

# An illustrated key to the genera and subgenera of the Recent azooxanthellate Scleractinia (Cnidaria, Anthozoa), with an attached glossary

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## Abstract

The 120 presently recognized genera and seven subgenera of the azooxanthellate Scleractinia are keyed using gross morphological characters of the corallum. All genera are illustrated with calicular and side views of coralla. All terms used in the key are defined in an illustrated glossary. A table of all species-level keys, both comprehensive and faunistic, is provided covering the last 40 years.

## Keywords

Azooxanthellate, Illustrated Key, Genera, Glossary, Scleractinia

## Introduction

The ready identification of azooxanthellate Scleractinia (determined herein by depth of occurrence and previously published observations) to the genus and species levels has been hampered by a lack of a comprehensive key to the genera as well as a lack of species level keys. For instance, the last comprehensive set of keys to the genera was published by Vaughan and Wells (1943) almost 70 years ago, and relied in part on microstructural characters that were both hard to observe (requiring thin sectioning) and interpret.

Since then the number of Recent azooxanthellate genera and species has almost doubled, and new observations on apozooxanthellate species (species that have facultative symbiosis with zooxanthellae) are also available. Furthermore, what keys exist to the species level of various taxa or geographic regions are scattered throughout the literature and of variable quality (Table 1). In this Table, tabular keys are included, as they provide as much if not more information than a conventional dichotomous key. As result of the application of molecular data (e.g. Fukami et al. 2008, Kitahara et al. 2010a, Huang et al. 2011, Stolarski et al. 2011, Arrigoni et al. 2012), the higher taxonomic ranks of the order Scleractinia were shown to be polyphyletic. As such, a key to this taxonomic rank seems premature. Thus, it is the purpose of this paper to provide a single, comprehensive, illustrated key to the presently recognized 120 azooxanthellate scleractinian genera and 7 additional subgenera. We constructed the key using gross morphological characteristics of the corallum, which, when used in conjunction with the glossary and illustrations, we hope will provide a guide to the proper genus identification. But one must keep in mind that this key, as most, will not necessarily supply a definitive identification of the genus, as its use depends on the interpretation of the characters as well as the variation of that character state. We have used many of the dichotomies published by Vaughan and Wells (1943), but avoided the microstructural characters, and updated the taxa. Whereas microstructure is undoubtedly a valuable set of characters to define genera, in most cases it is not necessary to identify the genera. Among the 120 extant azooxanthellate scleractinian genera, 74 are illustrated with its type species (~61%). Within the remaining 46 genera, 20 (~43.5%) have an extinct species as type, represented by a fossil coral. For them and the remaining 26 genera, the illustrated species present very well the most important morphological characters of their respective genus.

**Table 1.** Previously published keys to azooxanthellate taxa, divided as comprehensive keys to all taxa with in a monophyletic taxon, and partial (faunistic) keys of species. Taxa listed alphabetically by taxon name. Tabular keys (T) are included.

<b>Comprehensive keys</b>	
<i>Anthemiphyllia</i> , species (T)	Cairns (1999: 290)
<i>Asterosmilia</i> , species (T)	Cairns and Wells (1987: 38)
<i>Aulocyathus</i> , species	Cairns (1999: 104)
<i>Caryophyllia</i> , species (T)	Cairns (1991: 12)
<i>Caryophyllia</i> , species	Kitahara et al. (2010b: 112)
<i>Conocyathus</i> , species	Cairns (2004a: 290)
<i>Crispatotrochus</i> , species	Kitahara and Cairns (2008: 62)
<i>Deltoocyathus</i> , species	Kitahara and Cairns (2009: 236)
Dendrophylliidae, genera (T)	Cairns (2001: 5)
Flabellidae, genera (T)	Zibrowius (1974: 26); Cairns (1989: 45)
Guyniidae, genera (T)	Cairns (1989: 41); Stolarski (2000: 23)
<i>Javania</i> , species	Cairns (2004b: 10)
Micrabaciidae, genera	Cairns (1989: 13)
<i>Placotrochides</i> , species	Cairns (2004a: 307)
Scleractinia, families and genera	Vaughan and Wells (1943)

<b>Comprehensive keys</b>	
<i>Stephanophyllia</i> , species	Cairns (1989: 21)
<i>Trochocyathus</i> ( <i>Aplocyathus</i> ), species (T)	Cairns (1999: 85)
Turbinoliidae, genera	Cairns (1988a: 711; 1989: 25; 1997: 5 [T]); Filkorn (1994: 44)
<b>Faunistic keys</b>	
<i>Astrangia</i> , E. Pacific	Durham and Barnard (1952: 60)
Azooxanthellate Scleractinia, Antarctica	Cairns (1990: 18 [book])
Azooxanthellate Scleractinia, E. Gulf of Mexico	Cairns (1977a: 5)
Azooxanthellate Scleractinia, New Zealand	Squires and Keyes (1967: 13); Tracey et al. (2012)
Azooxanthellate Scleractinia, NE Pacific	Cairns (1994: 13)
Azooxanthellate Scleractinia, NW Pacific	Cairns (1994: 75)
Azooxanthellate Scleractinia, S. Australia	Cairns and Parker (1992: 4)
Azooxanthellate Scleractinia, Cold Temp. NE Atl.	Cairns (1981:3)
Azooxanthellate Scleractinia, Brazil	Kitahara (2007: 510)
<i>Balanophyllia</i> , W. Atlantic	Cairns (1977b: 133)
<i>Balanophyllia</i> , Japan	Ogawa et al. (1998: 145 [in Japanese])
<i>Balanophyllia</i> , W. Atlantic (T)	Cairns (2000: 163)
<i>Caryophyllia</i> , New Zealand	Cairns (1995: 43)
<i>Caryophyllia</i> , W. Atlantic	Cairns (1979: 46)
<i>Caryophyllia</i> , W. Pacific	Cairns and Zibrowius (1997: 87, 96)
<i>Caryophyllia</i> and <i>Premocyathus</i> , Japan	Ogawa et al. (1999: 115 [in Japanese])
<i>Conotrochus</i> and <i>Trochocyathus</i> , Japan	Ogawa et al. (2003: 57 [in Japanese])
<i>Culicia</i> , Australia	Cairns (2004a: 274)
<i>Deltocyathus</i> , W. Atlantic	Cairns (1979: 91)
<i>Deltocyathus</i> , W. Pacific	Cairns and Zibrowius (1997: 121)
<i>Dendrophyllia</i> , Japan	Ogawa and Takahashi (1995: 25 [in Japanese])
<i>Flabellum</i> , New Zealand	Cairns (1995: 96)
<i>Flabellum</i> , Japan	Ogawa and Takahashi (2005: 56 [in Japanese])
<i>Fungiacyathus</i> , W. Pacific (T)	Cairns (1989: 6, 7; 1999: 55)
<i>Fungiacyathus</i> , Japan	Ogawa and Takahashi (2004: 11 [in Japanese])
<i>Heterocyathus</i> , W. Pacific	Hoeksema and Best (1991: 222)
<i>Heterocyathus</i> , Japan	Ogawa and Takahashi (2008: 248 [in Japanese])
<i>Heteropsammia</i> , W. Pacific	Hoeksema and Best (1991: 222)
<i>Heteropsammia</i> , Japan	Ogawa and Takahashi (2008: 248 [in Japanese])
<i>Madracis</i> , W. Atlantic	Wells (1973: 19)
<i>Paracyathus</i> and <i>Polycyathus</i> , Japan	Ogawa et al. (2000: 55 [in Japanese])
<i>Trochocyathus</i> , W. Pacific	Cairns and Zibrowius (1997: 105)
<i>Truncatoflabellum</i> , W. Pacific	Cairns (1989a: 62)
<i>Truncatoflabellum</i> , SW Indian Ocean	Cairns and Keller (1993: 264)
<i>Truncatoflabellum</i> , Australia (T)	Cairns (1998: 397)
<i>Truncatoflabellum</i> , Japan	Ogawa (2006: 13 [in Japanese])
<i>Tubastraea</i> , Red Sea	Scheer and Pillai (1983: 173)
<i>Tubastraea</i> , Galapagos	Cairns (1991: 27)
<i>Tubastraea</i> , Japan	Ogawa and Takahashi (1993: 97 [in Japanese])
Turbinoliidae, Japan	Ogawa et al. (2002: 27 [in Japanese])

## Methods

Some genera are keyed two or even three times because of the variation within those genera regarding the characters used in the key. In theory, all variations of that genus will be correctly keyed. Although most couplets are dichotomous, some are polychotomous, such as the columella or colony shape, which allows the reader to clearly see the multiple states of a particular character.

Although it would be desirable to follow the generic key with keys to all of the approximately 720 azooxanthellate species, it is a simple fact that not many species level keys have been published. Those that have been published in the last 35 years are listed in Table 1, separated as to whether they are keys to all of the taxa within a monophyletic taxon (comprehensive) or to a more limited fauna of a region (faunistic). Keys made before 1970 were found to be, in general, not up to date and are thus not included. It should be noted that fully one-third of the genera (40) are monotypic, and thus do not require a key following a correct genus identification, and another 22 genera have but two species. Finally, although they do not include keys, the treatises of Wells (1956) and Chevalier and Beauvais (1987) include diagnoses of all genera, including those represented only by extinct species, and thus provide a rich source of taxonomic information.

Other sources of useful taxonomic information include a list of all extant Recent scleractinian species as of 1999 (Cairns et al. 1999), which also includes a rough indication of their geographic range. The azooxanthellate component of this list is kept up to date as an on-line resource ([www.lophelia.org/online-appendices](http://www.lophelia.org/online-appendices)), which now includes junior synonyms and depth ranges of the species, and authors of the genera. A list of the 120 azooxanthellate genera, their authorship, and bathymetric ranges was also published in Roberts et al. (2009: Table 2.7)

Geographic ranges within brackets in the key are not meant to be considered as distinguishing characters, but simply informational, which may nonetheless hint at an incorrect identification. Abbreviations: Ant. = Antarctic or Subantarctic, Atl. = Atlantic, IP = Indo Pacific, IWP = Indo-West Pacific, Pac. = Pacific, SubAnt = Subantarctic; Cosmopolitan implies occurrence in all three oceans as well as Subantarctic and/or Antarctic. Museums and Institutions acronyms: AM = Australian Museum (Sydney); AU = Auckland University Museum (Auckland); CSIRO = Commonwealth Scientific and Industrial Research Organisation (Hobart); JCU = James Cook University (Townsville); MNHN = Muséum national d'Histoire naturelle (Paris); SBMNH = Santa Barbara Natural History Museum (Santa Barbara); SIO = Scripps Institute of Oceanography (San Diego); NZOI = New Zealand Oceanographic Institution (now the National Institute of Water and Atmospheric Research) (Wellington); USNM = United States National Museum (now the National Museum of Natural History, Smithsonian) (Washington, D.C.); YPM = Yale Peabody Museum (New Heaven).

Useful sources for more information about definitions of terms used in the glossary include: Wells (1956), and Cairns (1981, 1989, 1994).

**Key to the Genera and Subgenera of the Recent Azooxanthellate Scleractinia**

(An asterisk indicates genera that have azooxanthellate and zooxanthellate representatives)

1a	Corallum colonial .....	<b>2</b>
1b	Corallum solitary .....	<b>43</b>
2a	Corallum free of attachment (recumbent, usually curved with a broken or open base, or globular).....	<b>3</b>
2b	Corallum firmly attached (arborescent, bushy, encrusting, or reptoid) .....	<b>5</b>
3a	Corallum recumbent (composed of a large primary corallite from which smaller buds originate); no sipunculid commensalism.....	<b>4</b>
3b	Corallum globular; pores in lateral base of colony associated with commensal sipunculid..... [IWP] <i>Heteropsammia</i> * (in part) Plate 1, Figures A–B	
4a	Corallum not porous (solid); septa arranged normally .....	
	..... [Atl. + IP] <i>Anomocora</i> Plate 1, Figures C–D	
4b	Corallum, especially septa porous; septa arranged in a Pourtalès Plan .....	
	..... [Atl. + IWP] <i>Eguchipsammia</i> Plate 1, Figures E–F	
5a	Corallum arborescent or bushy .....	<b>6</b>
5b	Corallum encrusting or reptoid.....	<b>27</b>
6a	Branching intratentacular .....	<b>7</b>
6b	Branching extratentacular .....	<b>9</b>
7a	Equal distomadeal budding .....	<b>8</b>
7b	Unequal monostomaeous budding .....	
	..... [Cosmopolitan] <i>Lophelia</i> Plate 1, Figures G–H	
8a	Texture of corallum rough (like sandpaper), resulting from a porous theca; septa arranged in a weak Pourtalès Plan .....	
	..... [W. Pac.] <i>Dichopsammia</i> Plate 1, Figures I–J	
8b	Texture of corallum smooth or costate, solid; septa arranged normally .....	
	..... Cosmopolitan] <i>Solenosmilia</i> Plate 1, Figures K–L	
9a	Septal symmetry decamerale or octamerale, septa in only one cycle; columella styliform .....	
	..... [Atl. + IP] <i>Madracis</i> * (in part) Plate 2, Figures A–B	
9b	Septal symmetry hexamerale, septa arranged in multiple cycles; columella papillose, fascicular or absent.....	<b>10</b>
10a	Texture of theca and septa rough (like sandpaper), resulting from a porous theca.....	<b>11</b>
10b	Texture of theca smooth, granular, or ridged (solid) .....	<b>14</b>
11a	Septa arranged in a Pourtalès plan .....	<b>12</b>
11b	Septa arranged normally .....	<b>13</b>
12a	Corallum small (bushy), most corallites budding from a common basal coenosteum or from the edge zone of corallites that originate from the basal coenosteum..... [Atl. + Pac.] <i>Cladopsammia</i> Plate 2, Figures C–D	

- 12b Corallum large (bushy to arborescent), with multiple successive generations of budding forming an erect colony ..... [Atl. + IP] *Dendrophyllia* Plate 2, Figures E–F
- 13a Corallum porosity only apparent near calicular edge; found in deep-water: 110–2165 m ..... [Atl. + IWP] *Enallopsammia* Plate 2, Figures G–H
- 13b Corallum porosity uniform: shallow-water: 0–110 m ..... [Atl. + IP] *Tubastraea* (in part) Plate 2, Figures I–J
- 14a Columella absent ..... **15**
- 14b Columella present (papillose, trabecular or fascicular) ..... **16**
- 15a Corallum large (arborescent), with numerous budding cycles, adjacent corallites often linked with hollow, tubular coenosteal bridges; tabular endothelial dissepiments common ... [I–P + Subant.] *Goniocorella* Plate 2, Figures K–L
- 15b Corallum a small bush, corallites originating from a common basal coenosteum or from the sides of other corallites and from relatively few budding cycles; endothelial dissepiments not prominent ..... [E. Atl. + New Zealand] *Hoplangia* (in part) Plate 5, Figures L–M
- 16a Columella fascicular ..... **17**
- 16b Columella papillose or trabecular ..... **18**
- 17a Pali before septa of third cycle (P3) ..... [N. Atl.] *Pourtalosmilia* Plate 3, Figures A–B
- 17b Pali absent ..... [W. Pac.] *Confluphyllia* Plate 3, Figures C–D
- 18a Columella trabecular, composed of slender (flattened laths); corallum never with more than 4 generations of budding ..... [Atl. + W. Pac.] *Coenosmilia* Plate 3, Figures E–F
- 18b Columella papillose (composed of rods); corallum composed of many generations of budding ..... **19**
- 19a Axial septal edges dentate ..... [W. Pac.] *Sympodangia* Plate 3, Figures G–H
- 19b Axial septal edges smooth ..... **20**
- 20a Pali absent ..... [Cosmopolitan] *Madrepora* (in part) Plate 3, Figures I–J
- 20b Pali present ..... **21**
- 21a Pali arranged in multiple crowns before septa of all but last cycle; axial edge of septa minutely dentate ..... **22**
- 21b Pali arranged in two crowns before S2 and S3 or S1–3; axial edges of septa smooth ..... **24**
- 22a Coenosteum costate ..... [Atl. + Pac.] *Cladocora* Plate 3, Figures K–L
- 22b Coenosteum not costate ..... **23**
- 23a Axial corallite associated with each branch ..... [SW Pac.] *Petrophyllia* Plate 4, Figures A–B
- 23b Axial corallites absent ..... [Atl. + Pac.] *Oculina*\* Plate 4, Figures C–D
- 24a P1–3 arranged in two palmar crowns ..... [IWP] *Cyathelia* Plate 4, Figures E–F
- 24b One palmar crown of P2 or P3 ..... **25**
- 25a Only P2 present ..... **26**
- 25b Only P3 present ..... [SW Atl. + E. Pac.] *Bathelia* Plate 4, Figures G–H

- 26a Columella massive ..... [SE Atl.] ***Sclerbelia*** Plate 4, Figures I–J
- 26b Columella rudimentary.....  
..... [Cosmopolitan] ***Madrepora*** (in part) Plate 4, Figures K–L
- 27a Septal symmetry decamer or octamer, septa in only one cycle; columella styliform ..... [Atl. + IP] ***Madracis***\* (in part) Plate 5, Figures A–B
- 27b Septal symmetry hexamer, septa arranged in multiple cycles; columella papillose, fascicular, spongy, lamellar or absent..... **28**
- 28a Texture of corallum rough (like sandpaper), resulting from a porous theca... **29**
- 28b Texture of corallum smooth or costate, solid ..... **31**
- 29a Corallum increases by stoloniferous budding (reptoid), the connection among corallites often obscured, thus sometimes appearing to be solitary; Pourtalès Plan present.. [W. Atl. + IP] ***Rhizopsammia*** Plate 5, Figures C–D
- 29b Corallum increases by budding from a common basal coenosteum, the connection among polyps quite evident; septa normally inserted..... **30**
- 30a Columella massive; epitheca surrounds each corallite.....  
..... [E. Atl.] ***Astroides*** Plate 5, Figures E–F
- 30b Columella of moderate to small size; epitheca lacking.....  
..... [Atl. + IP] ***Tubastraea*** (in part) Plate 5, Figures G–H
- 31a Columella absent ..... **32**
- 31b Columella present..... **33**
- 32a Corallites united by thin basal stolons (reptoid).....  
..... [Atl. + IWP] ***Thalamophyllia*** Plate 5, Figures I–K
- 32b Corallites bud from a common basal coenosteum .....  
..... [E. Atl. + New Zealand] ***Hoplanguia*** (in part) Plate 5, Figures L–M
- 33a Axial edges of some or all cycles of septa finely dentate or beaded .....  
..... (Rhizangiidae) **34**
- 33b Axial edges of all septa smooth..... **38**
- 34a Thin epitheca encircles corallites; axial edges of S1-2 smooth, sometimes lobate (but inner edges of S3-4 dentate)..... **35**
- 34b Epitheca absent; axial edges of all septa dentate..... **36**
- 35a Corallite base polycyclic; one crown of large P3.....  
..... [Atl.+ Pac.] ***Colanguia*** Plate 6, Figures A–B
- 35b Corallite base monocyclic; pali, if present, of uniform size .....  
..... [IP] ***Culicia*** Plate 6, Figures C–D
- 36a Corallite base polycyclic; pali absent ..... [IP] ***Oulangia*** Plate 6, Figures E–F
- 36b Corallite base monocyclic; pali before septa of all but last cycle..... **37**
- 37a Corallum stoloniferous (reptoid) or cerioid; peritheca absent.....  
..... [Atl. + IP] ***Astranguia***\* Plate 6, Figures G–H
- 37b Corallum massive (subramose); peritheca unite corallites .....  
..... [Indian] ***Cladanguia*** Plate 6, Figures I–J
- 38a Pali or paliform lobes on axial edges of septal of all but last cycle..... **39**
- 38b Pali or paliform lobes present only on septa of penultimate cycle (usually P3)..... **41**

39a Corallum stoloniferous (reptoid).... [IWP] *Rhizosmilia* Plate 6, Figures K–L

39b Corallites bud from a common basal coenosteum ..... **40**

40a Corallites monocyclic; pali before septa of all but last cycle, and all of approximately the same size..... [IWP] *Polycyathus* Plate 7, Figures A–B

40b Corallites polycyclic; pali before septa of all but last cycle, those of P3 crown much larger than others ..... [W. Atl.] *Phacelocyathus* Plate 7, Figures C–D

41a Columella fascicular..... **42**

41b Columella trabecular..... [Atl. + IP] *Phyllangia* Plate 7, Figures E–F

42a Occurrence of pali variable: usually P4, occasionally also P3, occasionally absent ..... [E. Pac.] *Bathycyathus* Plate 7, Figures G–H

42b Pali in one crown before septa of third cycle (P3) ..... [Atl. + Pac.] *Coenocyathus* Plate 7, Figures I–J

43a Corallum firmly attached (fixed) ..... **44**

43b Corallum unattached (free) ..... **67**

44a Theca granular, the granules usually occurring on longitudinally oriented costae ..... **45**

44b Theca smooth (epithecate or stereome-reinforced), sometimes with fine transverse ridges encircling the theca..... **53**

44c Theca and septa porous, although in some genera a smooth epitheca may cover the basal portion of the corallum ..... **61**

44d Theca absent (corallum discoidal) ..... [E. Pac.] *Nomlandia* Plate 7, Figure K

45a Columella papillose ..... **46**

45b Columella fascicular..... **51**

45c Columella absent ..... **52**

45d Columella labyrinthiform... [Atl. + IP] *Labyrinthocyathus* Plate 8, Figures A–B

46a Pali or paliform lobes absent; base polycyclic ..... [W. Atl. + W. Pac.] *Oxysmilia* Plate 8, Figures C–D

46b Pali or paliform lobes present; base monocyclic ..... **47**

47a Coralla usually arranged in pseudocolonial assemblages ..... [W. Pac.] *Lochmaetrochus* Plate 8, Figures G–H

47b Coralla discrete ..... **48**

48a Pali before S1-2 (P1, P2), indistinguishable from columellar elements..... [W. Atl. + IWP] *Monohedotrochus* Plate 8, Figures E–F

48b Pali before septa of all but last cycle; palar crowns discrete ..... **49**

49a Multiple slender paliform lobes on axial edge of every lower cycle septum, not arranged in crowns..... [Atl. + IP] *Paracyathus* Plate 8, Figures I–J

49b Two crowns of discrete pali or paliform lobes (P1+P2 and P3), only one palus or paliform lobe per septum..... **50**

50a True pali present, the P1-2 smaller than P3 but not significantly ..... [Atl. + IP] *Trochocyathus (Trochocyathus)* (in part) Plate 8, Figures K–L

50b Paliform lobes present, the P1-2 much smaller than the broad P3 ..... [W. Atl. + W. Pac.] *Vaughanella* Plate 9, Figures A–B

