of Thomson & Simpson (1909: 228) does not reveal anything characteristic. Their remarks, "The coenenchyme is thick and dense. It consists of an almost uniform outer layer of scales, underlying which are warty, irregular spindles and a few double-clubs with very prickly warts," even suggests it is not a species of *Bebryce* at all, but in those days this was a description used for sclerites of this genus. According to the authors the species approaches *B. hicksoni*. The holotype is stored in the Indian Museum in Kolkata and not available for re-examination.

Distribution. India, Gulf of Bengal, off Gopalpur.

Bebryce thomsoni Nutting, 1910

(Figs. 21b-c, 35-36)

Bebryce thomsoni Nutting, 1910: 49, pl. 7 figs. 4, 4a, pl. 20 fig. 8. (Indonesia, west coast of Flores; Kei Islands); Thomson & Dean, 1931: 206; Soest, 1979: 87.

Pseudobebryce thomsoni; Kükenthal, 1924: 208. Not *Pseudobebryce thomsoni*; Stiasny, 1940: 168. (= *B. inermis*). Not *Bebryce thomsoni*; Song, 1980: 27, pl. 1 figs. 15–21. *Bebryce indica* (part); Nutting, 1910: 48.

Material examined. ZMA 2260, Siboga sta. 260, Indonesia, off Nuhu Jaan, west coast of Great Kei Island, 5°36.5'S 132°55.2'E, 90 m, 16 December 1899, one small colony, the holotype; *Bebryce indica*: USNM 43159, Siboga sta. 310, Indonesia, Flores Sea, east end of Sumbawa: 8°30'S 119°07.5'E, 73 m, 12 February 1900, three incomplete colonies; ZMA 2258 (partly, see Fig. 21b–c), Siboga sta. 310, Indonesia, Flores Sea, east end of Sumbawa, 8°30'S 119°07.5'E, 73 m, 12 February 1900.

Diagnosis. *Bebryce* with rosettes that are large and coarse, intergrading with thick, tuberculate disks with central process, which predominate in the coenenchyme.

Description. The anthocodial armature consists of bent spindles up to 0.30 mm long (Fig. 35a) en chevron in each of the eight points above a transverse crown of bow-shaped spindles up to 0.45 mm long (Fig. 35b). The tentacles have dragon-wing sclerites up to 0.17 mm long (Fig. 35c).

The rosettes of this species (Fig. 35d–e) are large and coarse, up to 0.16 mm wide and 0.10 mm high, intergrading with thick, tuberculate disks with central boss, which predominate in the coenenchyme (Fig. 35g). Asymmetrical rosettes near the calycular margins are up to 0.20 mm long and not strongly developed (Fig. 35f).

FIGURE 35. *Bebryce thomsoni* Nutting, 1910, ZMA 2260, holotype; a, point spindles; b, collaret spindles; c, tentacle sclerites; d–e, rosettes; f, calyx sclerites; g, tuberculate disks of inner coenenchyme. Scale at d only applies to d.

Remarks. The holotype of *B. thomsoni* is a small colony originally 6.3 cm tall (Nutting, 1910: pl. 7, fig. 4), from which the lowermost side branch and the upper part of the main stem with the uppermost side branch were snipped off by Nutting in the course of preparing his description. He mentions a larger specimen from station 258 (1910: 50), but this can no longer be found either in the Zoological Museum at Amsterdam or in the samples of Siboga specimens that Nutting retained that are now deposited in the U.S. National Museum of Natural History.

Direct comparison of the type colony with specimens from Siboga station 310 identified by Nutting as *Bebryce indica* Thomson (1910: 48) conclusively demonstrates that those specimens of presumed *B. indica* are, in fact, *B. thomsoni*. Stiasny (1942: 195) referred one of the specimens in the Zoological Museum Amsterdam identified by Nutting as *B. indica* to a new species, *Bebryce nuttingi*, with the primary distinguishing character "Grosse massive Spicula von paxillenahnlicher Form." This seems to fit the specimen from Siboga station 305 (ZMA 2261),

whereas those from station 310 (USNM 43159, ZMA 2258) are undoubtedly *B. thomsoni*. For comparison the sclerites of USNM 43159 are depicted in Fig. 36.

Nutting's description and illustrations of *B. thomsoni* do not adequately define the species. The illustrations of sclerites, drawn apparently without aid of a camera lucida, for the most part agree with the verbal description although one figure that does not correspond with any form occurring in the species seems to have been artistically invented to match the description of sclerites of a form "much like that of a mushroom," which could only have been the result of a brisk imagination.

The appearance of the type colony is well conveyed by the photograph (Nutting, 1910: pl. 7, fig. 4) reproduced at natural size.

Remarks. Song (1980) misidentified three specimens from Wimi Ri, Korea as this species. Song's sclerite figures do not show the characteristic large rosettes.

Distribution. Flores Sea (Indonesia).

Comparisons. The species resembles *Bebryce* species A but has larger tuberculate disks and the calycular rosettes have a less developed blade.

FIGURE 36. *Bebryce thomsoni* Nutting, 1910, USNM 43159; a, point spindles; b, collaret spindles; c, rosettes; d, calyx sclerites; e, tuberculate disks of inner coenenchyme. Scale at c only applies to c.

Species incorrectly attributed to Bebryce:

Bebryce acanthoides Thomson and Russell, 1910, cannot be retained in *Bebryce*, but on the basis of comparison with *Placogorgia campanulifera* Nutting, 1910 and *P. bebrycoides* Nutting, 1910 is referred to the genus *Discogorgia* established by Kükenthal (1919, 1924) for those species.

Discogorgia acanthoides (Thomson & Russell, 1910), n. comb.