- 51a Pali before septa of penultimate cycle.....  
[Cosmopolitan] *Caryophyllia* (*Caryophyllia*) (in part) Plate 9, Figures C–D
- 51b Pali absent ..... [Cosmopolitan] *Crispatotrochus* Plate 9, Figures E–F
- 52a Corallum base monocentric; epitheca lacking; calice elliptical in outline; menianes lacking ..... [Cosmopolitan] *Desmophyllum* Plate 9, Figures G–H
- 52b Corallum polycentric; transverse epithecal bands near corallum base; calicular outline modified by calicular extensions; menianes on septal faces .....  
.....[W. Pac.] *Dactylotrochus* Plate 9, Figures I–J
- 53a Columella absent or simply a rudimentary fusion of lower axial edges of major septa deep in fossa ..... **54**
- 53b Columella present (papillose, fascicular or labyrinthiform) ..... **57**
- 54a Pedicel reinforced (thickened) with stereome deposits .....  
.....[Cosmopolitan] *Javania* Plate 9, Figures K–L
- 54b Pedicel reinforced with hollow rootlets, most easily seen in cross section of base or pedicel, or in a damaged corallum ..... **55**
- 55a Rootlets non-contiguous with pedicel, 2-20 adventitious rootlets anchoring the corallum ..... [IWP] *Rhizotrochus* Plate 10, Figures A–B
- 55b Rootlets (symmetrical or asymmetrical in placement) contiguous with pedicel, forming an integral part of the lower corallum..... **56**
- 56a Calicular edge jagged ..... [W. Atl. + IP] *Polymyces* Plate 10, Figures C–D
- 56b Calicular edge smooth ... [E. Atl. + W. Pac.] *Monomyces* Plate 10, Figures E–F
- 57a Columella papillose ..... **58**
- 57b Columella fascicular..... **60**
- 57c Columella labyrinthiform... [W. Pac.] *Stolarskicyathus* Plate 10, Figures G–I
- 58a Corallum base polycyclic; no notch between upper outer edges of septa and theca ..... **59**
- 58b Base monocyclic, but may have an accessory basal rootlet; septal notch present..... [W. Atl. + IWP] *Gardinieria* Plate 10, Figures J–K
- 59a Pali before septa of penultimate cycle.....  
..... [Atl. + E. Pac.] *Concentrotheca* Plate 10, Figures L–M
- 59b Paliform lobes present before septa of S1-2 (P1-2) .....  
..... [E. Atl. + E. Pac.] *Ceratotrochus* Plate 11, Figures A–B
- 59c Pali before septa of all but last cycle in two crowns .....  
..... [Atl. + Pac.] *Tethocyathus* Plate 11, Figures C–D
- 60a Corallum cylindrical and very small (calicular diameter less than 2 mm); a row of thecal spots or pores present in every interseptal region; octameral septal symmetry; only 1 columellar element.....  
..... [Atl. + IWP] *Guynia* Plate 11, Figures E–G
- 60b Corallum trochoid and larger (adult calicular diameter over 10 mm); thecal spots and pores lacking; hexameral symmetry; numerous columellar elements..... [IWP] *Conotrochus* (in part) Plate 11, Figures H–I
- 61a Septa arranged in a Pourtalès Plan ..... **62**

61b	Septa arranged normally .....	<b>63</b>
62a	Corallum base polycyclic; theca costate.....	
	..... [Cosmopolitan] <i>Balanophyllia (Balanophyllia)*</i> Plate 11, Figures J–K	
62b	Corallum base monocyclic; theca hispid (not costate).....	
	..... [W. Atl. + SW Pac.] <i>Thecopsammia</i> Plate 11, Figures L–M	
63a	Columella absent or rudimentary.....	<b>64</b>
63b	Columella spongy.....	<b>65</b>
64a	Corallum trochoid; theca costate .....	
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## References

- Arrigoni R, Stefani F, Pichon M, Galli P, Benzoni F (2012) Molecular phylogeny of the Robust clade (Faviidae, Mussidae, Merulinidae and Pectiniidae): an Indian Ocean perspective. *Molecular Phylogenetics and Evolution* 65: 183–193. doi: 10.1016/j.ympev.2012.06.001
- Cairns SD (1977a) Caryophylliina and Dendrophyllina (Anthozoa: Scleractinia). *Memoires of the Hourglass Cruises* 3(4): 1-27.
- Cairns SD (1977b) A review of the Recent species of *Balanophyllia* in the western Atlantic, with description of four new species. *Proceedings of the Biological Society of Washington* 90(1): 132–148.
- Cairns SD (1978) New genus and species of ahermatypic coral (Scleractinia) from the western Atlantic. *Proceedings of the Biological Society of Washington* 91(1): 216–221.
- Cairns SD (1979) The deep-water Scleractinia of the Caribbean and adjacent waters. *Studies on the Fauna of Curaçao and other Caribbean Islands* 57(180): 1–341.

- Cairns SD (1981) Marine flora and fauna of the northeastern United States. NOAA Technical Report, NMFS Circular 438: 1–14.
- Cairns SD (1988a) *Cryptotrochus*, new genus and two new species of deep-water corals (Scleractinia: Turbinoliinae). Proceedings of the Biological Society of Washington 101(4): 709–716.
- Cairns SD (1988b) Asexual reproduction in solitary Scleractinia. In: Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia) 2: 641–646.
- Cairns SD (1989) A revision of the ahermatypic Scleractinia of the Philippine islands and adjacent waters. Part 1. Fungiacyathidae, Micrabaciidae, Turbinoliinae, Guyniidae, and Flabellidae. Smithsonian Contributions to Zoology 486: 1–136. doi: 10.5479/si.00810282.486
- Cairns SD (1990) Antarctic Scleractinia: keys and notes for the identification of the species. Koeltz Scientific Books (Synopsis of the Antarctic Benthos), 1–78.
- Cairns SD (1991) A revision of the ahermatypic Scleractinia of the Galápagos and Cocos Islands. Smithsonian Contributions to Zoology 504: 1–44. doi: 10.5479/si.00810282.504
- Cairns SD (1994) Scleractinia of the temperate North Pacific. Smithsonian Contributions to Zoology 557: 1–150.
- Cairns SD (1995) The marine fauna of New Zealand: Scleractinia (Cnidaria Anthozoa). New Zealand Oceanographic Institute Memoir 103: 1–210.
- Cairns SD (1997) A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria: Scleractinia). Smithsonian Contributions to Zoology 591: 1–55.
- Cairns SD (1998) Azooxanthellate Scleractinia (Cnidaria: Anthozoa) of western Australia. Records of the Western Australian Museum 18: 361–417.
- Cairns SD (1999) Cnidaria Anthozoa: deep-water azooxanthellate Scleractinia from Vanuatu, and Wallis and Futuna Islands. Mémoires du Muséum National d'Histoire Naturelle 180: 31–167.
- Cairns SD (2000) A revision of the shallow-water azooxanthellate Scleractinia of the western Atlantic. Studies on the Natural History of the Caribbean Region 75: 1–215.
- Cairns SD (2001) A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). Smithsonian Contributions to Zoology 615: 1–75. doi: 10.5479/si.00810282.615
- Cairns SD (2004a) The azooxanthellate Scleractinia (Coelenterata: Anthozoa) of Australia. Records of the Australian Museum 56: 259–329. doi: 10.3853/j.0067-1975.56.2004.1434
- Cairns SD (2004b) A new shallow-water species of *Javania* (Scleractinia: Flabellidae) from Indonesia. Raffles Bulletin of Zoology 52: 7–10.
- Cairns SD, Keller NB (1993) New taxa and distributional records of azooxanthellate Scleractinia (Cnidaria, Anthozoa) from the tropical southwest Indian Ocean, with comments on their zoogeography and ecology. Annals of the South African Museum 103(5): 213–292.
- Cairns SD, Parker SA (1992) Review of the Recent Scleractinia of South Australia, Victoria, and Tasmania. Records of the South Australian Museum (Monograph Series) 3:1–82.
- Cairns SD, Wells JW (1987) Neogene paleontology in the northern Dominican Republic. 5. The suborders Caryophylliina and Dendrophylliina (Anthozoa: Scleractinia). Bulletins of American Paleontology 93: 23–43.
- Cairns SD, Zibrowius H (1997) Cnidaria Anthozoa: azooxanthellate Scleractinia from the Philippines and Indonesian regions. Mémoires du Muséum National d'Histoire Naturelle (Paris) 172: 27–243.

- Cairns SD, Hoeksema BW, van der Land J (1999) Appendix: List of extant stony corals. Atoll Research Bulletin 459: 13–46.
- Chevalier JP, Beauvais L (1987) Order des Scléractiniaires. In: Grassé PP (Ed.) *Traité de Zoologie* tome III, fasc. 3. Masson, Paris.
- Durham JW, Barnard JL (1952) Stony corals of the Eastern Pacific collected by the Velero III and Velero IV. Allan Hancock Pacific Expedition 16(1): 1–110.
- Filkorn HF (1994) Fossil scleractinian corals from James Ross Basin, Antarctica. Antarctic Research Series 65: 96 pp. doi: 10.1029/AR065
- Hoeksema BW, Best MB (1991) New observations on scleractinian corals from Indonesia, 2: Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heteropsammia*. Zoologische Mededelingen 65(16): 221–245.
- Huang D, Licuanan WY, Baird AH, Fukami H (2011) Cleaning up the ‘Bigmessidae’: Molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. BMC Evolutionary Biology 11: 1–37. doi: 10.1186/1471-2148-11-37
- Kitahara MV (2007) Species richness and distribution of azooxanthellate Scleractinia in Brazil. Bulletin of Marine Science 81(3): 497–518.
- Kitahara MV, Cairns SD (2008) New records of the genus *Crispatotrochus* (Scleractinia; Caryophylliidae) from New Caledonia, with description of a new species. Zootaxa 1940: 59–68.
- Kitahara MV, Cairns SD (2009) Revision of the genus *Deltocyathus* (Cnidaria, Scleractinia), with a description of a new species from New Caledonia. Zoosystema 31(2): 233–249. doi: 10.5252/z2009n2a2
- Kitahara MV, Cairns SD, Stolarski J, Blair D, Miller DJ (2010a) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. Plos One 5: e11490. doi: 10.1371/journal.pone.0011490
- Kitahara MV, Cairns SD, Miller DJ (2010b) Monophyletic origin of the *Caryophyllia* (Scleractinia; Caryophylliidae), with description of six new species. Systematics and Biodiversity 8: 91–118. doi: 10.1080/14772000903571088
- Ogawa K (2006) A revision of Japanese ahermatypic corals around the coastal region with guide to identification. XII. *Truncatoflabellum*, *Placotrochus* and *Placotrochides*. Nankiseibutu (The Nanki Biological Society) 48(1): 13–20. [In Japanese]
- Ogawa K, Takahashi K (1993) A Revision of Japanese Ahermatypic Corals around the Coastal Region with a Guide to Identification, I: Genus *Tubastraea*. Nankiseibutu (The Nanki Biological Society) 35(2): 95–109. [In Japanese]
- Ogawa K, Takahashi K (1995) A Revision of Japanese ahermatypic corals around the coastal region with a guide to identification, II. Genus *Dendrophyllia*. Nankiseibutu (The Nanki Biological Society) 35(14): 15–33. [In Japanese]
- Ogawa K, Takahashi K (2004) A revision of Japanese ahermatypic corals around the coastal region with guide to identification, X. *Fungiacyathus*, *Letepsammia*, and *Anthemiphyllia*. Nankiseibutu (The Nanki Biological Society) 46(1): 11–17. [In Japanese]
- Ogawa K, Takahashi K (2005) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, XI. *Guynia*, *Truncatoguyinia* and *Flabellum*. Nankiseibutu (The Nanki Biological Society) 47(1): 55–62. [In Japanese]

- Ogawa K, Takahashi K (2008) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, XIV. *Endopachys*, azooxanthellate *Heterocyathus* and *Heteropsammia*. Nankiseibutu (The Nanki Biological Society) 50(2): 247–251. [In Japanese]
- Ogawa K, Takahashi K, Chiba J (1998) A revision of Japanese ahermatypic corals around the coastal region with guide to identification, IV. Genus *Balanophyllia*. Nankiseibutu (The Nanki Biological Society) 37(1): 15–33. [In Japanese]
- Ogawa K, Takahashi K, Tachikawa H (1999) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, V. Genera *Caryophyllia* and *Premocyathus*. Nankiseibutu (The Nanki Biological Society) 41(2): 116–124. [In Japanese]
- Ogawa K, Takahashi K, Tachikawa H, Sakai K, Chiba J (2000) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, VI. Genera *Paracyathus*, *Polycyathus*, *Endopsammia* and *Leptopsammia*. Nankiseibutu (The Nanki Biological Society) 42(1): 55–63. [In Japanese]
- Ogawa K, Tachikawa H, Takahashi K (2002) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, VIII. Family Turbinoliidae. Nankiseibutu (The Nanki Biological Society) 44(1): 27–36. [In Japanese]
- Ogawa K, Tachikawa H, Takahashi K (2003) A revision of the Japanese ahermatypic corals around the coastal region with guide to identification, IX. *Conotrochus*, *Trochocyathus*, and *Bourneotrochus*. Nankiseibutu (The Nanki Biological Society) 45(1): 57–63. [In Japanese]
- Roberts JM, Wheeler AJ, Freiwald A, Cairns SD (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, xvi + 334 pp.
- Scheer G, Pillai CSG (1983) Report on the stony corals from the Red Sea. Zoologica 133: 198 pp.
- Squires DF, Keyes IW (1967) The marine fauna of New Zealand: scleractinian corals. New Zealand Oceanographic Institute Memoir 43: 1–46.
- Stolarski J (1995) Ontogenetic development of the thecal structures in Caryophylliinae scleractinian corals. Acta Palaeontologica Polonica 40(1): 19–44.
- Stolarski J (2000) Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data. Lethaia 33: 13–38. doi: 10.1080/00241160050150276
- Stolarski J, Kitahara MV, Miller DJ, Cairns SD, Mazur M, Meibom A (2011) The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. BMC Evolutionary Biology 11: 2–15. doi: 10.1186/1471-2148-11-316
- Tracey DM, Anderson OG, Naylor JR (editors) (2011) A guide to common deepsea invertebrates in New Zealand waters. New Zealand Aquatic Environment and Biodiversity Report 86: 1–317.
- Vaughan TW, Wells JW (1943) Revision of the suborders, families and genera of the Scleractinia. Special Papers of the Geological Society of America 44: 1–363.
- Wells JW (1956) Scleractinia. In: Moore RC (Ed) Treatise on Invertebrate Paleontology, Part F. Coelenterata. Geological Society of America, Lawrence, F328-F444.
- Wells JW (1973) New and old corals from Jamaica. Bulletin of Marine Science 23(1): 16–55.
- Zibrowius H (1974) Révision du genre *Javania* et considérations générales sur les Flabellidae (Scléractiniaux). Bulletin de l'Institut Océanographique (Monaco) 71(1429): 1–48.

## Glossary

**Anthocaulus:** See Transverse Division.

**Anthocyathus:** See Transverse Division.

**Apozooxanthellate:** Species that have facultative symbiotic relationships with unicellular photosynthetic dinoflagellates (*Symbiodinium* spp.).

**Axial Corallite:** See Corallite.

**Axial Septal Margin:** See Septum.

**Azooxanthellate:** Species that do not have symbiotic relationships with unicellular photosynthetic dinoflagellates (*Symbiodinium* spp.).

**Base (Figure 1):** The lower several millimeters of a solitary corallum, usually solid and composed of an accretion of thecal layers (a **monocyclic base**) (e.g. **Plate 24, Fig. B**), but in some genera composed of concentric rings of partitioned chambers, called a **polycyclic base** (e.g. **Plate 24, Fig. C**) (Cairns 1978). The base usually expands basally as a thin layer facilitating adhesion to the substrate.

**Budding:** The process of asexual reproduction that adds new mouths (or polyps) to a corallum, often resulting in a colony. **Intratentacular budding** adds new polyps to the oral disc inside the ring of tentacles surrounds its mouth (e.g. **Plate 1, Fig. K–L**). **Extratentacular budding** adds new polyps outside the ring of tentacles (e.g. **Plate 2, Fig. H**). (The third form of asexual reproduction is **transverse division** - Cairns 1988b).

**Calice (Figure 1) (pl. Calices):** The skeletal analog of the polyp, cupping the polyp from below, and consisting of the septa, and, if present, the columella and pali (e.g. **Plate 1, Figs C, E, G; Plate 9, Figs A, C, E, G, I, K**).

**Ceratoid Corallum:** See Solitary Corallum.

**Coenosteum:** The skeletal structure found between the individual corallites of a colonial corallum, including the costae, and various kinds of dissepiments; sometimes called **peritheca** (e.g. **Plate 24, Fig. E**).

**Colonial Corallum:** See Corallum.

**Columella (Figure 1):** An axial structure of diverse shape and composition that projects from the center of a calice. If in the shape of a single lamella (called **lamellar**) (e.g. **Plate 20, Fig. I**), if a maze of interconnected lamellae (**labyrinthiform**) (e.g. **Plate 8, Fig. A**), if a set of twisted lamellae (**fascicular**) (e.g. **Plate 20, Figs C, E**), if a simple rod (**styliform**) (e.g. **Plate 13, Fig. A**), if a group of rods (**papillose**) (e.g. **Plate 8, Fig. K**), if a fine porous mass (**spongy**) (e.g. **Plate 12, Fig. G**), and if an irregular group of twisted elements (**trabecular**) (e.g. **Plate 16, Fig. K**).

**Conical Corallum:** See Solitary Corallum.

**Corallite:** The vertical, usually cylindrical, structure produced by an individual polyp, consisting of endothecal dissepiments and the calice at the upper end (e.g. **Plate 1, Fig. F**). If a corallite occurs at the tip of a colony's branch, it is termed an **axial corallite** (e.g. **Plate 24, Fig. F**).

**Corallum (Figure 1) (pl. Coralla):** The aragonitic calcium carbonate skeleton of a scleractinian coral. If the coral has only one mouth (or calice), it is termed **solitary** (e.g.

**Plate 10, Figs A–M; Plate 17, Figs A–M**, if polystomatous (or more than one calice), then a **colonial** (e.g. **Plate 2, Fig. A–L; Plate 3, Figs A–L**).

**Costae** (**Figure 1**) (sing. **Costa**; adj. **Costate**): Continuation of a septum on the outside of the corallite wall, often as a ridge or low linear mound (e.g. **Plate 24, Figs A, D, G, M**).

**Crest**: See Edge Spine.

**Crown** (**Figure 1**): See Palus.

**Cuneiform Corallum**: See Solitary Corallum.

**Cupolate Corallum**: See Solitary Corallum.

**Cycle**: See Septum.

**Cylindrical Corallum**: See Solitary Corallum.

**Discoidal Corallum**: See Solitary Corallum.

**Dissepiments**: Thin horizontal (**tabular dissepiments**, e.g., **Plate 2, Fig. K**) or blister-like plates that form within a corallite (**endothecal**) or beneath the coenosteum outside corallites (**exothecal**), which separate the polyp from the lower part of the corallum that it no longer occupies.

**Distomodeal Budding**: A mode of intratentacular budding in which two polyps (or calices) develop within the common tentacular ring (e.g., **Plate 1, Figs I–K**).

**Edge Spine/Crest/Spur**: The external thecal edges of a solitary coral, those associated with the principal septa, sometimes bears a low thin crest, or a series of hollow spines. If the crest is limited to the basal portion of the corallum and project outward in the shape of a fish tail, they may be called spurs (e.g. **Plate 24, Figs H–M**).

**Edge Zone**: The fold of the polyp body that extends over the edge of the theca (e.g. **Plate 25, Fig. A**).

**Endothecal**: See Dissepiments.

**Epitheca**: Thin, external, smooth or wrinkled, non-trabecular sheath surrounding individual corallites, formed by centripetal (inward) growth (e.g. **Plate 10, Figs I, K; Plate 11, Figs D, I; Plate 12, Fig. F**). **Tectura** is very similar in outward appearance by originates by centrifugal (outward) growth (e.g. **Plate 25, Fig. B**) (Stolarski 1995).

**Exothecal**: See Dissepiments.

**Extratentacular Budding**: See Budding.

**Fascicular Columella**: See Columella.

**Free**: An unattached corallum (e.g. **Plate 14, Figs A–L; Plate 17, Figs A–M; Plate 18, Figs A–Q**).

**Globular Corallum**: See Solitary Corallum.

**Imperforate Theca**: See Theca.

**Intratentacular Budding**: See Budding.

**Labyrinthiform Columella**: See Columella.

**Lamellar Columella**: See Columella.

**Marginal Shelf**: A low rim encircling a solitary corallum composed of greatly reduced septa and costae, or costal spines (Cairns 1989) (e.g. **Plate 25, Fig. D**).

**Menianes:** Short ledge-like features on septal faces formed by aligned lateral extensions of trabeculae (e.g. **Plate 25, Fig. C**).

**Monocyclic Base:** See Base.

**Monostomaeous/Monostomatous:** A single-mouthed corallum, i.e., a solitary form (e.g. **Plate 8, Figs A–F**).

**Normal Arrangement of Septa:** Arrangement of septa within a calice in which the septa are independent and all aligned with the center of the calice. (See Pourtalès Plan) (e.g. **Plate 8, Fig. E; Plate 9, Fig. E**).

**Paliform Lobes:** Small, flattened lobes on the axial septal edge of various cycles, often more than one per septum, and part of the septum to which they are attached (e.g., **Plate 17, Fig. I**).

**Palus (Figure 1) (pl. Pali):** Small flattened lobes on the axial septal edge of various cycles, always one per septum, and not part of the septum to which it is attached but ontogenetically different. Groups of pali occurring on the same cycle of septa and thus stand at the same distance from the center of the calice are called **crowns** of pali (e.g. **Figure 1**).

**Papillose Columella:** See Columella.

**Parricidal Budding:** A mode of intratentacular budding in which new polyps are generated from the inner surface of a fragment of a parent corallum that has longitudinally split apart (e.g. **Plate 16, Fig. J, L–M**).

**Pedical (Figure 1):** The stem-like region of a solitary coral just above the base and below the calicular surface.

**Perforate Theca:** See Theca.

**Peritheca:** See Coenosteum.

**Polycyclic Base:** See Base.

**Polystomaeous/Polystomatous:** See Corallum.

**Portalès Plan:** A form of septal arrangement in which the axial edges of pairs of higher cycle septa bend in front of and unite before their adjacent lower cycle septum (e.g. **Plate 25, Fig. E**). See Cairns (1994: fig. 2).

**Reptoid Budding:** A type of extratentacular budding in which polyps are asexually generated from a thin, reticulate, encrusting ribbon (similar to stoloniferous budding) (e.g. **Plate 6, Fig. B; Plate 7, Fig. F**).

**Scolecoïd Corallum:** See Solitary Corallum.

**Septum (pl. Septa):** Radially arranged longitudinal partitions of a corallite (**Figure 1**), usually arranged in hexamerall symmetry. Septa are added in **cycles**, the first cycle composed of 6 septa, the second also of 6, the third of 12, the fourth of 24, the fifth of 48, etc. resulting in corallites consisting of 6, 12, 24, 48, or 96, etc. septa per calice. Septa can bear smooth, dentate, or lacinate axial margin (**Figure 1**).

**Solitary Corallum:** Solitary coralla exist in a variety of shapes, the shape being one of the criteria used to differentiate genera and species. Many solitary coralla are shaped as an inverted cone (**conical**), and may be attached and straight or free and usually curved. If the edges of the cone diverge at a hypothetical basal angle of 10–40°, this corallum is called **ceratoid** (e.g. **Plate 10, Figs H–I**), if the angle is 40–60°, then

**trochoid** (e.g. **Plate 8, Fig. F**), if the angle is 60–80°, **turbinate** (e.g. **Plate 13, Fig. H**), and if the angle is 160–180° and the corallum is low, **discoidal** (e.g. **Plate 18, Fig. P**). Coralla may also be **cylindrical** (e.g. **Plate 22, Fig. N**), and if the cylinder is irregular in shape, **scolecoid** (e.g. **Plate 12, Fig. D**). Others are wedge-shaped (**cuneiform**) or **bowl-shaped** (e.g. **Plate 17, Figs F, H, J, M**). Still others have a flat base with a convex upper surface (**cupolate**) (e.g. **Plate 19, Figs A–F**) and others are simply onion-shaped or irregular (**globular**) (e.g. **Plate 18, Fig. B**).

**Spongy Columella:** See Columella.

**Stereome:** A general term for thick calcareous deposits, generally thickening various parts of the corallum.

**Stoloniferous Budding:** A type of extratentacular budding in which polyps are asexually generated from a thin, elongate, encrusting coenenchymal ribbon, the connecting ribbon often obscured by encrusting organisms (e.g. **Plate 5, Fig. B; Plate 6, Fig. D**).

**Styliform Columella:** See Columella.

**Synapticular Plate:** Ribbons of calcium carbonate linking adjacent fungiacyathid septa, first appearing as vertical rods midway between septa, later bifurcate, the two ends fusing to adjacent septal faces (T- or Y-shaped) (Cairns 1989a) (e.g. **Plate 25, Fig. F**).

**Trabecular Columella:** See Columella.

**Tabular Endothecal Dissepiment:** See Dissepiment.

**Tectura:** See Epitheca.

**Theca** (**Figure 1**): The skeletal sides, or walls, of solitary coralla or corallites of colonial corals, that enclose the polyps. If the theca is solid, it is termed **imperforate** (e.g. **Plate 9, Figs D, L**); if the theca is porous, **perforate** (e.g. **Plate 22, Figs I–J**).

**Thecal spots/pores:** Some genera have longitudinal series of small pores aligned with the interseptal spaces of various cycles, termed thecal pores. In other genera, these analogous structures do not penetrate the theca but are visible only as slightly differently colored spots of a construction consistently different from the remaining theca, these termed spots (e.g. **Plate 11, Figs F–G; Plate 22, Fig. N**).

**Thecal spur:** See Edge Spine.

**Trabecular Columella:** See Columella.

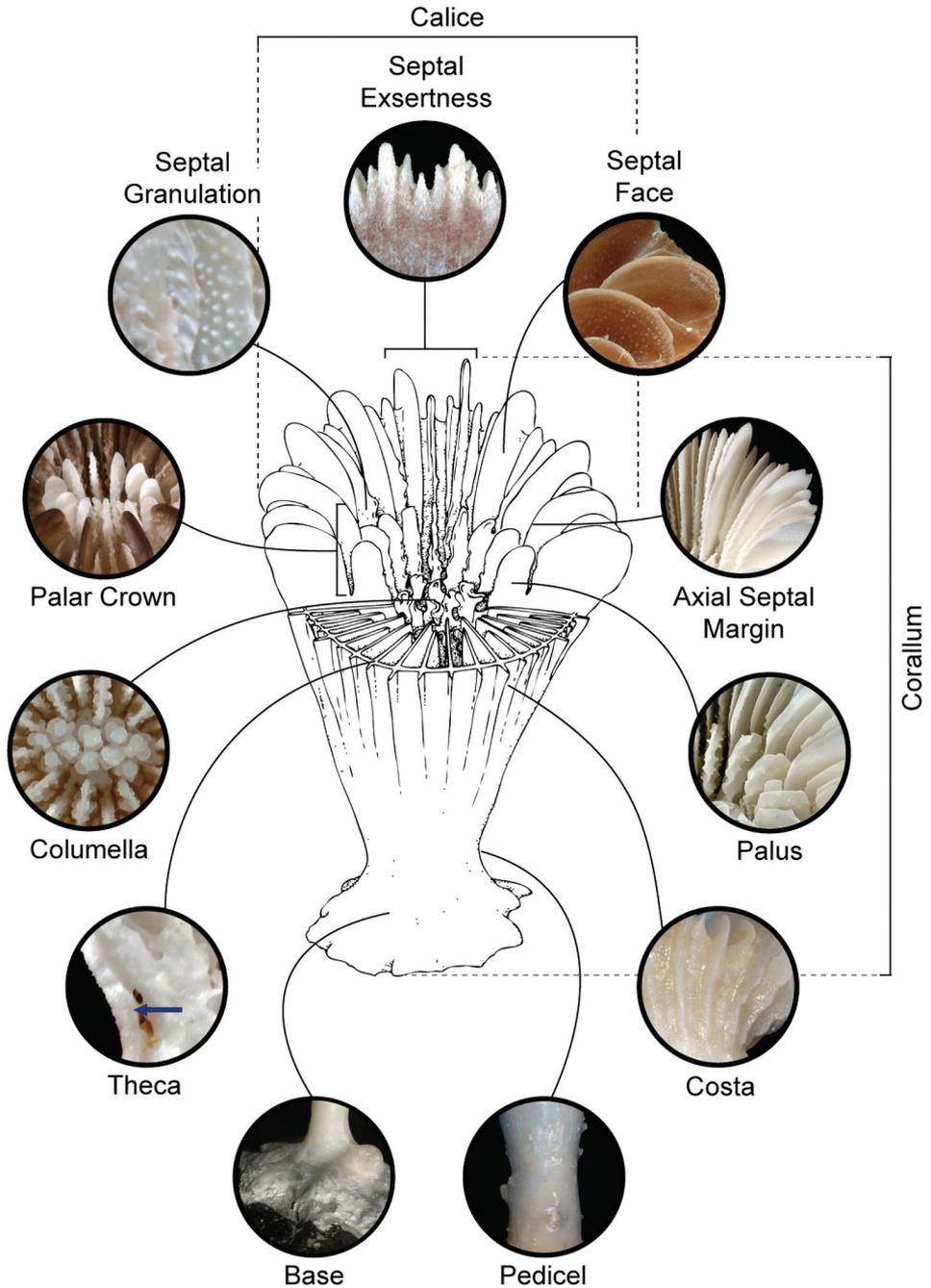
**Transverse Division:** One of the three main methods of asexual reproduction among the Scleractinia (Cairns 1988b). In this method an attached sexually produced solitary corallum (called the **anthocaulus** - e.g. **Plate 25, Figs H, J**) transversely divides it corallum usually along a crescent-shaped line of thecal weakness, producing an asexually generated distal corallum (the **anthocyathus** - e.g. **Plate 25, Figs G, I**), which falls to the substrate as an unattached (free) corallum, the base of which retains a scar of previous attachment (e.g. **Plate 25, Figs I–J**).

**Trochoid Corallum:** See Solitary Corallum.

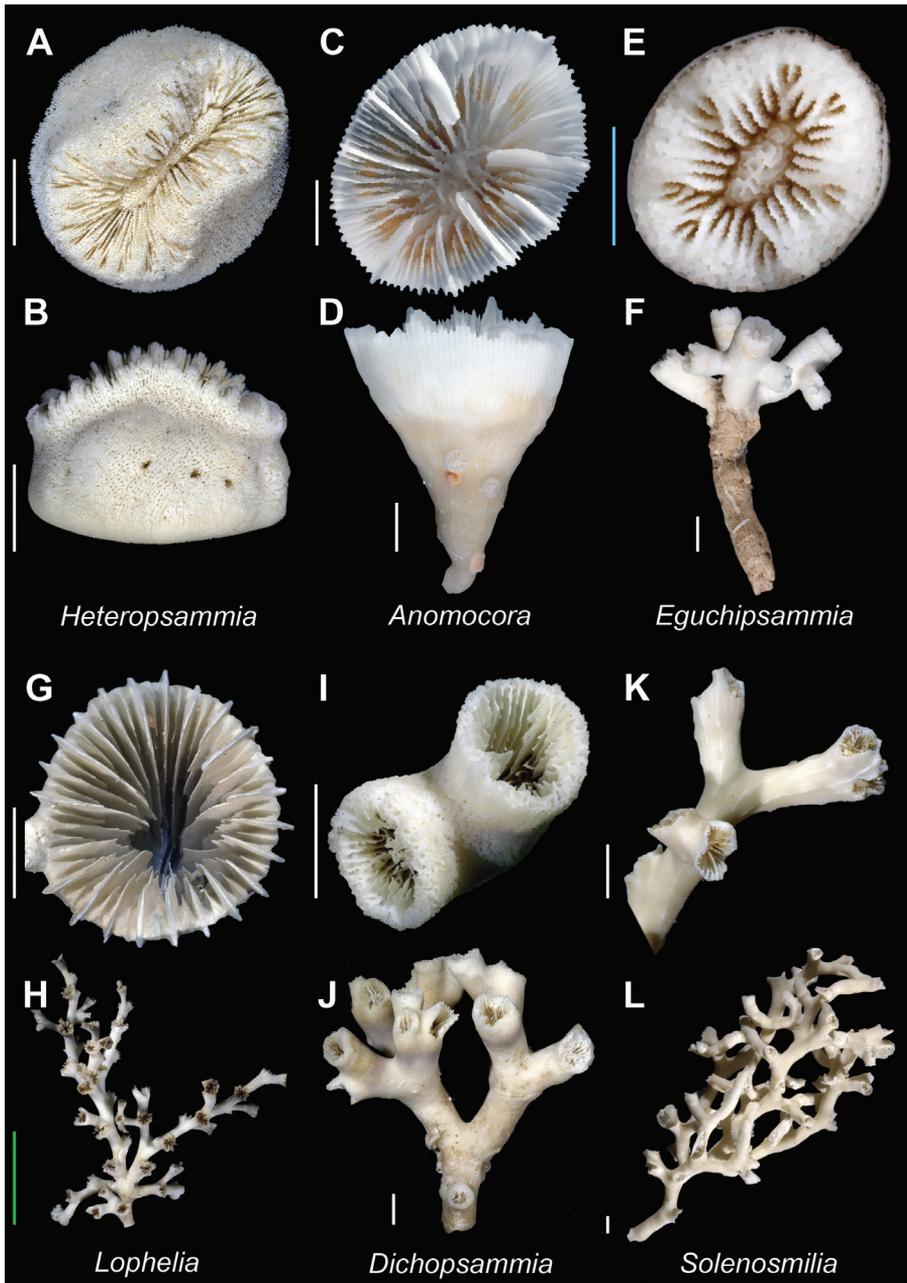
**Turbinate Corallum:** See Solitary Corallum.

**Zooxanthellate:** Species that have symbiotic relationships with unicellular photosynthetic dinoflagellates (*Symbiodinium* spp.).

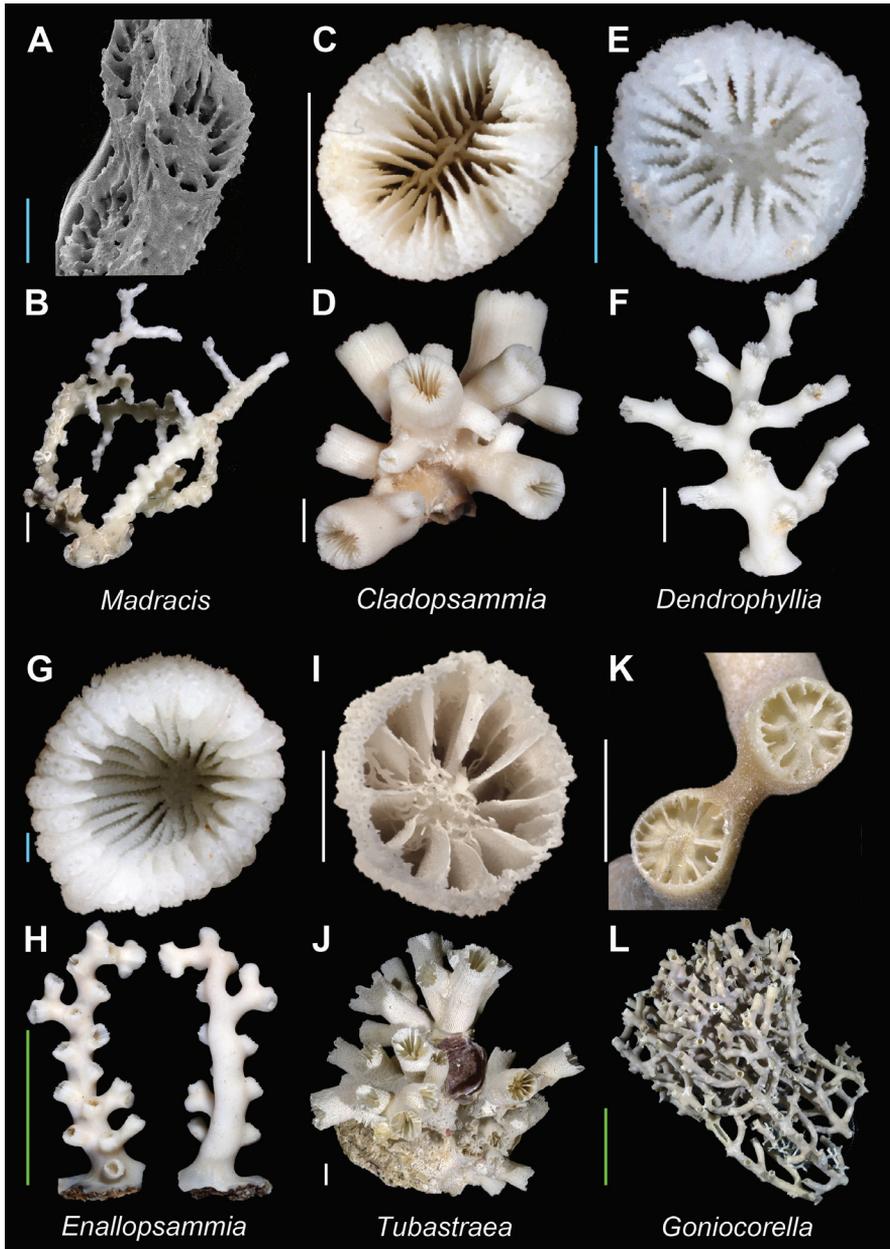
Figure and plates



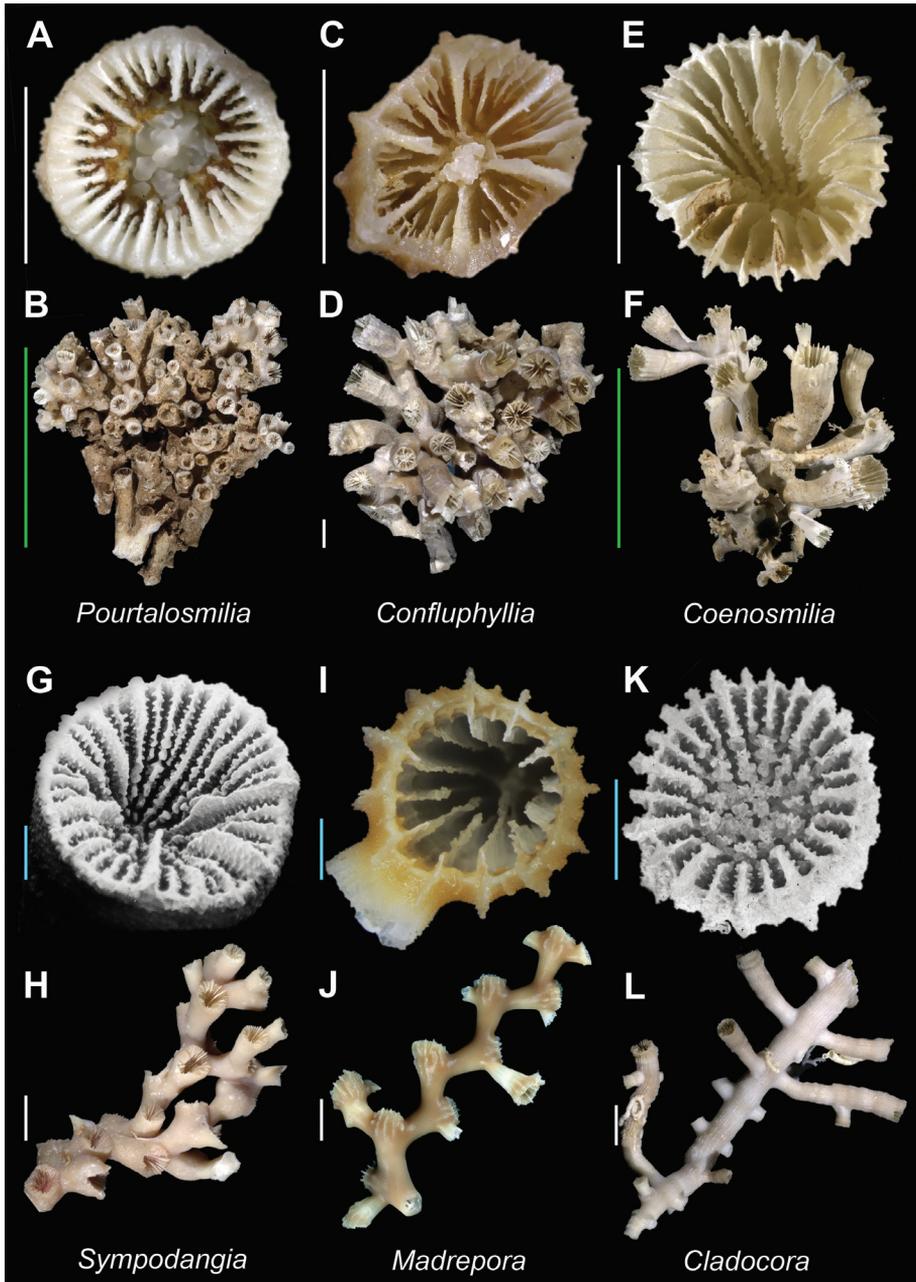
**Figure 1.** Cutaway diagram of a species of *Caryophyllia* illustrating the basic morphological features of an attached, solitary scleractinian (Modified from Cairns 1994). Small circular photos are from different scleractinian species and are intended to illustrate basic morphological characters used in the taxonomy of the group.



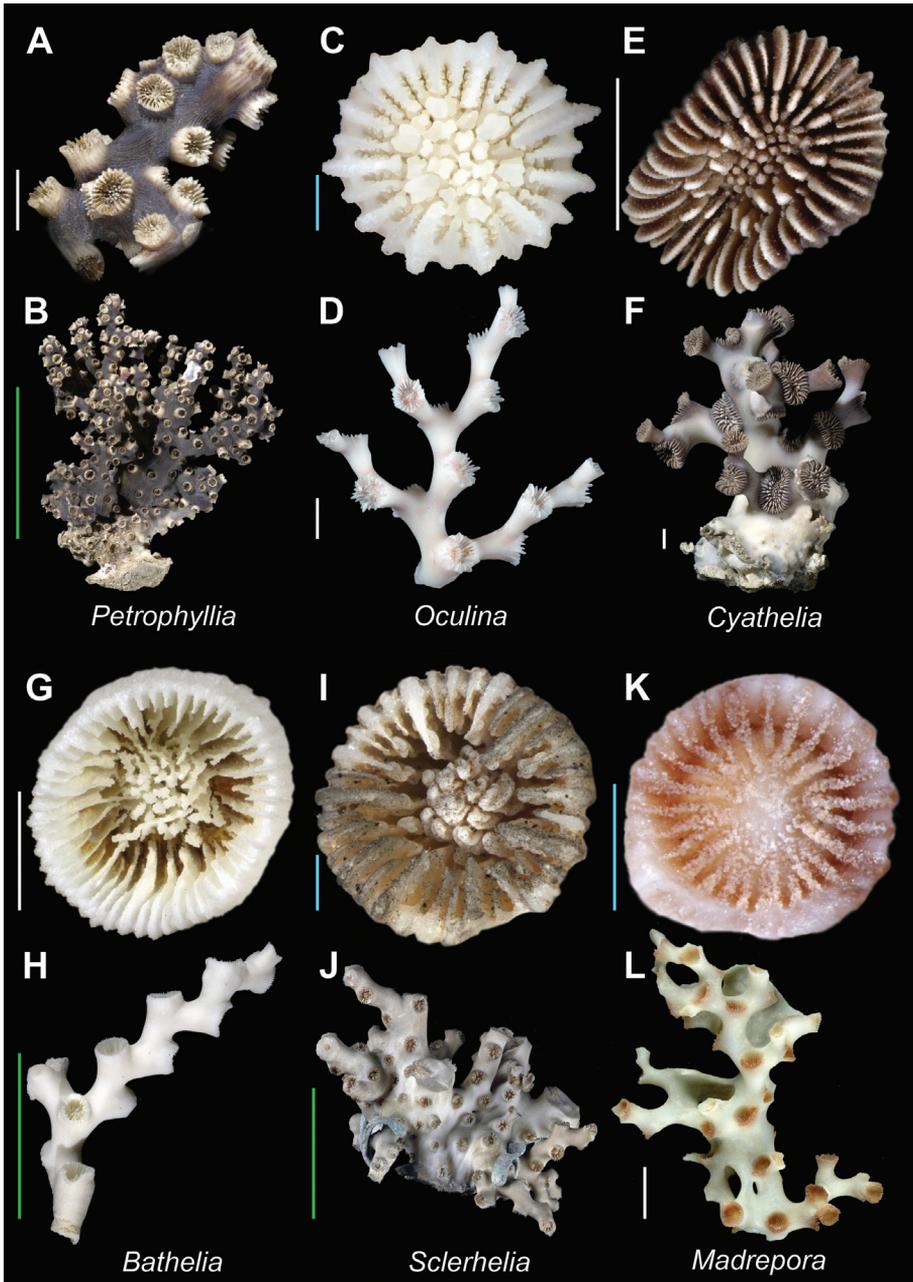
**Plate I.** *Heteropsammia cochlea* **A** (USNM 97652) and **B** (USNM 73772): Calicular and lateral view respectively; *Anomocora gigas* (MNHN uncatologued, Terrasses stn. CP3091) **C** and **D** Calicular and lateral view respectively; *Eguchipsammia fistula* (USNM uncatologued, Norfolk 2 stn. 2024) **E** and **F** Calicular and colony view respectively; ***Lophelia pertusa*** (USNM 1071877) **G** and **H** Calicular and colony view respectively; *Dichopsammia granulosa* (USNM 15847, holotype) **I** and **J** Calicular and colony view respectively; *Solenosmilia variabilis* (USNM 47426) **K** and **L** Distal branch and colony view respectively. Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