Bebryce acanthoides Thomson & Russell, 1910: 151, pl. 7 figs. 3, 6; Hickson, 1940: 264. *Placogorgia bebrycoides* Nutting, 1910: 83, pl. 13 fig. 4, 4a; pl. 22 fig. 11. *Discogorgia bebrycoides*; Kükenthal, 1924: 213. Not *Bebryce acanthoides*; Tixier-Durivault, 1966: 399, 1972: 33 (= *Bebryce*).

Material examined. BMNH 1912.02.24.009, Providence I., Indian Ocean, syntype of *Bebryce acanthoides*; USNM 43079, Siboga sta. 274, Indonesia, Aru Islands, 5°28.2'S, 134°53.9'E, 57 m, illustrated syntype of *Placogorgia bebrycoides* and another syntype from sta. 274.

Description. See Thomson and Russell, 1910: 151; Nutting, 1910: 83.

Remarks. Colonial form of *B. acanthoides* and *P. bebrycoides* as illustrated by Thomson & Russell (1910: pl. 7, figs. 3, 6) and Nutting (1910: pl. 13, figs. 4, 4a) is in reasonable agreement.

The sclerites of *Bebryce acanthoides* include abundant tuberculate rods and stout spindles, chiefly in the deeper layers of coenenchyme, in addition to large, tuberculate spheroids and oval forms concentrated in the outer coenenchyme, but no rosettes. The tubercles on the outer surface of the large spheroids are larger and smoother than those of the inner surface; some of the oval and rod-like forms can be somewhat larger at one end, no doubt representing the club-like shapes reported in the original description. The curved spindles of the anthocodial armature are arranged as a distinct crown and points.

The sclerites of the illustrated colony of *Placogorgia bebrycoides* Nutting (1910: pl. 13, fig. 4) are very similar to those of *Bebryce acanthoides*, consisting of tuberculate rods and spindles, with many spheroids especially in the surface layer; those of the axial sheath are small capstans and belted spindles. The anthocodiae are armed with curved spindles converging toward the tentacles, above an indistinct transverse crown. The large, tuberculate spheroids can be as much as 0.36 mm in diameter, somewhat larger than those of *B. acanthoides*, which are about 0.22 mm in diameter.

Examination of two syntype specimens of *Placogorgia bebrycoides* from Siboga sta. 274 retained by Nutting (now USNM 43079) shows that the species is composite. Consequently, the colony illustrated on Nutting's plate 13, fig. 4 (presumed to be the specimen from sta. 305 by the process of elimination), is here recognized as lectotype in order to restrict the nominal species to a single taxonomic entity. The paralectotypes from sta. 274 are here determined to be *Placogorgia campanulifera* Nutting and therefore referable to the genus *Discogorgia* Kükenthal.

Stiasny (1942: 197) placed *Placogorgia bebrycoides* in *Paracis*, but the species clearly has nothing to do with *Paracis*, and can reasonably be referred to *Discogorgia*. It also is similar to some species referred by Kükenthal to the genus *Euplexaura* Verrill, but the anthocodial armature is stronger than usual for *Euplexaura* and is more typical of *Bebryce*, and the spheroidal sclerites predominant in the outer coenenchyme are similar to those of some species of *Bebryce* (cf. *B. thomsoni*, Figs. 35–36). The numerous spindle- and rod-shaped sclerites are unlike any reported for any species of *Bebryce*, and, together with the absence of sclerites representing any variation of the rosette type, may be accepted as definitively excluding *P. bebrycoides* from *Bebryce*.

In spite of the difference in size of the large spheroidal sclerites, which could be due to individual or geographical variation, or even to differences in sample preparation, both *Placogorgia bebrycoides* and *Bebryce acanthoides* are treated as a single species of *Discogorgia*, pending a thorough revision of that genus and its relationship with *Euplexaura* and *Thesea*.

Discussion

Many re-examined specimens showed signs of disintegrated sclerites, probably caused by acidity. We assume this

must have happened by initially storing specimens in formalin after collecting and only later transferring them to alcohol. For several species only fragmentary material is left, i.e., *Bebryce bocki*, *B. boninensis*, *B. hicksoni*, *B. indica*, *B. philippii*, *B. stellata*, and *B. studeri*, further hampering this study of the genus.

As a consequence of older, rather incomplete descriptions species were seldom described or identified, and when done so mostly based on wrong assumptions. For instance, Samimi-Namin and Ofwegen (2010) based their new species *B. inermis* on the statement that there were only three Indo-Pacific species of *Bebryce* with rosettes with bristle-like projections, while the present study shows six had been described already; now five as we here synonymized *B. stellata* with *B. studeri*. Moreover, sequences from two specimens identified to the species level have been deposited in GenBank (*nd2* mitochondrial gene), *B. indica* and *B. thomsoni*, most likely, based on identifications of Song (1980), which are here shown to be incorrect. Many more misidentifications occur in the natural products literature.

As a first result of this overview we could identify a species of *Bebryce* from Palau, with sequences in GenBank (McFadden *et al.*, 2014) as *B. crucifera*.

Still very little is known about the distribution of *Bebryce* in the Indo-Pacific, as most species are only known from one or a few locations. This study shows the distribution range of two species to be much greater than known from the literature. *Bebryce studeri* is now identified from Funafuti, New Caledonia and Indonesia, *B. inermis* from Oman and the Red Sea. It is today accepted that the Atlantic-Mediterranean species of *Bebryce* do not occur in the Indo-Pacific. Therefore, *B. mollis* findings for the Indo-Pacific (See *B. mollis*) are considered misidentifications.

The sclerite characters used by us in this overview to describe species of *Bebryce* should be evaluated using recent collections, but from a preliminary study of NBC specimens it became obvious that rosette type, internal sclerite form, and modification of calyx rim rosettes are useful. The anthocodial sclerites seem to vary more regarding shape and size.

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