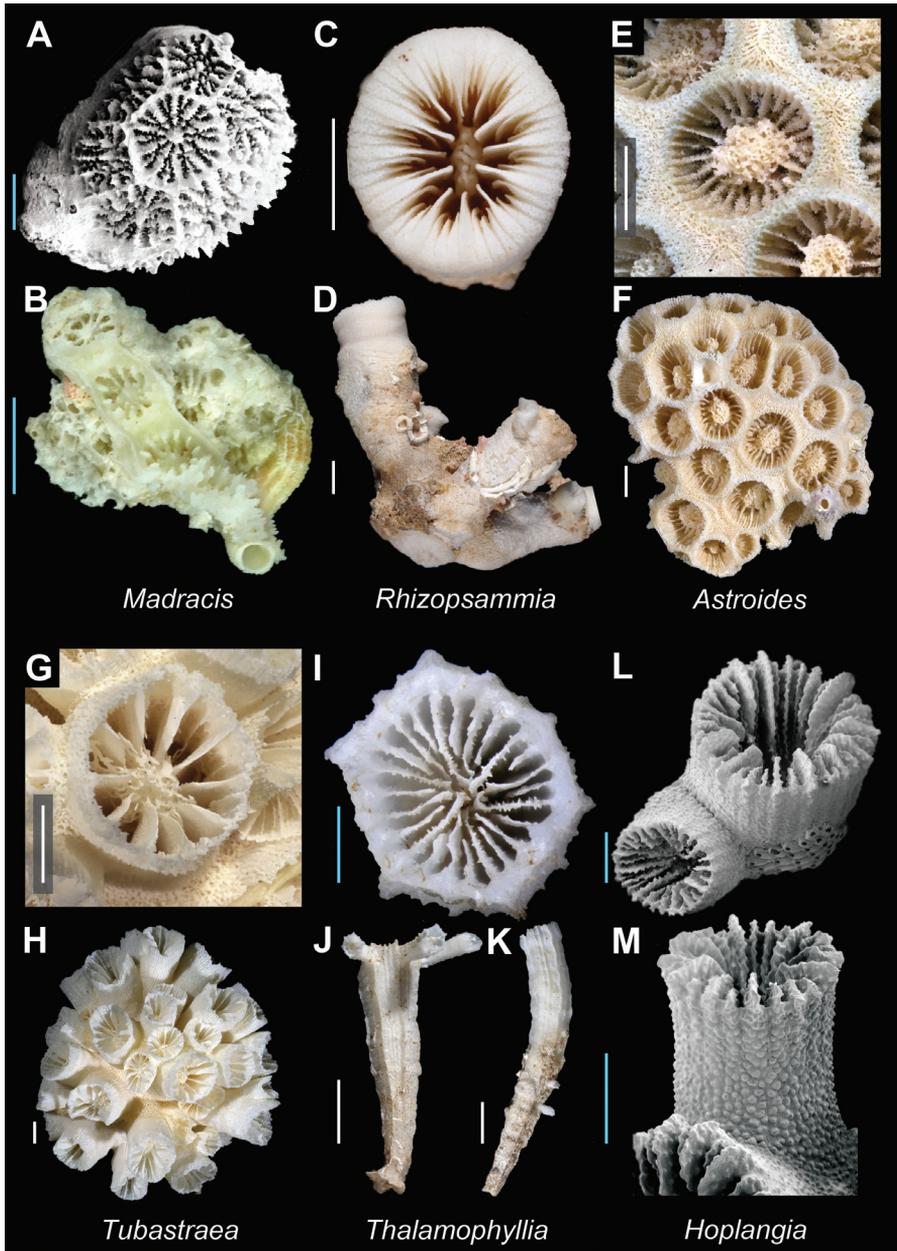
**Plate 2.** *Madracis asperula* **A** (SEM, USNM 99068) and **B** (USNM 99056): Calicular and colony view respectively; *Cladopsammia* sp. (USNM uncatalogued, Norfolk 2 stn. 2023) **C** and **D** Calicular and colony view respectively; *Dendrophyllia alcocki* (USNM uncatalogued, Norfolk 2 stn. 2135) **E** and **F** Calicular and colony view respectively; *Enallopsammia rostrata* (USNM uncatalogued, Norfolk 2 stn. DW 2056) **G** and **H** Calicular and colony (calicular and acalicular side) view respectively; *Tubastraea coccinea* (USNM 46973) **I** Calicular view; *Tubastraea diaphana* (USNM 83677) **J** Colony view; *Goniocorella dumosa* (USNM 47505) **K** and **L** Calicular and colony view respectively. Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



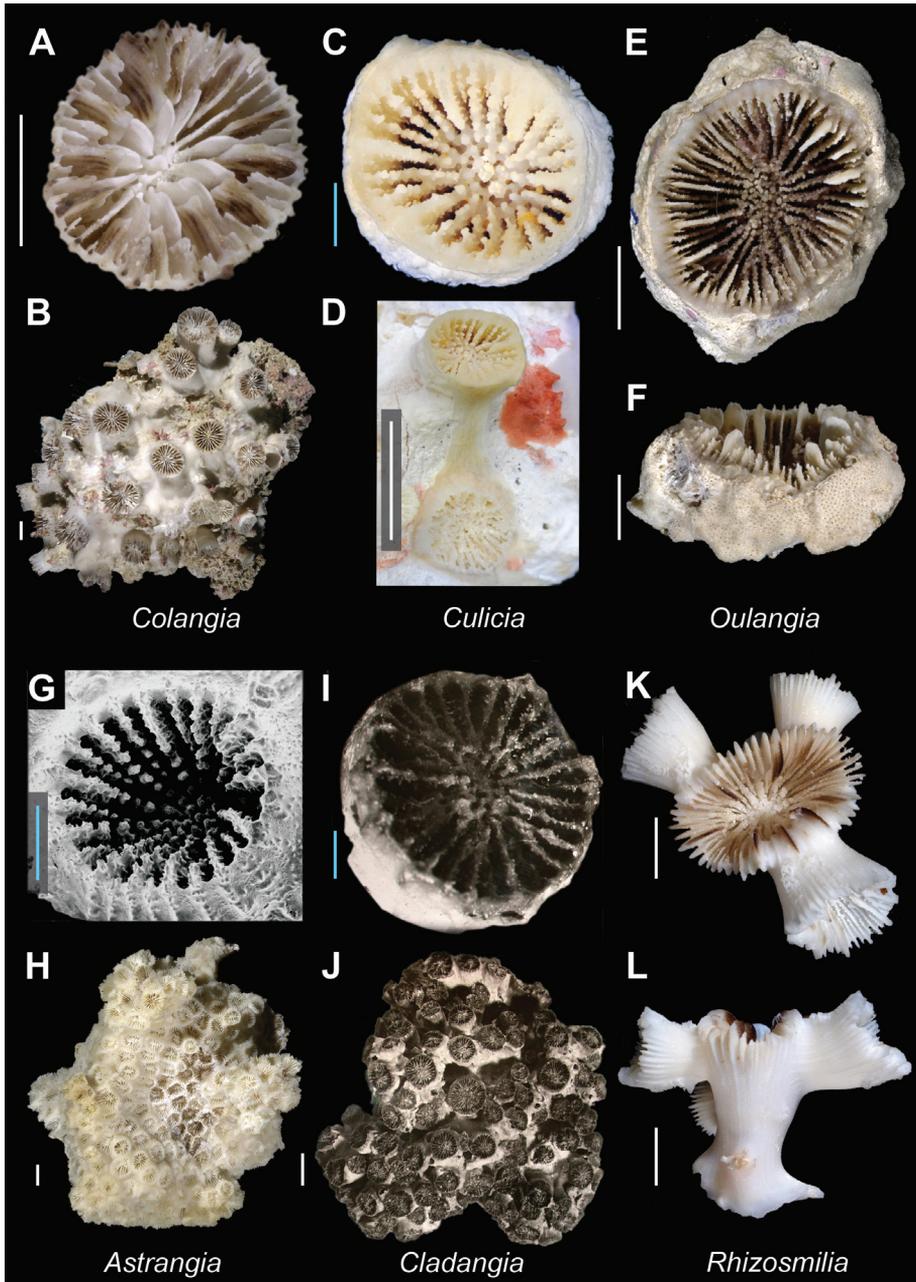
**Plate 3.** *Pourtalesmilia anthophyllites* **A** (USNM 1174947) and **B** (USNM 117494): Calicular and colony view respectively; *Confluphyllia juncta* (USNM 97316, paratype) **C** and **D** Calicular and colony view respectively; *Coenosmilia arbuscula* (USNM 97312) **E** and **F** Calicular and colony view respectively; *Sympodangia albatrossi* (USNM 97308, holotype) **G** (SEM) and **H** Calicular and colony view respectively; *Madrepora oculata* (MNHN uncatologued, Halipro 2 stn. BT104) **I** and **J** Calicular and colony view respectively; *Cladocora debilis* **K** (USNM 10452, SEM) and **L** (USNM 62351): Calicular and colony view respectively. Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



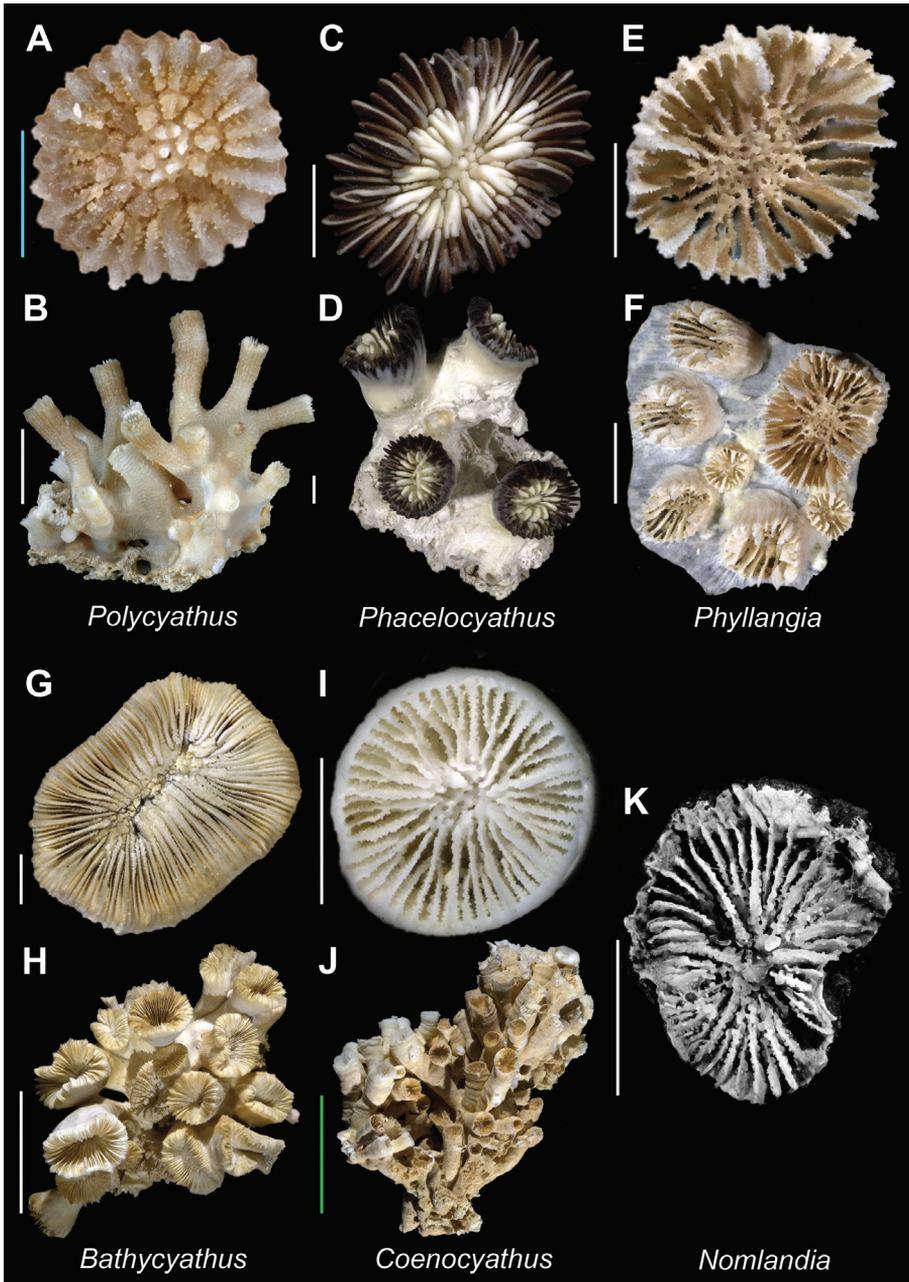
**Plate 4.** *Petrophyllia rediviva* (USNM 82696) **A** and **B** Distal branch and colony view respectively; *Oculina virgosa* (MNHN uncatalogued, SMIB 5 stn. DW101) **C** and **D** Calicular and colony view respectively; *Cyathelia axillaris* (USNM 92665) **E** and **F** Calicular and colony view respectively; **Bathelia candida** (USNM 47512) **G** and **H** Calicular and colony view respectively; *Sclerhelia hirtella* (MNHN Michellin collection) **I** and **J** Calicular and colony view respectively; *Madrepora minutiseptum* (MNHN uncatalogued, SMIB 5 stn. DW101) **K** and **L** Calicular and colony view respectively. Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



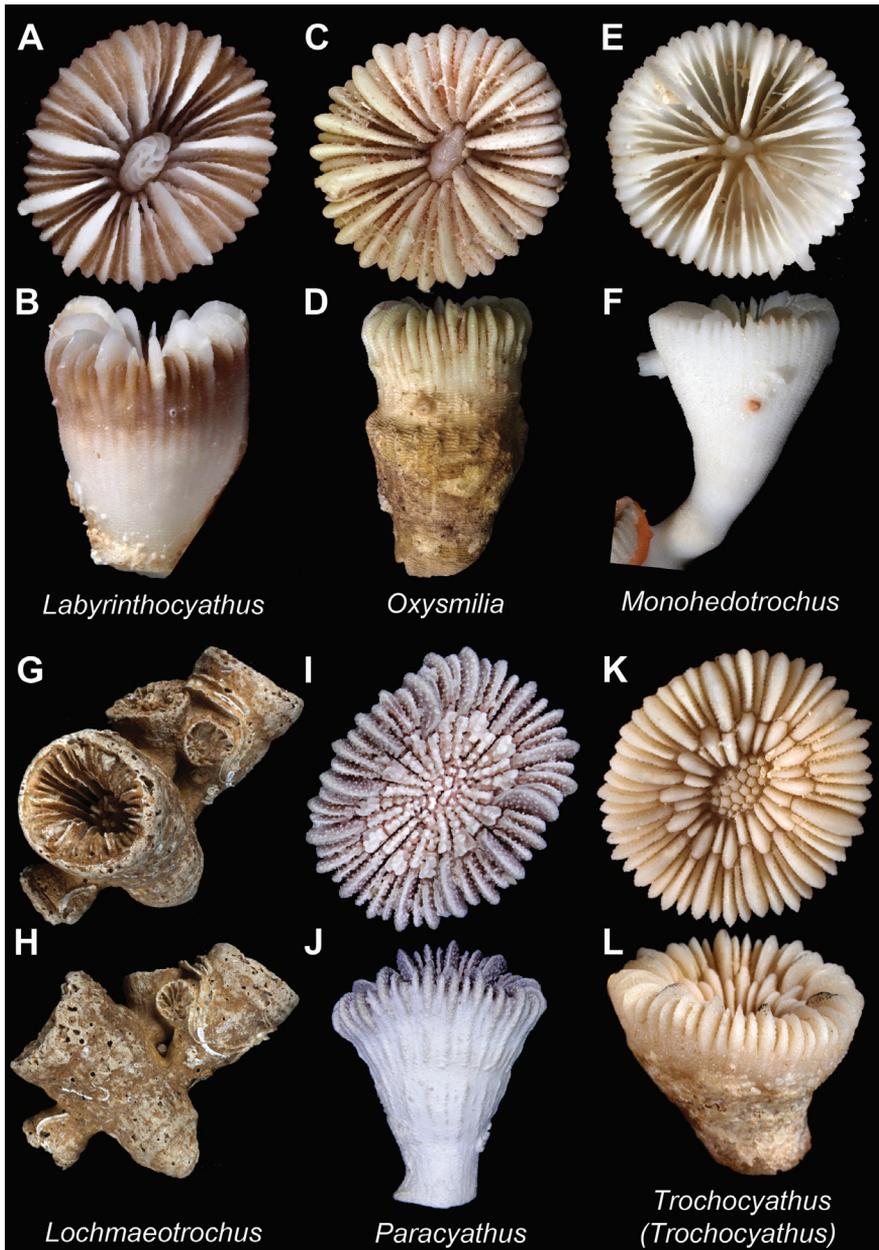
**Plate 5.** *Madracis pharensis* **A** (USNM 96676, SEM): Colony view; *Madracis* sp. **B** (MNHN uncatalogued, New Caledonia): Colony view; *Rhizopsammia* sp. (USNM uncatalogued, Bathus 4 stn. DW 941) **C** and **D** Calicular and colony view respectively; *Astroides calycularis* (USNM 78767) **E** and **F** Calice detail and colony view respectively; *Tubastraea coccinea* (USNM 46973) **G** and **H** Calicular and colony view respectively; *Thalamophyllia tenuescens* **I** (MNHN uncatalogued, Bathus 3 stn. CH802), **J** and **K** (Norfolk 2 stn. 2095): Calicular and corallum views respectively; *Hoplangia durotrix* (AU 6097) **L** (SEM) and **M** (SEM): Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



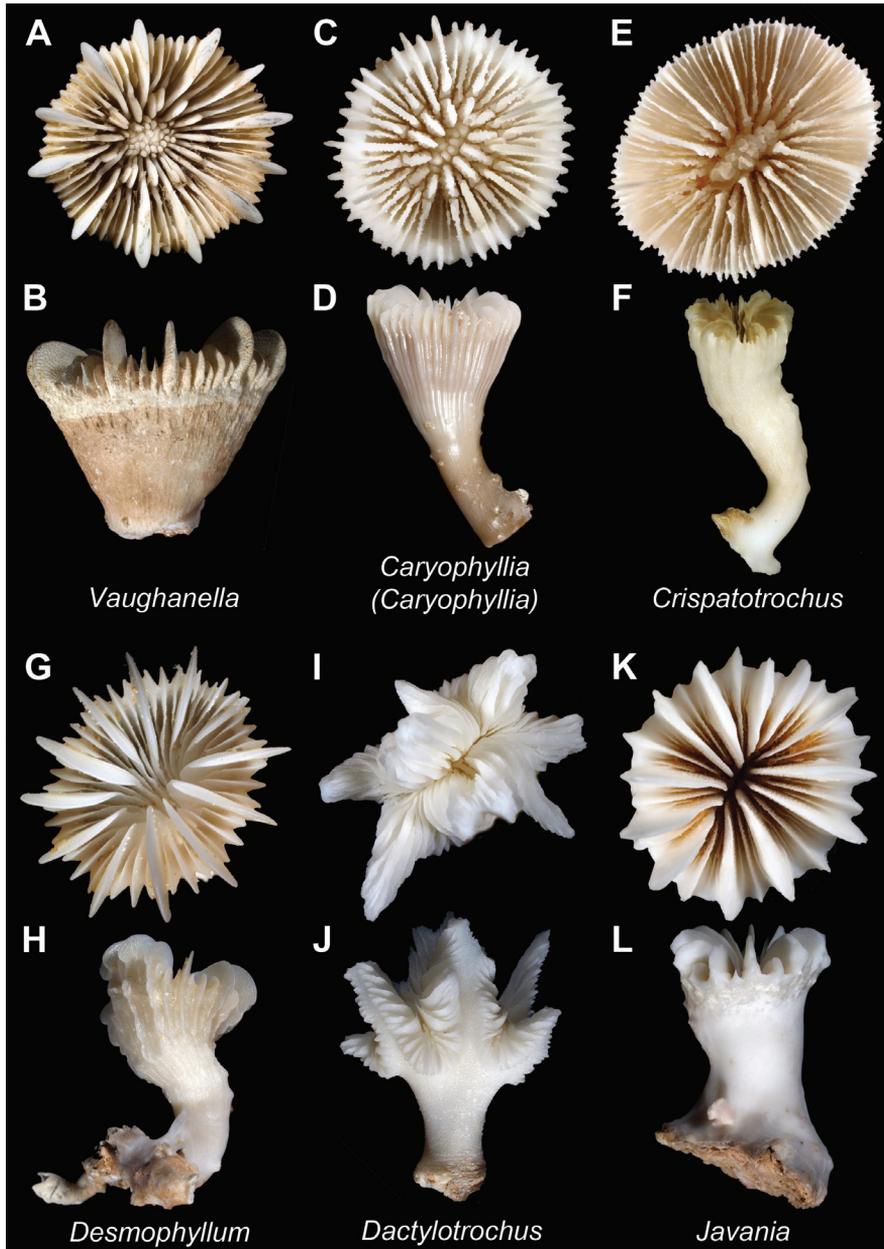
**Plate 6.** *Colangia immersa* (USNM 73917) **A** and **B** Calicular and colony view respectively; *Culicia stellata* (MNHN uncatalogued, New Caledonia) **C** and **D** Calicular and stolon connection view respectively; *Oulangia bradleyi* (USNM 92371) **E** and **F** Calicular and lateral view respectively; *Astrangia danae* (USNM 78507, SEM) **G** Calicular view; *Astrangia poculata* (USNM 80350, neotype) **G** and **H** calicular and colony view respectively; *Cladangia exusta* (YPM 1359, syntype ?) **I** and **J** Calicular and colony view respectively; *Rhizosmilia sagamiensis* (USNM uncatalogued, Norfolk 2 stn. 2124) **K** and **L** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



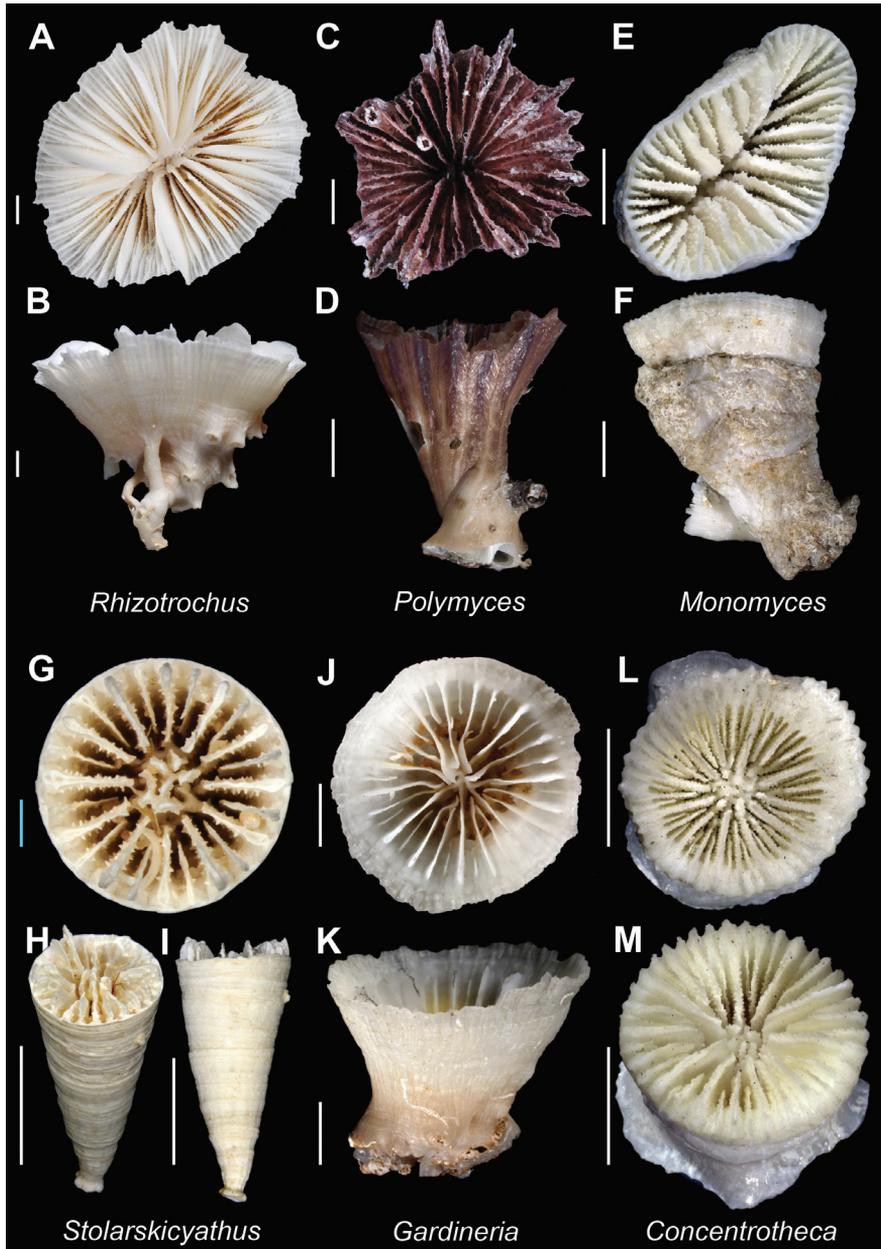
**Plate 7.** *Polycyathus* sp. (MNHN uncatalogued, Beryx 11 stn. DW11) **A** and **B** Calicular and colony view respectively; *Phacelocyathus flos* (USNM 46077) **C** and **D** Calicular and colony view respectively; *Phyllangia americana* (USNM 80881) **E** and **F** Calicular and colony view respectively; *Bathycyathus chilensis* (USNM 100711) **G** and **H** Calicular and colony view respectively; *Coenocyathus anthophyllites* (USNM 48694) **I** and **J** Calicular and colony view respectively; *Nomlandia californica* (SBMNH 35560, holotype) **K** Calicular view (after Cairns 1994). Scale bars: blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



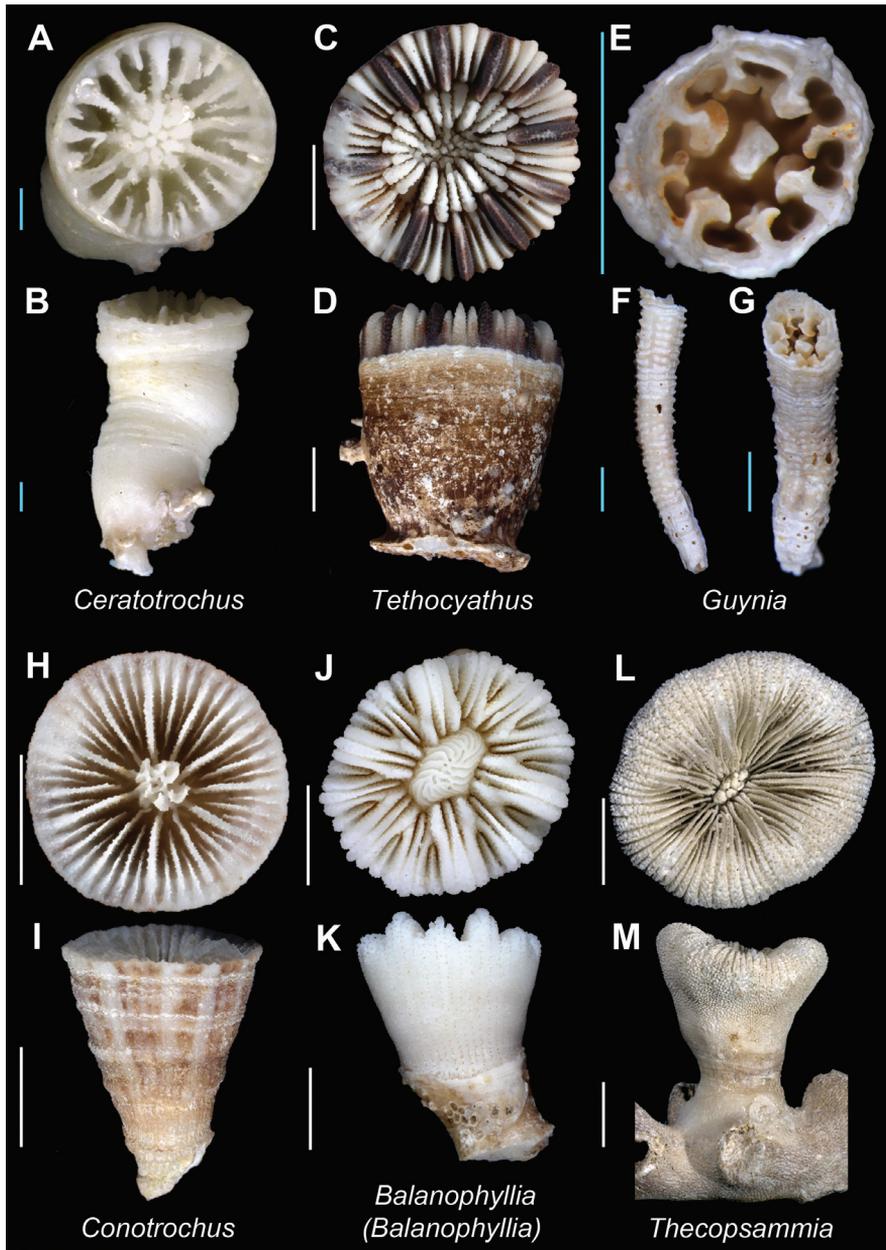
**Plate 8.** *Labyrinthocyathus limatulus* (USNM uncatalogued, Bathus 4 stn. DW 936) **A** and **B** Calicular and lateral view respectively; *Oxysmilia corrugata* (USNM uncatalogued, Norfolk 2 stn. DW2125) **C** and **D** Calicular and lateral view respectively; *Monohedotrochus circularis* (USNM uncatalogued, Norfolk 2 stn. DW2124) **E** and **F** Calicular and lateral view respectively; **Lochmaetrochus oculeus** (USNM uncatalogued, Musorstom 6 stn. DW394) **G** and **H** Calicular and "aggregation" view respectively; *Paracyathus* sp. (MNHN uncatalogued, Ebisco stn. DW2555) **I** and **J** Calicular and lateral view respectively; *Trochocyathus efateensis* (USNM uncatalogued, Bathus 4 stn. DW818) **K** and **L** Calicular and lateral view respectively. Scale bars represent 5 mm. Bold face indicates type species for the genus.



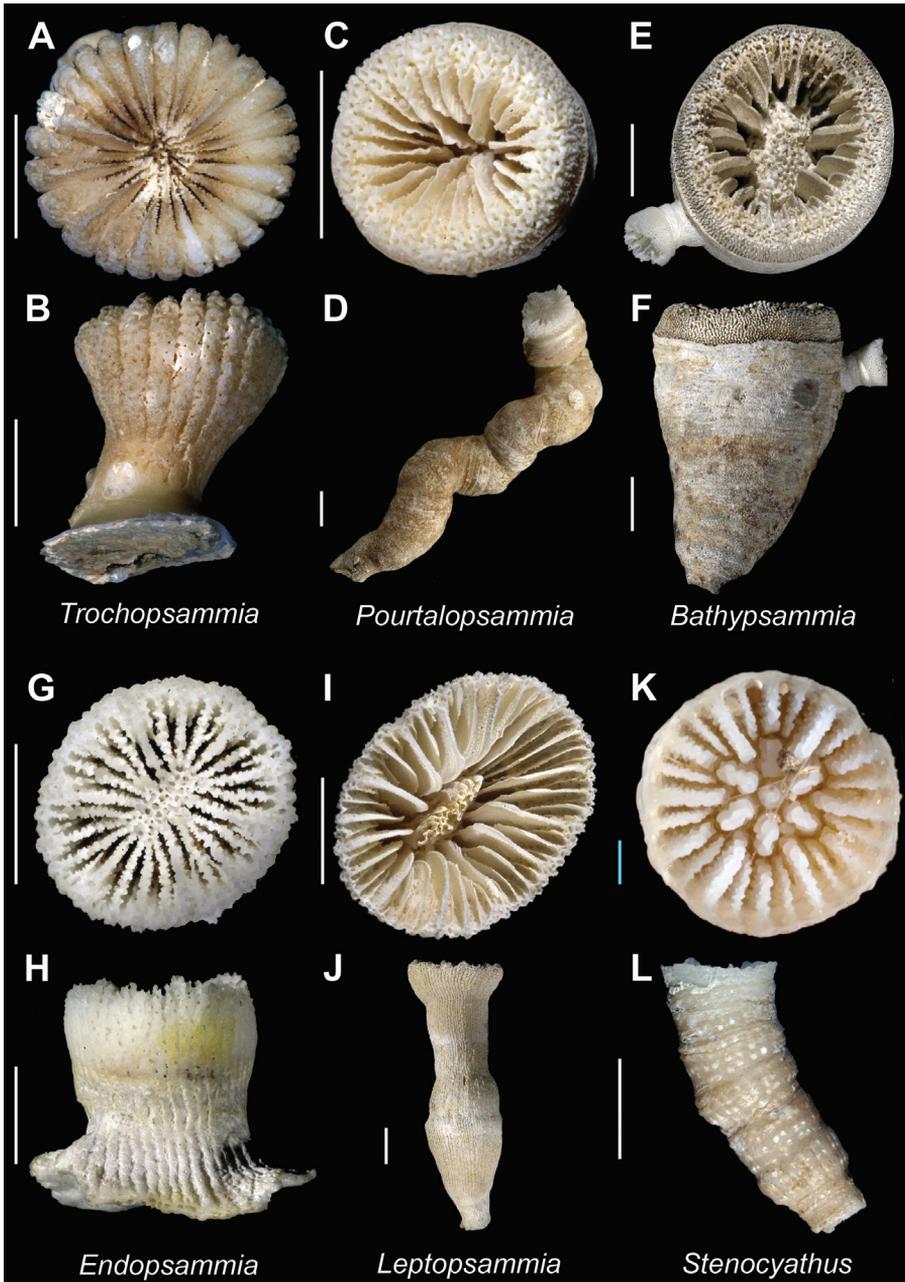
**Plate 9.** *Vaughanella concinna* (USNM uncatalogued, Norfolk 2 stn. DW2070) **A** and **B** Calicular and lateral view respectively; *Caryophyllia (Caryophyllia) diomedae* (USNM uncatalogued, Norfolk 2 stn. DW2086) **C** and **D** Calicular and lateral view respectively; *Crispatotrochus rubescens* (USNM uncatalogued, Bathus 3 stn. CP833) **E** and **F** Calicular and lateral view respectively; **Desmophyllum dianthus** (USNM uncatalogued, Halipro 1 stn. CP877) **G** and **H** Calicular and lateral view respectively; *Dactyloctrochus cervicornis* (USNM uncatalogued, SMIB 10 stn. DW208) **I** and **J** Calicular and lateral view respectively; *Javania insignis* (USNM uncatalogued, Norfolk 2 stn. DW2023) **K** and **L** Calicular and lateral view respectively. Scale bars represent 5 mm. Bold face indicates type species for the genus.



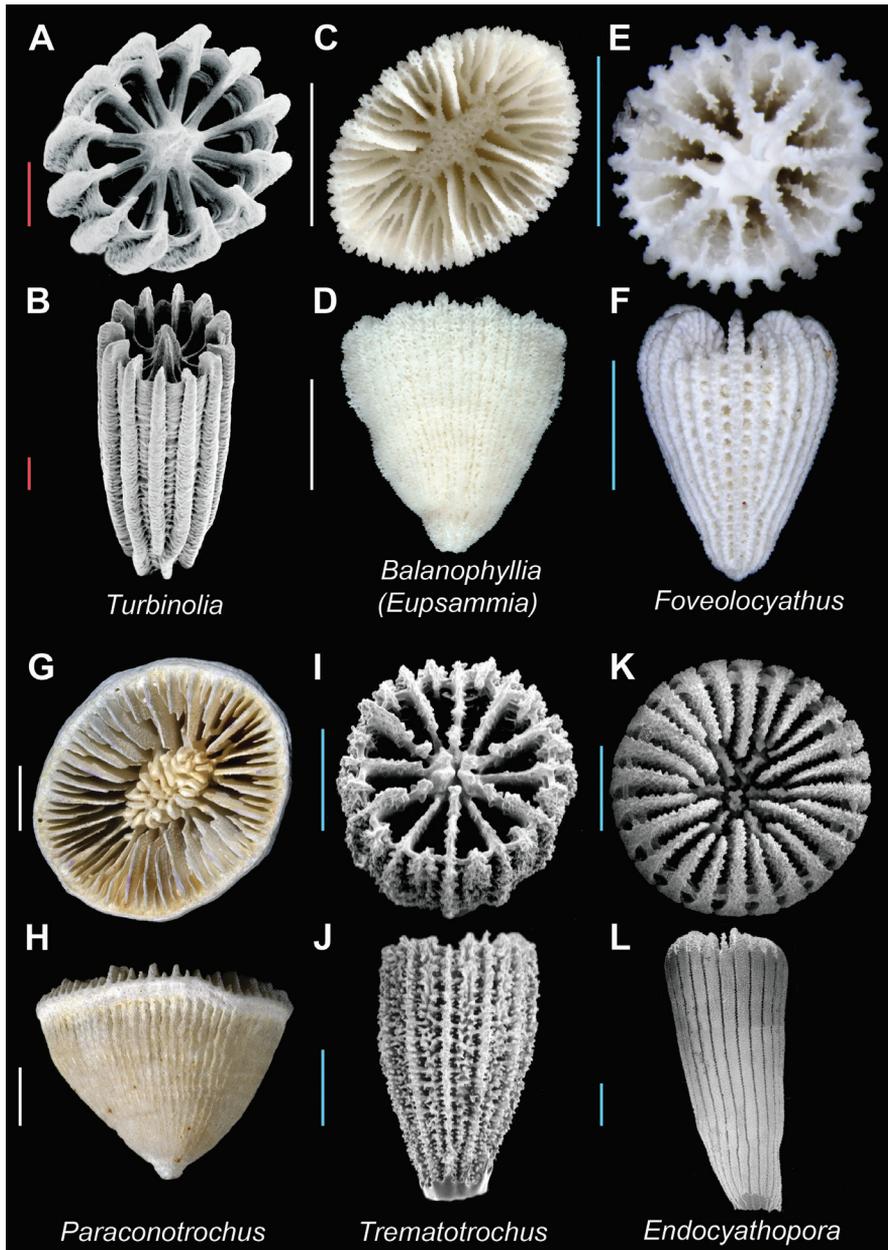
**Plate 10.** *Rhizotrochus typus* (USNM uncatalogued, Norfolk 2 stn. DW2024) **A** and **B** Calicular and lateral view respectively; *Polymyces wellsii* **C** (MNHN uncatalogued, Ebisco stn. DW2618) and **D** (MNHN uncatalogued, New Caledonia): Calicular and lateral view respectively; *Monomyces pygmaea* (USNM 48561) **E** and **F** Calicular and lateral view respectively; *Stolarskicyathus pocilliformis* (MNHN uncatalogued, Ebisco stn. DW2573) **G**, **H**, and **I** Calicular, oblique, and lateral view respectively; *Gardineria hawaiiensis* (USNM uncatalogued, Norfolk 2 stn. DW2086) **J** and **K** Calicular and lateral view respectively; *Concentrotheca laevigata* (USNM 80748) **L** and **M** Calicular and oblique view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



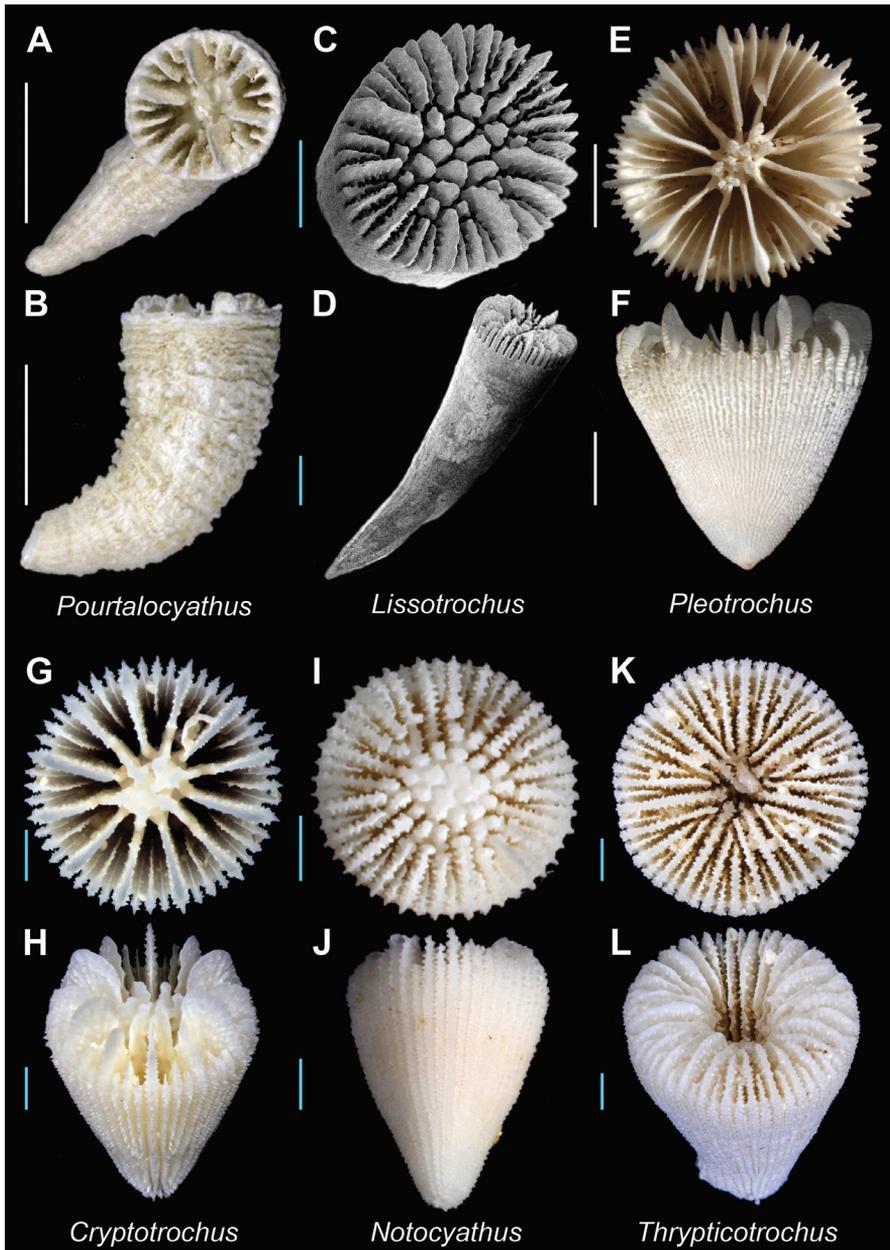
**Plate II.** *Ceratotrochus magnaghii* (USNM 48780) **A** and **B** Calicular and lateral view respectively; *Tethocyathus virgatus* (USNM uncatalogued, SMIB 10 stn. DW205) **C** and **D** Calicular and lateral view respectively; *Guynia annulata* (MNHN uncatalogued, Biogeocal stn. DW253) **E**, **F** and **G** Calicular, lateral, and oblique view respectively; *Conotrochus funicolumna* (USNM uncatalogued, Bathus 4 stn. CP967) **H** and **I** Calicular and lateral view respectively; *Balanophyllia (Balanophyllia) laysanensis* (MNHN uncatalogued, Musorstom 6 stn. DW407) **J** and **K** Calicular and lateral view respectively; *Thecopsammia socialis* (USNM 61828) **L** and **M** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



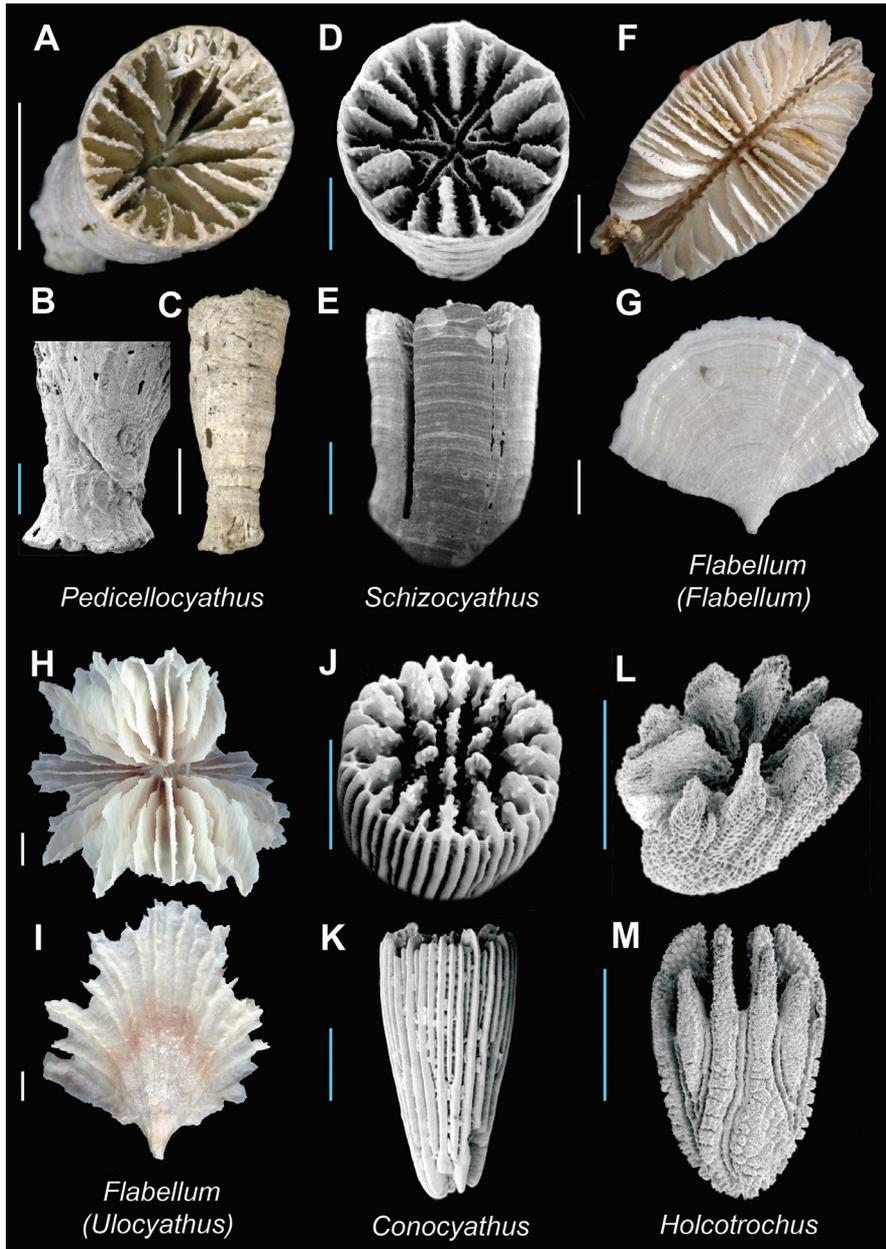
**Plate 12.** *Trochopsammia infundibulum* (USNM 46722) **A** and **B** Calicular and lateral view respectively; *Portalopsammia togata* (USNM 91792) **C** and **D** Calicular and lateral view respectively; *Bathypsammia tintinnabulum* (USNM 14569) **E** and **F** Calicular and lateral view respectively; *Endopsammia philippensis* (USNM 83006) **G** and **H** Calicular and lateral view respectively; *Leptopsammia stokesiana* (USNM 78603) **I** and **J** Calicular and lateral view respectively; *Stenocyathus verniformis* (USNM uncatalogued, Norfolk 2 stn. ?) **K** and **L** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



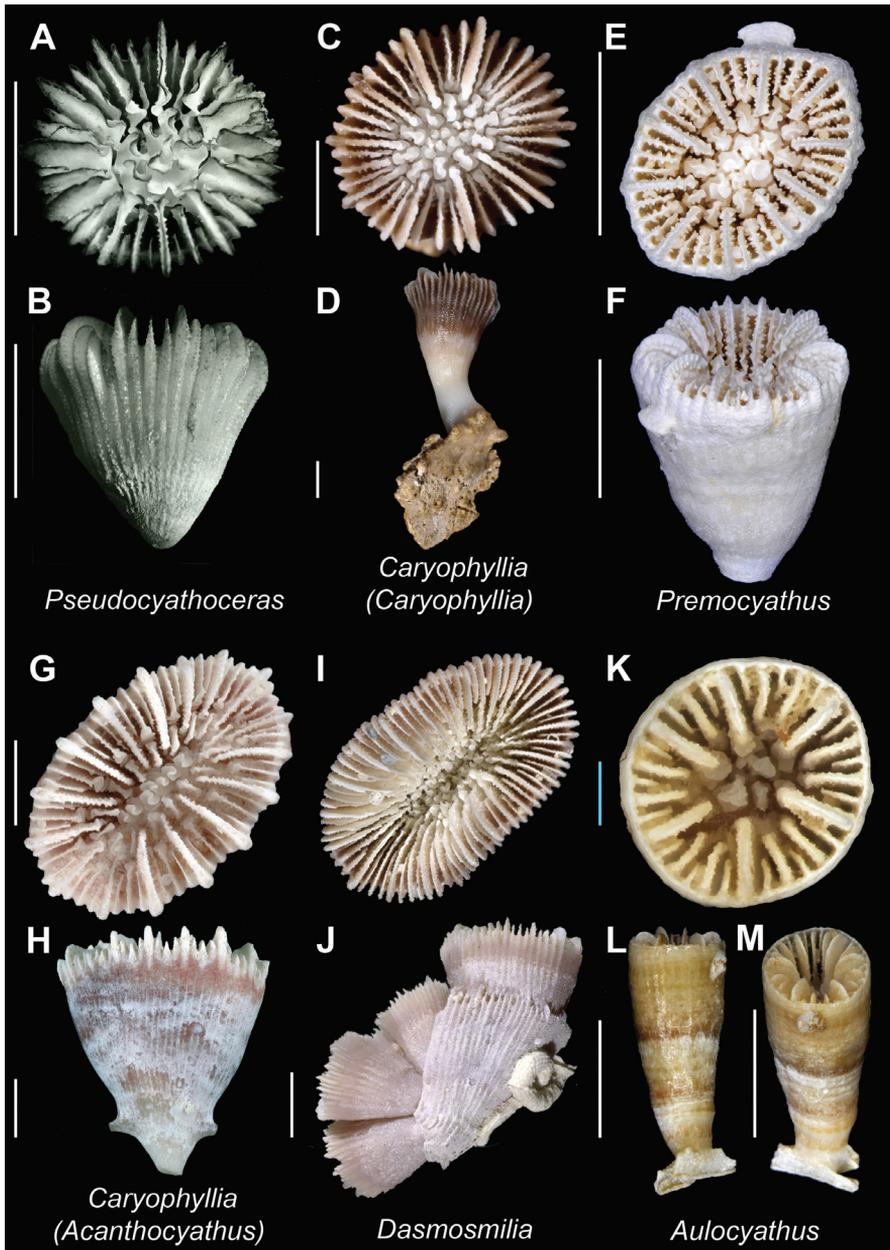
**Plate 13.** *Turbinolia stephensoni* (USNM 80014) **A** (SEM) and **B** (SEM): Calicular and oblique view respectively; *Balanophyllia (Eupsammia) carinata* (MNHN uncatologued, Chalcal stn. D22) **C** and **D** Calicular and lateral view respectively; *Foveocyathus parkeri* (MNHN uncatologued, Musorstom 5 stn. 280) **E** and **F** Calicular and lateral view respectively; *Paraconotrochus zeidlerii* (USNM 85677, paratype) **G** and **H** Calicular and lateral view respectively; *Trematotrochus corbicula* (USNM 46477) **I** (SEM) and **J** (SEM): Calicular and lateral view respectively; *Endocyathopora laticostata* (USNM 81894) **K** (SEM) and **L** (SEM): Calicular and lateral view respectively. Scale bars: red = 0.25 mm; blue = 1 mm; white = 5 mm; green = 50 mm. Bold face indicates type species for the genus.



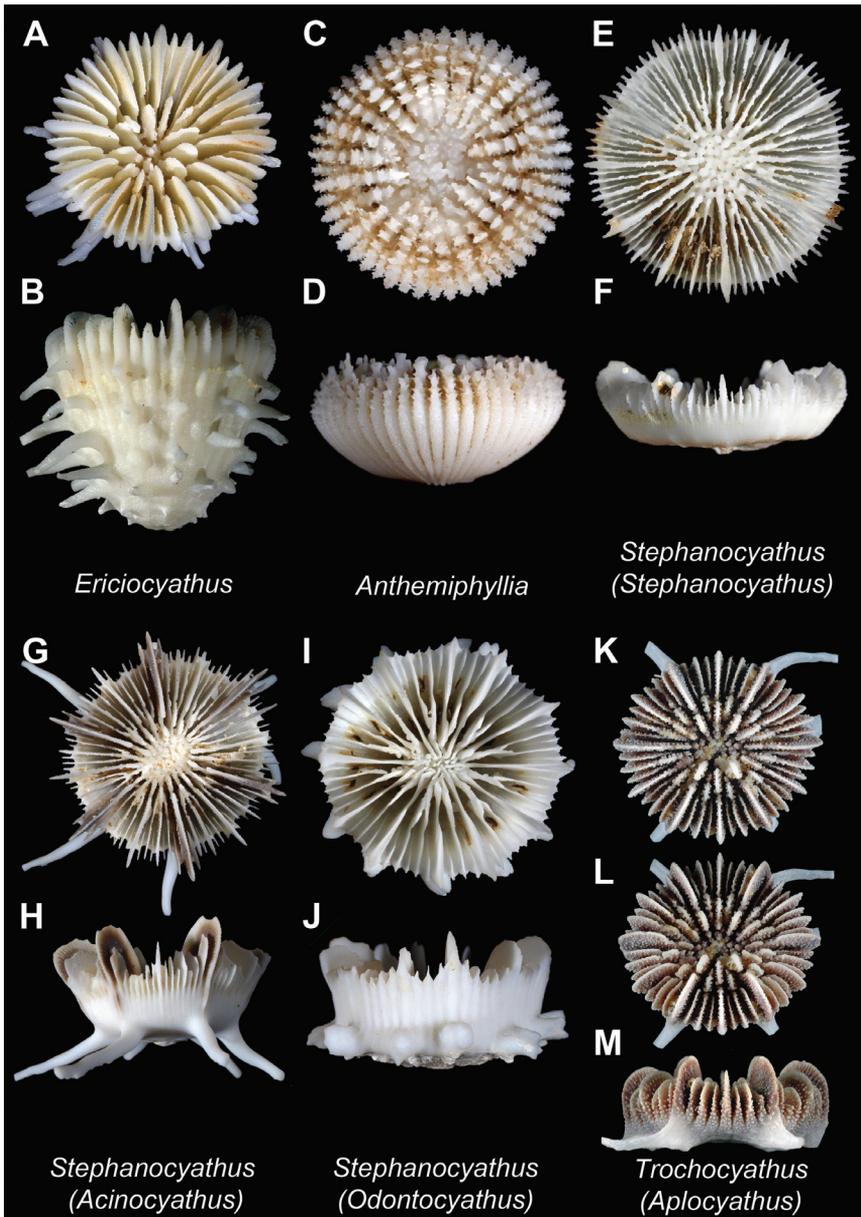
**Plate 14.** *Portalocyathus hispidus* (USNM 61928) **A** and **B** Calicular and lateral view respectively; *Lissotrochus curvatus* (AM G16745) **C** (SEM) and **D** (SEM): Calicular and oblique view respectively; *Pleotrochus venustus* (USNM uncatalogued, Norfolk 2 stn. DW 2104) **E** and **F** Calicular and lateral view respectively; *Cryptotrochus* sp. (MNHN uncatalogued, Ebisco stn. DW2603) **G** and **H** Calicular and oblique view respectively; *Notocyathus venustus* (USNM uncatalogued, Bathus 4 stn. DW 958) **I** and **J** Calicular and lateral view respectively; *Thrypticotrochus petterdi* (MNHN uncatalogued, Ebisco stn. DW2561) **K** and **L** Calicular and oblique view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



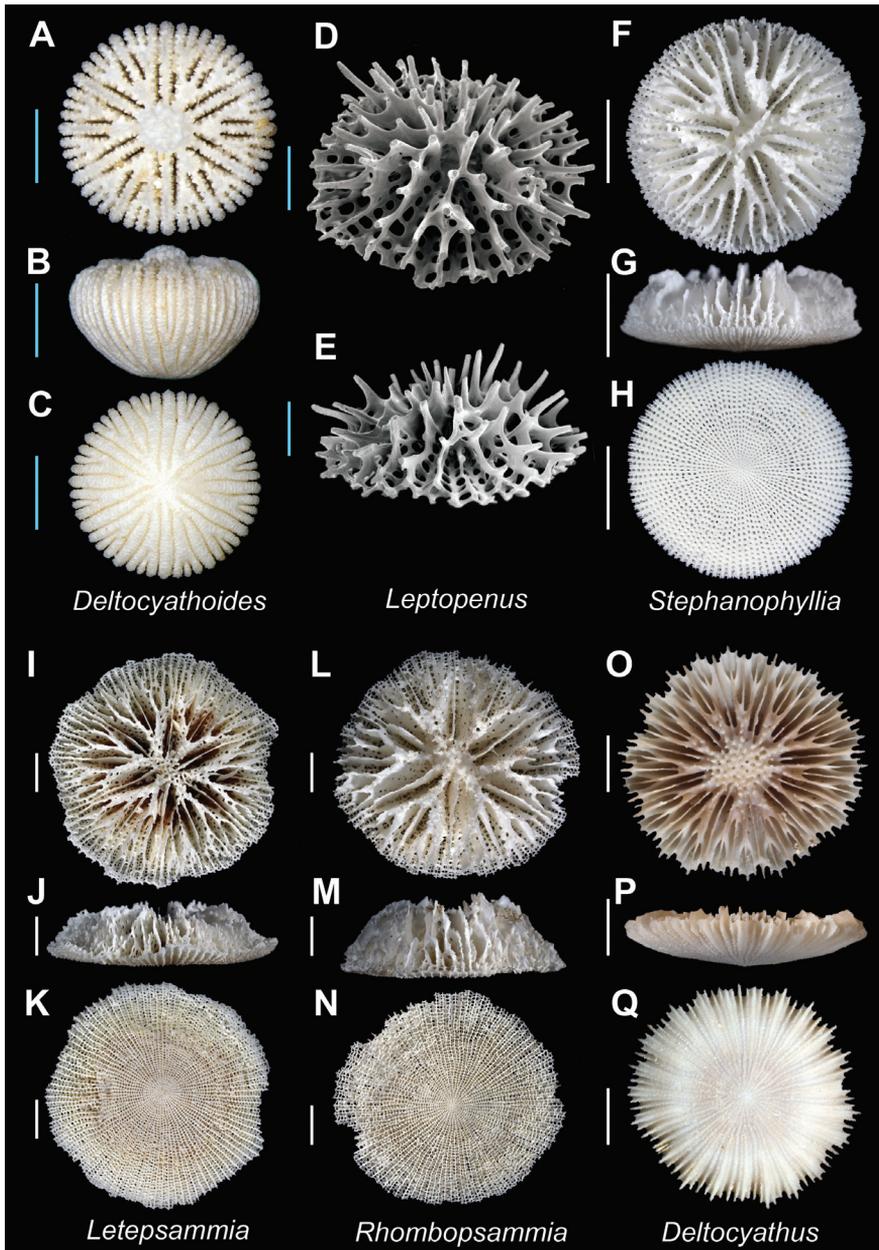
**Plate 15.** *Pedicellocyathus keyesi* (USNM 94268, paratype) **A**, **B** (SEM), and **C** Calicular, pedicel detail, and lateral view respectively; *Schizocyathus fissilis* (USNM 61747) **D** (SEM) and **E** (SEM): Calicular and lateral view respectively; *Flabellum (Flabellum) politum* (USNM uncatalogued, Bathus 4 stn. DW933) **F** and **G** Calicular and lateral view respectively; *Flabellum (Ulocyathus) messum* (MNHN uncatalogued, Bathus 1 stn. DW661) **H** and **I** Calicular and lateral view respectively; *Conocyathus zelandiae* (USNM 85713) **J** (SEM) and **K** (SEM): Oblique and lateral view respectively; *Holcotrochus scriptus* (USNM 85687) **L** (SEM) and **M** (SEM): Oblique and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



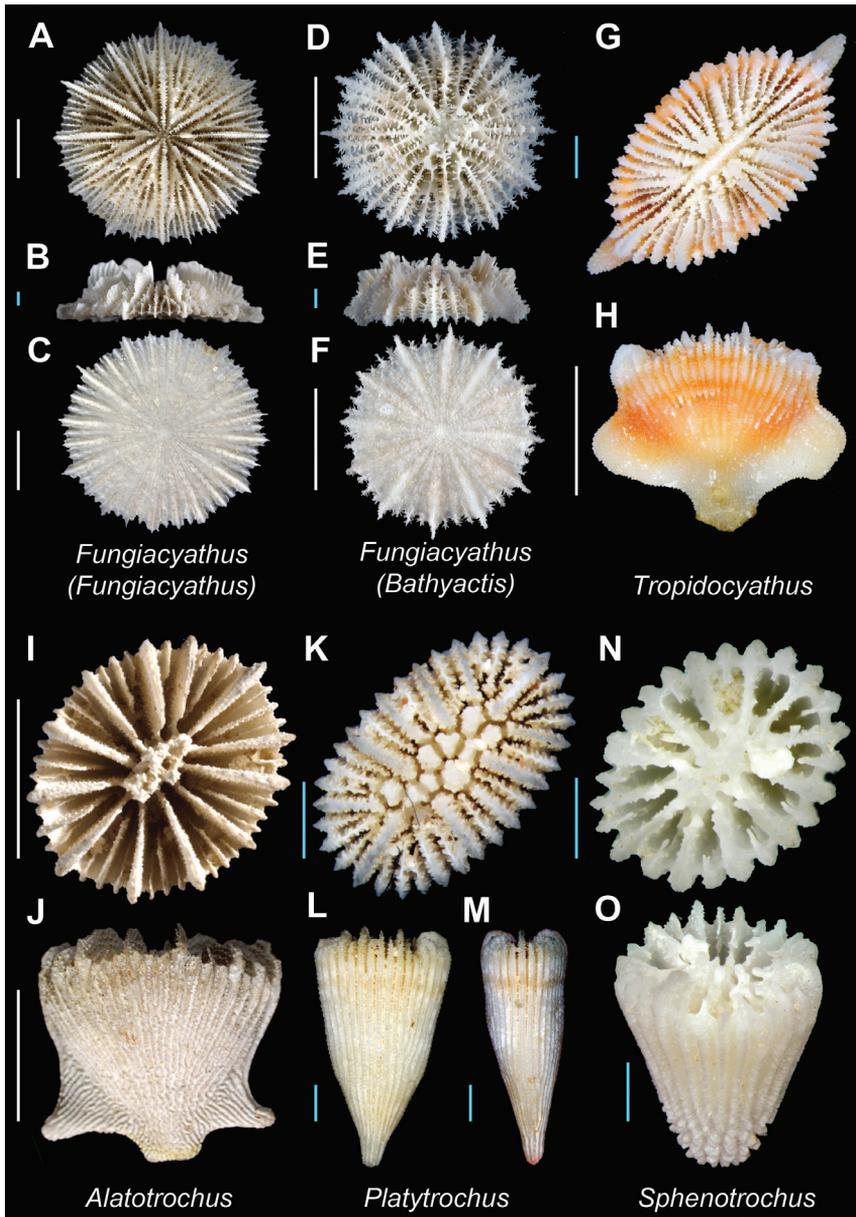
**Plate 16.** *Pseudocyathoceras avis* (USNM 46962, holotype) **A** and **B** Calicular and lateral view respectively; *Caryophyllia* (*Caryophyllia*) *quadragenaria* (USNM uncatologued, PrFO, New Caledonia) **C** and **D** Calicular and oblique view respectively; *Premocyathus dentiformis* (MNHN uncatologued, Ebisco stn. DW2573) **E** and **F** Calicular and oblique view respectively; *Caryophyllia* (*Acanthocyathus*) *grayi* (MNHN uncatologued, Ebisco stn. DW2559) **G** and **H** Calicular and lateral view respectively; *Dasmosmilia lymani* (USNM 82997) **I** and **J** Calicular and lateral (aggregation) view respectively; *Aulocyathus juvenescens* (MNHN uncatologued, Lifou 2000 stn. DW37) **K**, **L**, and **M** Calicular, lateral, and oblique view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



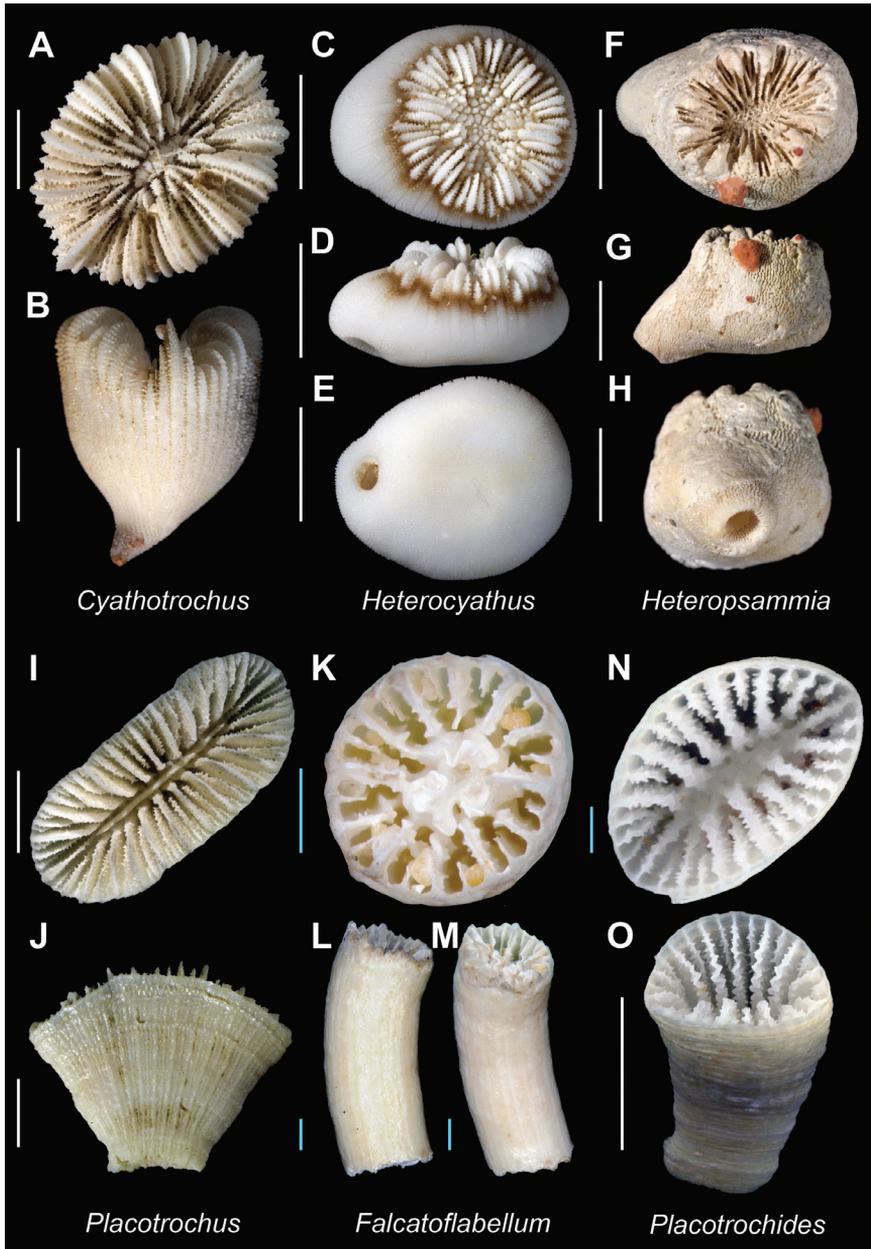
**Plate 17.** *Eriocyathus echinatus* (USNM 97169, holotype) **A** and **B** Calicular and lateral view respectively; *Anthemiphyllia patera costata* (USNM uncatalogued, Norfolk 2 stn. 2066) **C** and **D** Calicular and lateral view respectively; *Stephanocyathus* (*Stephanocyathus*) *regius* (USNM uncatalogued, Bathus 3 stn. 858) **E** and **F** Calicular and lateral view respectively; *Stephanocyathus* (*Acinocyathus*) *spiniger* (USNM uncatalogued, Bathus 3 stn. CP877) **G** and **H** Calicular and lateral view respectively; *Stephanocyathus* (*Odontocyathus*) *coronatus* (USNM uncatalogued, Bathus 4 stn. CP950) **I** and **J** Calicular and lateral view respectively; *Trochocyathus* (*Aplocyathus*) *brevispina* (MNHN uncatalogued, Musorstom 8 stn. DW960) **K**, **L**, and **M** Calicular, oblique, and lateral view respectively. Scale bars represent 5 mm. Bold face indicates type species for the genus.



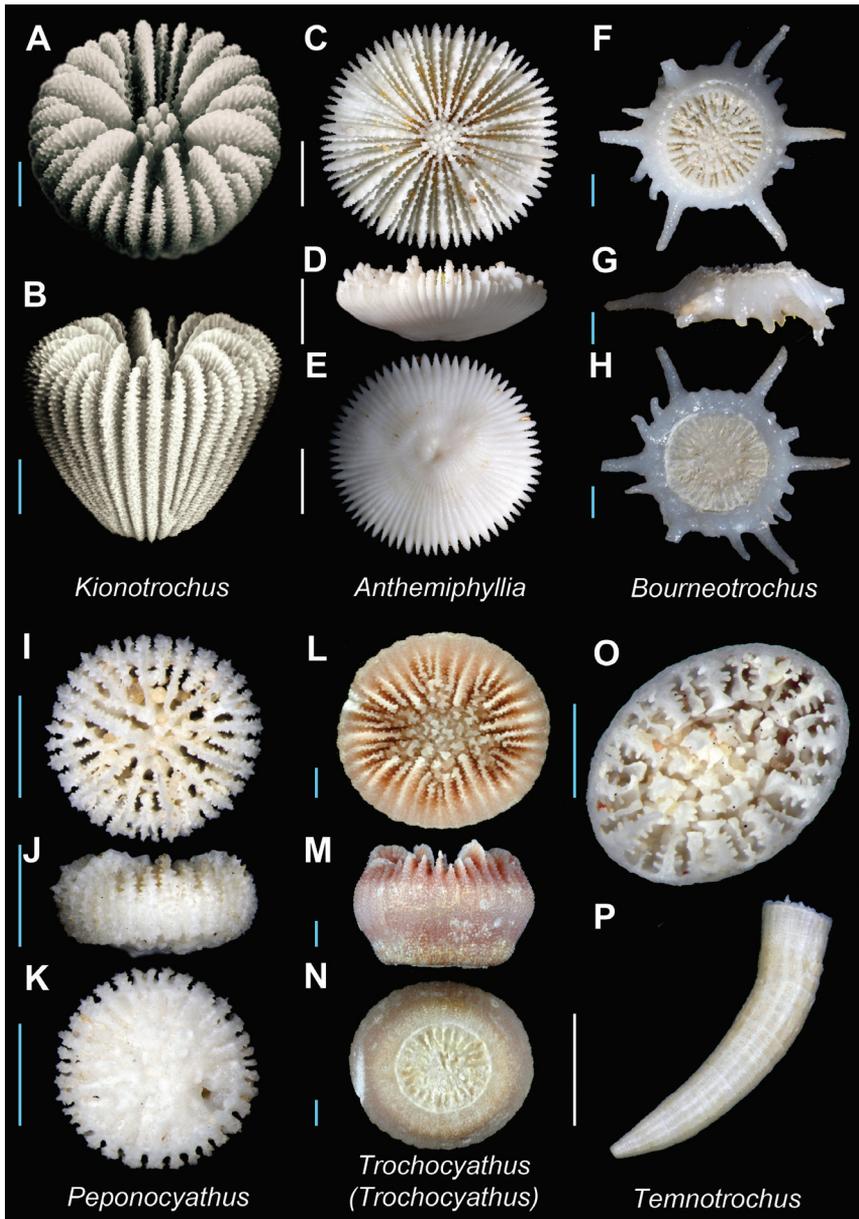
**Plate 18.** *Deltocyathoides orientalis* (MNHN uncatalogued, Bathus 3 stn. DW829) **A**, **B** and **C** Calicular, lateral, and base view respectively; *Leptopenus discus* (SIO Co-1271) **D** (SEM) and **E** (SEM): Oblique views respectively; *Stephanophyllia complicata* (USNM uncatalogued, New Caledonia) **F**, **G**, and **H** Calicular, lateral, and base view respectively; *Letepsammia formosissima* (USNM uncatalogued, Norfolk 2 stn. DW2032) **I**, **J**, and **K** Calicular, lateral, and base view respectively; *Rhombopsammia niphada* (USNM uncatalogued, Norfolk 2 stn. DW2069) **L**, **M**, and **N** Calicular, lateral, and base view respectively; *Deltocyathus rotulus* (MNHN-Sci.2008-0004) **O**, **P**, and **Q** Calicular, lateral, and base view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



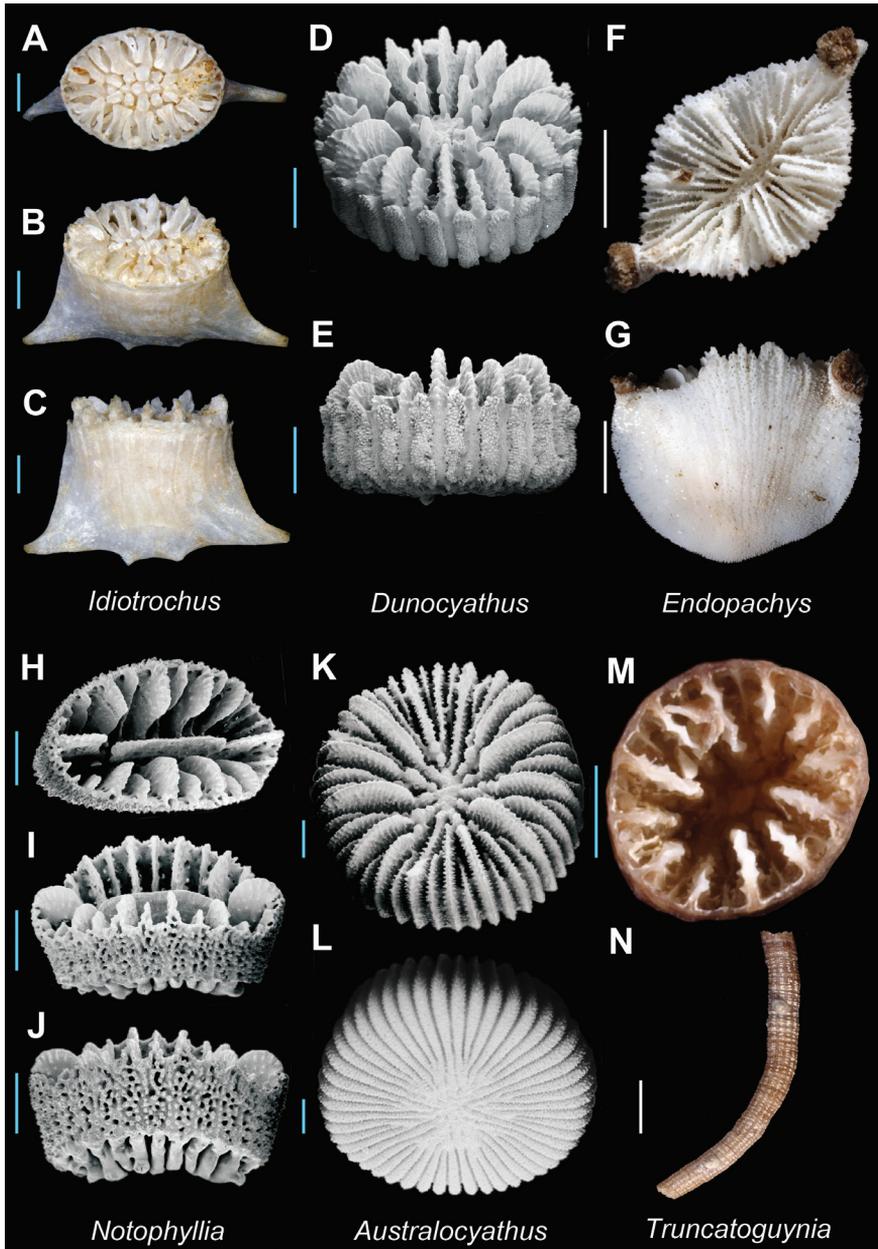
**Plate 19.** *Fungiacyathus* (*Fungiacyathus*) *paliferus* (USNM uncatalogued, Bathus 3 stn. DW 887) **A**, **B** and **C** Calicular, lateral, and base view respectively; *Fungiacyathus* (*Bathyactis*) *variegatus* (MNHN uncatalogued, Lagoon NO stn. DC933) **D**, **E**, and **F** Calicular, lateral, and base view respectively; *Tropidocyathus* *lessoni* (MNHN uncatalogued, Musorstom 8 stn. DW1105) **G** and **H** Calicular and lateral view respectively; *Alatotrochus* *rubescens* (USNM uncatalogued, Bathus 4 stn. DW 908) **I** and **J** Calicular and lateral view respectively; *Platytrochus* *hastatus* (MNHN uncatalogued, Ebisco stn. DW2559) **K**, **L**, and **M** Calicular and lateral (GCD and LCD) views respectively; *Sphenotrochus* *hancocki* (MNHN uncatalogued, Ebisco stn. DW2617) **N** and **O** Calicular and oblique view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



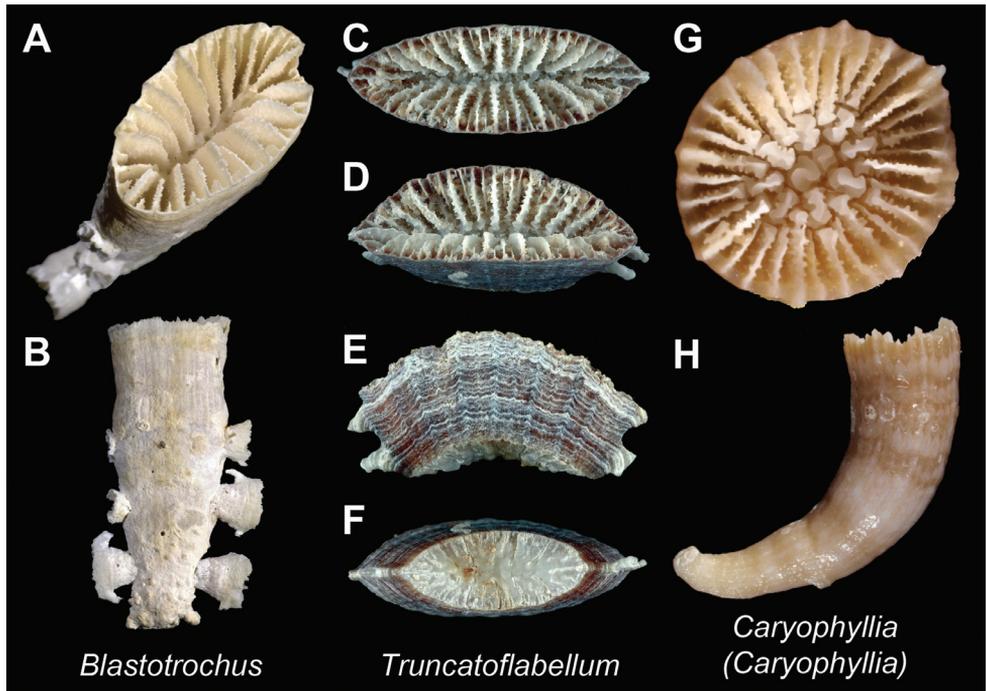
**Plate 20.** *Cyathotrochus pileus* (USNM uncatalogued, Bathus 3 stn. CP833) **A** and **B** Calicular and lateral view respectively; *Heterocyathus aequicostatus* (USNM uncatalogued, Bathus 4 stn. DW933) **C**, **D**, and **E** Calicular, lateral, and base view respectively; *Heteropsammia cochlea* (USNM uncatalogued, Bathus 3 stn. DW894) **F**, **G**, and **H** Calicular, lateral, and base view respectively; *Placotrochus laevis* (USNM 81989) **I** and **J** Calicular and lateral view respectively; *Falcatoflabellum raoulensis* (MNHN uncatalogued, Ebisco stn. DW2603) **K**, **L**, and **M** Calicular, lateral, and oblique view respectively; *Placotrochides scaphula* (MNHN uncatalogued, Chalcal stn. DW75) **N** and **O** Calicular and oblique view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



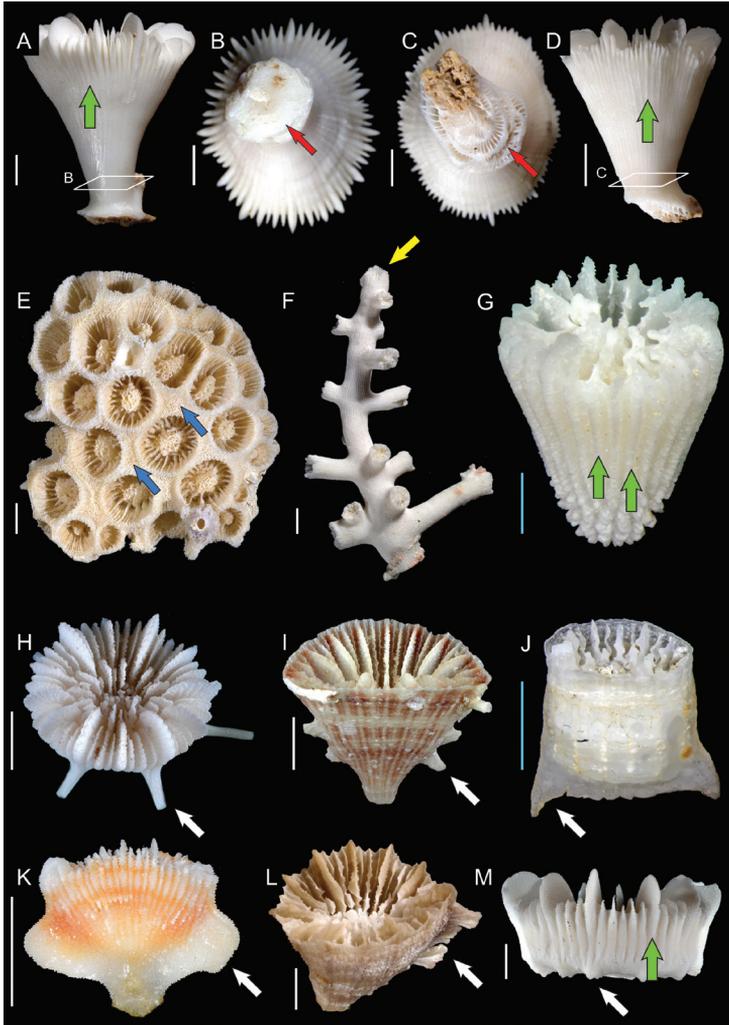
**Plate 21.** *Kionotrochus suteri* (NZOI F915) **A** (SEM) and **B** (SEM): Calicular and lateral view respectively; *Anthemiphyllia dentata* (USNM uncatalogued, Bathus 4 stn. DW914) **C**, **D**, and **E** Calicular, lateral, and base view respectively; *Bourneotrochus stellulatus* (USNM uncatalogued, Bathus 3 stn. DW877) **F**, **G**, and **H** Calicular, lateral, and base view respectively; *Peponocyathus folliculus* (MNHN uncatalogued, Norfolk 1 stn. DW1697) **I**, **J**, and **K** Calicular, lateral, and base view respectively; *Trochocyathus* (*Trochocyathus*) *discus* (MNHN uncatalogued, Biocal stn. DW46) **L**, **M**, and **N** Calicular, lateral, and base view respectively; *Temnotrochus kermadecensis* (MNHN uncatalogued, Musorstom 5 stn. DW328) **O** and **P** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



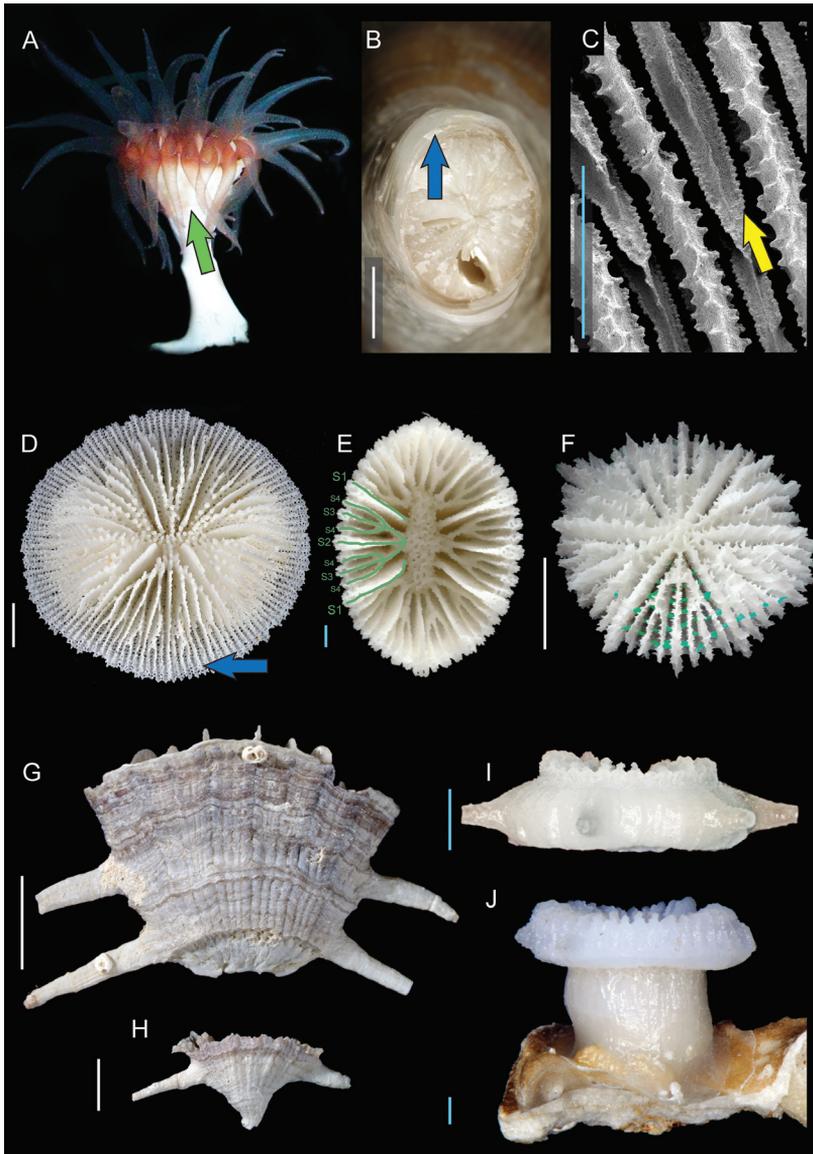
**Plate 22.** *Idiotrochus emarciatus* (MNHN uncatalogued, Ebisco stn. DW2632) **A**, **B**, and **C** Calicular, oblique, and lateral view respectively; *Dunocyathus parasiticus* (USNM 85697) **D** (SEM) and **E** (SEM): Oblique and lateral view respectively; *Endopachys grayi* (USNM uncatalogued, Norfolk 2 stn. DW2158) **G** and **H** Calicular and lateral view respectively; *Notophyllia recta* (USNM 85752) **H**, **I**, and **J** Calicular, oblique, and lateral view respectively; *Australocyathus vincentinus* (USNM 85699) **K** and **L** Oblique views respectively; *Truncatoguyunia irregularis* (USNM uncatalogued, Norfolk 2 stn. DW2117) **M** and **N** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



**Plate 23.** *Blastotrochus nutrix* (USNM 97553)– **A** and **B** Calicular and lateral view respectively; *Truncatoflabellum* sp. (MNHN uncatalogued, Concalis stn. DW2934) **C**, **D**, **E**, and **F** Calicular, oblique, lateral, and basal scar view respectively; *Caryophyllia* (*Caryophyllia*) *abrupta* (MNHN-Scl.2009-0067) **G** and **H** Calicular and lateral view respectively. Scale bars: blue = 1 mm; white = 5 mm. Bold face indicates type species for the genus.



**Plate 24.** **A** and **B** *Caryophyllia ralphae* (MNHN-Scl.2009-0077, **A** lateral view and **B** pedicel section): Green and red arrows indicating costae and monocyclic base respectively **C** and **D** *Rhizosmilia robusta* (USNM uncatalogued, Norfolk 2 stn. DW2114 **C** pedicel section and **D** lateral view): Red and green arrows indicating polycyclic base and costae respectively **E** *Astroides calycularis* (USNM 78767, colony view): Blue arrows indicating coenosteum **F** *Dendrophyllia ijimai* (USNM uncatalogued, Bathus 4 stn. DW933, lateral colony view): Yellow arrow indicating the axial polyp **G** *Sphenotrochus hancocki* (MNHN uncatalogued, Ebisco stn. DW2617, oblique view): Green arrows indicating costae **H** *Trochocyathus hastatus* (MNHN uncatalogued, Ebisco stn. DW2497, oblique view): White arrow indicating costal spines **I** *Truncatoflabellum vigintifarium* (MNHN uncatalogued, Ebisco stn. DW2578, oblique view): White arrow indicating lateral edge spines **J** *Idiotrochus emarciatus* (MNHN uncatalogued, Ebisco stn. DW2632, lateral view): White arrow indicating lateral edge spines (fish tail) **K** *Tropidocyathus lessoni* (MNHN uncatalogued, Musorstom 8 stn. DW1105, lateral view): White arrow indicating alate edge crests **L** *Caryophyllia unicristata* (MNHN-Scl.2009-0094, oblique view): White arrow indicating very sinuous lateral crest **M** *Stephanocyathus weberianus* (MNHN uncatalogued, Musorstom 5 stn. DW313, lateral view): White and green arrows indicating tubercles and costae respectively; Scale bars: blue = 1 mm; white = 5 mm.



**Plate 25.** **A** Indeterminate Caryophylliina (lateral view of live specimen, Roatan, Honduras ~200 m deep): Green arrow indicating the edge zone **B** *Javania* sp. (USNM uncatalogued, Norfolk 2 stn. CH 2115, broken pedicel section): Blue arrow indicating tectura layers **C** *Leptoseris gardineri* (JCU uncatalogued, Australia, septal detail [SEM]): Yellow arrow indicating meniane **D** *Letepsammia franki* (MNHN uncatalogued, Musorstom 6 stn. CP464, oblique view): Blue arrow indicating marginal shelf **E** *Balanophyllia carinata* (MNHN uncatalogued, Chalcal stn. D22, calicular view): Green diagram indicating a complete septal system arranged in a Pourtalès Plan configuration **F** *Fungiacyathus* sp. (MNHN uncatalogued, Biocal stn. CP17, oblique view): Synapticular plates highlighted in green **G** and **H** *Truncatoflabellum candeanum* (CSIRO uncatalogued, SS102005 stn. 170-086, lateral views) **G** anthocyathus and **H** anthocaulus **I** and **J** *Bourneotrochus stellulatus* (MNHN uncatalogued, Musorstom 4 stn. DW162, lateral views) **I** anthocyathus and **J** a specimen undergoing transverse division. Scale bars: blue = 1 mm; white = 5 mm.



# *Profundulus kreiseri*, a new species of *Profundulidae* (Teleostei, Cyprinodontiformes) from northwestern Honduras

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## Abstract

A new species of *Profundulus*, *P. kreiseri* (Cyprinodontiformes: *Profundulidae*), is described from the Chamelecón and Ulúa Rivers in the northwestern Honduran highlands. Based on a phylogenetic analysis using cytochrome *b* and the presence of synapomorphic characters (dark humeral spot, a scaled preorbital region and between 32–34 vertebrae), this new species is placed in the subgenus *Profundulus*, which also includes *P. (P.) oaxaca*, *P. (P.) punctatus* and *P. (P.) guatemalensis*. *Profundulus kreiseri* can be distinguished from other members of the subgenus *Profundulus* by having less than half of its caudal fin densely scaled. *Profundulus kreiseri* can further be differentiated from *P. (P.) oaxaca* and *P. (P.) punctatus* by the absence of rows of dark spots on its flanks. The new species can further be differentiated from *P. (P.) guatemalensis* by the presence of fewer caudal- and pectoral-fin rays. The new species is distinguished from congeners of the profundulid subgenus *Tlaloc* (viz., *P. (T.) hildebrandi*, *P. (T.) labialis*, *P. (T.) candalarius* and *P. (T.)*

*portillorum*) by having a scaled preorbital region and a dark humeral spot. *Profundulus kreiseri* and *P. portillorum* are the only two species of *Profundulus* that are endemic to the region south of the Motagua River drainage in southern Guatemala and northwestern Honduras.

### Keywords

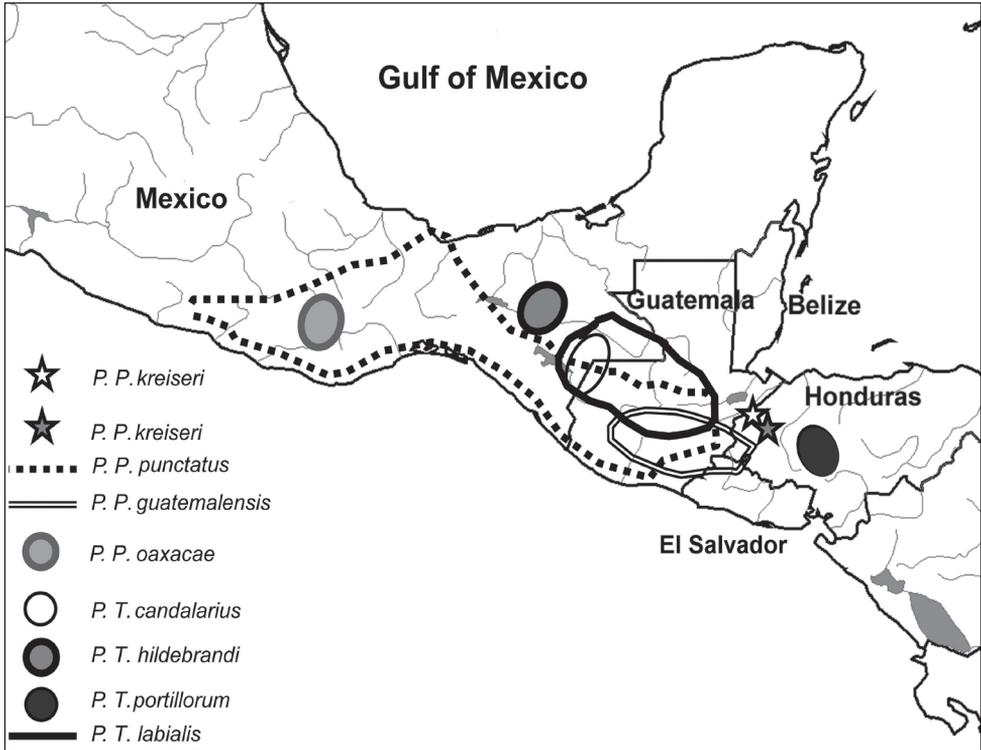
Central America, nuclear Middle America, Cyprinodontiformes, Kreiser's Killifish, phylogeny, systematics

### Introduction

The genus *Profundulus* Hubbs, 1924, is a depauperate lineage of northern Central American and southern Mexican (Fig. 1) cyprinodontiforms that belong to Profundulidae. The family comprises a single genus, *Profundulus*, which has seven valid species (Matamoros and Schaefer 2010). The northernmost distributed species, *Profundulus oaxacae* (Meek, 1902), is found in the Río Verde basin, in the Mexican Pacific slope in the state of Oaxaca (Miller et al. 2005). The southernmost boundary of the genus is delimited by the distributional range of *P. portillorum* Matamoros and Schaefer, 2010, which is found in the headwaters of the Ulúa and Nacaome River basins in the Atlantic and Pacific slopes of Honduras (Matamoros et al. 2009; Matamoros and Schaefer 2010; Matamoros et al. 2012).

Taxonomic relationships within Profundulidae were inferred by Miller (1955), who erected two subgenera (*Tlaloc* and *Profundulus*). The subgenus *Tlaloc* was diagnosed by having a preorbital region that has either two inconspicuously embedded scales or is naked, small scales on the body, and a high vertebral count. *Tlaloc* includes *P. (T.) candalarius*, Hubbs 1924, *P. (T.) hildebrandi*, Miller 1950, *P. (T.) labialis* (Günther 1866) and the recently described *P. (T.) portillorum*. The subgenus *Profundulus* is diagnosed by having a preorbital region covered with conspicuous (not deeply embedded) scales, a prominent humeral spot, and at least half (the anterior half) of the caudal fin densely scaled (Miller 1955). The subgenus *Profundulus* includes four species; *P. (P.) punctatus* (Günther, 1866), *P. (P.) guatemalensis* (Günther, 1866), *P. (P.) oaxacae* and the new species described herein.

Among neotropical members of Cyprinodontiformes, profundulids are the least studied. Although some progress has been made over the past two decades in advancing our understanding of the genetics (Doadrio et al. 1999; Valencia-Diaz and Espinoza-Perez 2011), morphometrics (Gonzales-Diaz et al. 2005) and conservation (Velazquez-Velazquez and Schmitter-Soto 2004; Velazquez-Velazquez et al. 2009) of the family, many aspects of the ecology, life history and general biology of *Profundulus* species remain unknown. Furthermore, most papers that address *Profundulus* are focused on Mexico, the northernmost range of the family, and little is known about the species that occur south of Mexico (e.g., *P. guatemalensis* and *P. portillorum*). Recent ichthyological work in Honduras (Matamoros et al. 2009) and El Salvador (McMahan pers. comm.) has produced new localities and records of undescribed species for the family (e.g. *P. portillorum*). The aim of this paper is to describe a new species of *Profundulus* from the Chamelecón and Ulúa River basins in the Atlantic slope of Honduras.



**Figure 1.** Map of Honduras and neighboring countries showing the distribution of all species of *Profundulus*. The type locality of *Profundulus kreiseri* (15.197667°N, 88.616°W) is represented by a white star, and a second known locality for the species (15.029520°N, 88.508°W) is represented by a dark star.

## Materials and methods

### Morphology

All specimens examined are housed at the University of Southern Mississippi Ichthyology Collection (USM), Louisiana State University Museum of Natural Science (LSUMZ), and University of Michigan Museum of Zoology (UMMZ). Measurements and counts were taken following Miller (1948), including standard length, snout length, head length, predorsal length, anal-fin origin to caudal-peduncle base, anal-fin length, eye diameter, head depth, caudal-peduncle depth, head width and maximum body width. All measurements were made using digital calipers. Counts include midline scales, scales around the caudal peduncle, anal-fin rays, dorsal-fin rays, pectoral-fin rays, and caudal-fin rays.

### Molecular phylogeny

Genomic DNA was extracted from ethanol-preserved fin tissue using a DNeasy Tissue Kit (QIAGEN Inc.). We amplified the mitochondrial cytochrome *b* gene using the

GluF and ThrR primers described by Machordom and Doadrio (2001). Initial sequences were generated with these two primers and used to design the following internal primers: ProcytbintF (5'-ACTCGATTCTTYGCCTTCCA-3') and ProcytbintR (5'-GGGTGAAATGARATTTTGTCG-3'). Subsequent amplifications and sequencing were conducted using the primer pairs GluF-ProcytbintR and ThrR-ProcytbintF. Amplifications were conducted in a total volume of either 25 ml or 50 ml using 50 mM KCl, 10 mM Tris-HCl (pH 8.3), 0.01% gelatin, 200 mM dNTPs, 2 mM MgCl<sub>2</sub>, 0.5 units of Taq polymerase (New England Biolabs), 0.3 mM of each primer, 20–150 ng of template DNA, and water to the final volume. Cycling conditions consisted of an initial denaturing step of 1 min at 95° C followed by 30 cycles of 1 min at 95° C, 1 min at 50° C and 1 min at 72° C. A final elongation step of 72° C for 3 min completed the reaction. PCR products were cleaned using the ExoSAP-IT system (USB Co.), and then used as the template in a cycle sequencing reaction with an ABI BigDye Terminator cycle sequencing kit (Foster City, CA, USA) using the primers described above. Sequencing reactions were cleaned using sephadex (Princeton Separations, Adelphia, NJ, USA) and then sent to the Iowa State University DNA Sequencing and Synthesis Facility. The sequences were edited and aligned using Sequencher v. 4.10.1 (GeneCodes Co.). Sample information and GenBank accession numbers for ingroup and outgroup species used in the analysis are listed in Table 1.

Sequence divergence (uncorrected p-distance) was estimated in PAUP\* (Swofford 2002). The AIC (Akaike's information criterion) model selection procedure was implemented in jModelTest (Posada 2008) and used to obtain an appropriate substitution model and parameter values for phylogenetic analysis. Phylogenetic relationships were inferred by maximum parsimony (MP) using PAUP\* (Swofford 2002) and Bayesian analysis (BA) using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). All valid species of *Profundulus* were included in the analysis. Two species from the family Goodeidae, *Allodontichthys hubbsi* Miller & Uyeno, 1980, and *Allophorus robustus*

**Table 1.** GenBank accession numbers and locality information of data used in the molecular analysis. Gu= Guatemala, Me= Mexico, Ho= Honduras.

Taxa	Accession No.	Locality	Source
<i>P. guatemalensis</i>	AY155568	Gu. Blanco River, San Miguel Duenas	Doadrio and Dominguez 2004
<i>P. labialis</i>	AY155567	Gu. Jeronimo River, San Jeronimo	Doadrio and Dominguez 2004
<i>P. punctatus</i>	AY155566	Me. Maniatepec Basin, San Juan Lachao	Doadrio and Dominguez 2004
<i>P. candalarius</i>	JQ254931	Me. Chiapas, Grijalva River basin	this study
<i>P. hildebrandi</i>	JQ254932	Me. Chiapas, San Cristobal de las Casas	this study
<i>P. kreiseri n. sp.</i>	JQ254935	Ho. Chamelecón River	this study; USM 39024
<i>P. kreiseri n. sp.</i>	JQ254934	Ho. Ulúa River	this study; USM 39028
<i>P. oaxacae</i>	JQ254933	Me. Oaxaca, Verde River basin	this study
<i>P. portillorum</i>	JQ254929	Ho. Nacaoeme River	this study; USM 31628
<i>P. portillorum</i>	JQ254930	Ho. Ulúa River	this study; USM 31597
<i>Allodontichthys hubbsi</i>	AF510835	Me. Jalisco, El Trampolin	Doadrio and Dominguez 2004
<i>Allophorus robustus</i>	AF510809	Me. Michoacán, Uruapan	Doadrio and Dominguez 2004

(Bean, 1982), were used as outgroups in the two phylogenetic analyses: these taxa were selected because Costa (1998) recovered goodeids as the sister group of Profundulidae. For the MP analysis, a heuristic search was performed to find the most parsimonious tree(s). Nonparametric bootstrapping (Felsenstein 1985) was used to measure clade support, with 1000 total pseudoreplicates and TBR branch-swapping with 10 random sequence addition replicates per pseudoreplicate. For BA analysis we performed four simultaneous analyses, each with ten Markov chain Monte Carlo simulations run for 1,000,000 generations, sampling trees every 1000 generations. At the end of the analysis, the average standard deviation of the split frequencies was < 0.01, indicating that the runs had converged. The first 100 trees from each run before reaching equilibrium were discarded as burn-in. The remaining trees were used for reconstruction of a 50% majority-rule consensus tree with posterior probabilities values. One of the paratypes (USM 39024; tissue 08-2921) was sequenced (GenBank accession number JQ254935) and therefore constitutes a “paragenotype cytochrome *b*” following the nomenclature of Chakrabarty (2010).

### Usage of “genotypes” nomenclature

The “genotypes” nomenclature was proposed by Chakrabarty (2010) to flag sequences from type specimens. Many genotypes can be created from a single specimen and these may be a single gene region or an entire genome; for instance “paragenotype COI” and “paragenotype ND2” could be added from USM 39024 at a later date, as could genotypes from other type specimens of this species (e.g., paratypes, holotype) from which DNA can be extracted. This nomenclature is simply a flag to alert molecular biologists and taxonomists that sequences are available from type specimens.

The genotype terminology is not used here in a strict nomenclatural sense, as it is not formally accepted by the International Code for Zoological Nomenclature. However, we consider this terminology useful and expect increased application in the future. The present paper is one of the first uses of the genotype terminology.

## Results

### Systematic Account

#### *Profundulus kreiseri*, sp. n.

urn:lsid:zoobank.org:act:97D8525F-9BDF-48EF-A7C5-21AD7917558B

[http://species-id.net/wiki/Profundulus\\_kreiseri](http://species-id.net/wiki/Profundulus_kreiseri)

Figure 2

*Profundulus* sp. 2 Matamoros et al. 2009

*Profundulus* sp. 2 Santa Barbara Matamoros et al. 2012

**Type material.** Holotype: USM 39022, field number WAM09-28, Honduras, Department of Santa Barbara, Municipality of Macuelizo. Drainage: Chamelecón, System: Chamelecón. Locality: small creek that drains to the Chamelecón River, near the Chamelecón Hydroelectric Dam 15.197667°N, 88.616°W; Collectors: W.A. Matamoros, M. Medina and J.C. Carrasco, 3 July 2009 (Fig. 2).

Paratypes: LSUMZ 14851 (n=9), field number WAM08-141, Honduras, Department of Santa Barbara, Drainage: Ulúa, small creek that drains into the main river, 15.029520°N, 88.508°W, Collectors: W.A. Matamoros, F. Elvir and H. Vega, 7 August 2008; LSUMZ 14852 (n=4), same data as the holotype; USM 39024 (n=9), same data as the holotype; USM 39025 (n=7), same data as LSUMZ 14851; USM 39026 (n=5), same data as LSUMZ 14851.

**Diagnosis.** *Profundulus kreiseri* is a new member of the subgenus *Profundulus* and shares with other members of that subgenus (viz., *P. (P.) punctatus*, *P. (P.) guatemalensis* and *P. (P.) oaxacae*) the following set of characters: dark humeral spot, a scaled preorbital region and between 32–34 vertebrae. It differs from all members of the subgenus by having less than half of its caudal fin densely covered with scales. It can further be distinguished from *P. (P.) oaxacae* and *P. (P.) punctatus* by the absence of conspicuous brown spots on the sides of the body; from *P. (P.) guatemalensis* by having fewer pectoral-fin rays (17–20 in *P. (P.) guatemalensis* versus 13–16 in *P. kreiseri*) and caudal-fin rays (19–23 in *P. (P.) guatemalensis* versus 13–18 in *P. (P.) kreiseri*); and from *P. (P.) guatemalensis* and *P. (P.) punctatus* by having a golden blotch that covers most of the operculum and reaches the base of the pectoral fin. *Profundulus (P.) kreiseri* is distinguishable from all members of the subgenus *Tlaloc* (viz., *P. (T.) candalarius*, *P. (T.) hildebrandi*, *P. (T.) labialis*, *P. (T.) portillorum*) by having a dark humeral spot and a scaled preorbital. *Profundulus (P.) kreiseri* can further be differentiated from *P. (T.) candalarius*, *P. (T.) hildebrandi* and *P. (T.) labialis* by having between 32–34 vertebrae (versus 35–39).

**Description.** Morphometric and meristic data for type material are summarized in Table 2. The largest specimen is 81.2 mm SL. The body is elongate with the dorsal and ventral profiles nearly symmetrical. The narrowest point on the body is the tip of the snout, with the body expanding gradually dorsally and ventrally to the deepest point slightly anterior to the verticals through the dorsal- and anal-fin origins. The vertical through the origin of the dorsal fin is slightly anterior to the origin of the anal fin. The body depth narrows in the region of these two unpaired fins, and the dorsal and ventral body margins are straight and parallel on the caudal peduncle before diverging out slightly at the origin of the caudal fin.

The head (including cheek, infraorbital and preorbital regions) is covered with scales that are deeply embedded in the skin. The mouth is terminal, the lower jaw protruding slightly beyond the upper. The posterior portion of the maxilla extends ventrally to a vertical through the anterior region of the orbit.

The number of dorsal-fin rays ranges from 10–12 (holotype=11). The number of pectoral-fin rays ranges from 13–16 (holotype=14). The posterior edge of the pectoral fin does not reach the pelvic-fin origin. The number of anal-fin rays ranges from 9–14



**Figure 2.** Photographs of preserved specimens of **A** *Profundulus kreiseri* sp. n., USM 39022, holotype, 53.2 mm SL, Río Chamelecón, Honduras **B** *Profundulus punctatus*, UMMZ 194154, 47.0 mm SL, Rio Nahualate, Guatemala; and **C** *Profundulus guatemalensis*, UMMZ 190542, 43.7 mm SL, Río Maria Linda, Guatemala. The diagnostic characters of each species (**A–C**) are shown in **D–F** the white bar shows the extent of squamation on the caudal fin **D** *Profundulus kreiseri* sp. n., USM 39022, holotype (note that scales cover less than half of the caudal fin, and there are no rows of dark spots on the caudal peduncle and caudal-fin base) **E** *Profundulus punctatus*, UMMZ 194154 (note that the entire anterior half of the caudal fin is covered with scales, and rows of dark dots occur on the caudal peduncle and caudal-fin base); and **F** *Profundulus guatemalensis*, UMMZ 190542 (note that scales extend beyond the midpoint of the caudal fin, and there are no rows of dark spots on the posterior portion of the caudal peduncle and caudal-fin base).

(holotype=12; mode=12). The caudal fin is rounded, the number of fin rays ranging from 13–18 (holotype=17). All specimens examined have six pelvic-fin rays. The number of scales along the midline of the body ranges from 33–34 (holotype=33). The

**Table 2.** Morphological data and counts from the holotype and 33 paratypes of the new species *P. kreiseri*. Measurements are presented as % of standard length (%SL) or % of head length (%HL). SD=standard deviation.

Morphological data	Holotype	Range	Mean	SD
Standard length	53.2	46.1–81.2	60.3	9.7
Snout length (%HL)	30.1	20.4–36.1	28.9	3.6
Head length (%SL)	26.0	24.0–28.8	25.8	1.2
Predorsal length (%SL)	70.9	20.4–74.9	68.9	2.2
Anal-fin origin to caudal-peduncle base (%SL)	32.0	29.6–35.7	31.9	1.7
Anal-fin length (%SL)	32.0	28.5–34.9	31.9	1.8
Eye diameter (%HL)	23.0	20.4–29.5	23.4	2.1
Head depth (%HL)	75.6	42.8–78.1	69.4	6.6
Maximum body depth (%SL)	24.9	18.1–25.7	23.2	2.0
Caudal-peduncle depth (%SL)	14.0	12.0–15.5	13.8	0.8
Head width (%HL)	66.9	36.2–68.1	61.2	6.6
Maximum body width (%SL)	17.4	10.2–19.5	16.0	1.8
Counts	Holotype	Range	Mean	Mode
Scales along midline	33	33–34	33.4	33
Scales around caudal peduncle	10	9–10	9.46	9
Anal-fin rays	12	9–14	11.73	12
Dorsal-fin rays	11	10–12	10.88	11
Pectoral-fin rays	14	13–16	14.23	14
Caudal-fin rays	17	13–18	15.69	16
Vertebrae	32	32–34	32.93	33

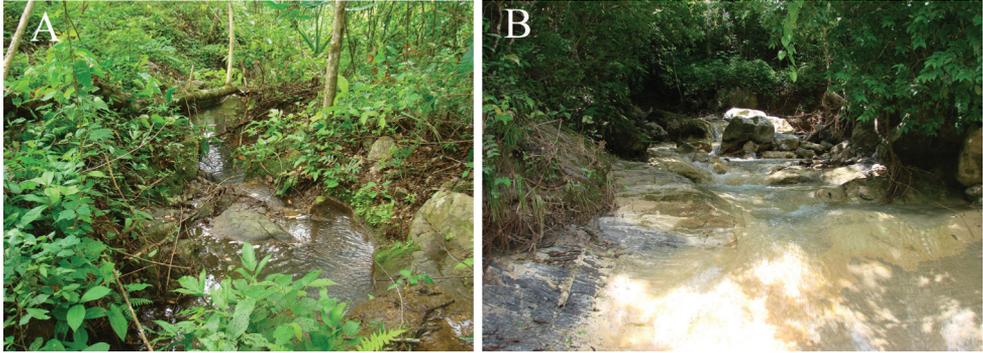
number of scales around the caudal peduncle ranges from 9-10 (holotype=10). The number of vertebrae ranges from 31-33 (holotype=32).

**Live coloration.** In life this species is brown, with a golden-yellow blotch that covers most of the operculum and reaches the base of the pectoral fin. An inconspicuous dark stripe is present along the midline of the body starting at a vertical between the dorsal- and anal-fin origins and terminating at the origin of the caudal fin.

**Preserved coloration.** The body is a uniform dusky brown with a prominent dark humeral spot posterior to the upper insertion of the pectoral fin. A dark stripe is present along the midbody; this stripe is more conspicuous in preservation than in life. The distal margins of the unpaired fins are opaque, but the basal  $\frac{3}{4}$  of the fins are covered with scattered melanophores.

**Distribution.** *Profundulus kreiseri* is only known from the middle reaches of the Chamelecón and Ulúa rivers in Honduras (Figs. 1, 3).

**Ecological notes.** The only known localities of *P. kreiseri* are both characterized as small tributaries ranging in width from 0.8 to 4 meters with stones (from pebbles to boulders) as the dominant substrate. The canopy cover of both localities is estimated to be 70–80%. Both creeks feature a variety of run, pool, riffle, rapid and small waterfall habitats (Fig. 3).



**Figure 3.** Photographs of the habitat of *P. kreiseri*. **A** Type locality of *P. kreiseri*, 15.197667°N, 88.616°W. A small creek that drains directly into the Chamelecón River, near the new hydroelectric dam. Department of Santa Barbara, Municipality of Macuelizo **B** Small creek that drains into the main river. Department of Santa Barbara, 15.029520°N, 88.508°W.

**Conservation.** The limited range of this species makes it vulnerable to extinction via habitat loss. The creation of a new hydroelectric dam on the Chamelecón River will likely drastically impact populations of this new species.

**Etymology.** The specific epithet is in honor of Dr. Brian R. Kreiser, the doctoral advisor and friend of the first author.

Suggested English name: Kreiser's Killifish

Suggested Spanish name: El Escamudo de Kreiser

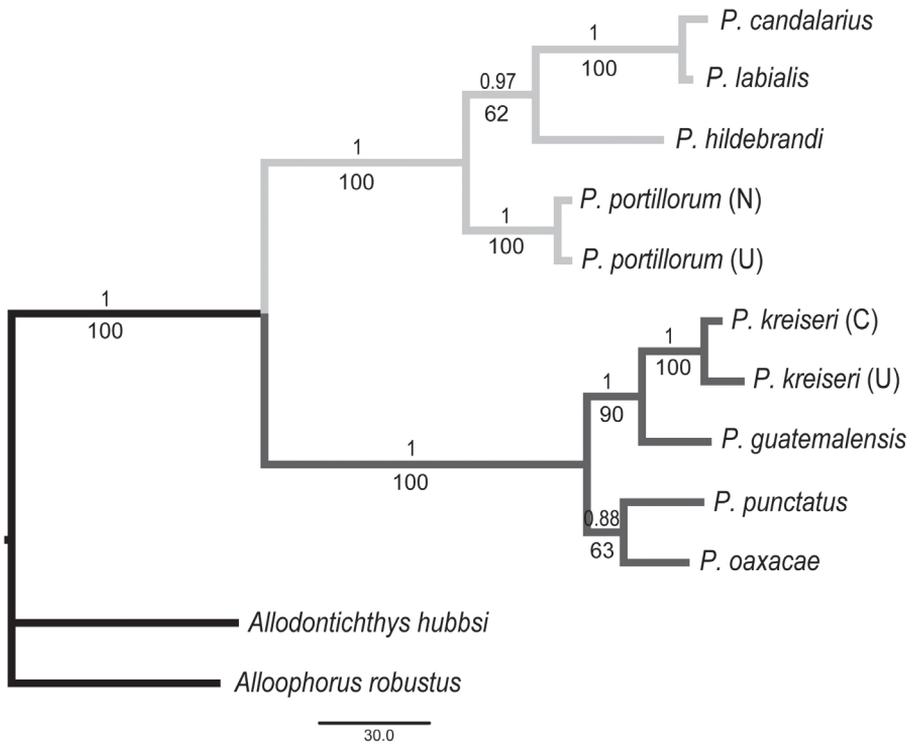
### Molecular analysis

The phylogenetic analysis included sequences from 12 taxa (10 in the ingroup and 2 outgroups). Novel sequences were deposited in GenBank under accession numbers JQ254929-JQ254935 (Table 1). A total of 990 bp of cytochrome *b* were analyzed, of which 280 sites (28.3%) were parsimony informative. The GTR + I + G model was selected as the best fit for the dataset by jModelTest using the AIC. The optimized parameters were: A=0.2692, C=0.2640, G=0.2334, T= 0.3335, Rmat=( 8.4428, 56.7004, 8.4428, 1.0000, 56.7004, 1.0000), the gamma distribution was 1.4610, and the proportion of invariable sites was 0.4970.

The same tree topology was recovered by MP (a single tree, length: 585, CI: 0.735; RI: 0.796) and BA (Fig. 4). Two monophyletic groups corresponding to the two subgenera were recovered. Node support was generally high throughout the tree (Fig. 4). The new species was recovered as the sister group of *P. guatemalensis* with high bootstrap and posterior probability values. P- distances between the members of the two subgenera ranged from 17.8 to 19.3%. Within the subgenus *Tlaloc*, sequence divergence ranged from 1 to 9.2%. The shortest genetic distance was found between *P. labialis* and *P. candalarius* (1%). Sequence divergence between the new species

**Table 3.** Uncorrected pairwise genetic divergence based on cytochrome *b* sequences. C= chamelecón river, u= ulúa river, n= nacaome river.

	1	2	3	4	5	6	7	8	9
1. <i>P. (P) kreiseri</i> (C)	0								
2. <i>P. (P) kreiseri</i> (U)	0.016	0							
3. <i>P. (P) guatemalensis</i>	0.041	0.047	0						
4. <i>P. (P) punctatus</i>	0.062	0.064	0.064	0					
5. <i>P. (P) oaxacae</i>	0.063	0.065	0.063	0.040	0				
6. <i>P. (T) portillorum</i> (U)	0.185	0.184	0.182	0.181	0.178	0			
7. <i>P. (T) portillorum</i> (N)	0.187	0.186	0.183	0.180	0.178	0.008	0		
8. <i>P. (T) hildebrandi</i>	0.191	0.191	0.186	0.183	0.184	0.080	0.080	0	
9. <i>P. (T) labialis</i>	0.192	0.193	0.183	0.187	0.186	0.087	0.087	0.078	0
10. <i>P. (T) candalarius</i>	0.192	0.193	0.183	0.183	0.187	0.090	0.092	0.083	0.010



**Figure 4.** Bayesian and maximum parsimony trees based on cytochrome *b* sequences. Number above each node represents Bayesian posterior probabilities. Number below each node represents nonparametric bootstrap support. Subgenus membership is shown with either light gray branches (*Tlaloc*) or dark gray branches (*Profundulus*). C = Chamelecón River, U = Ulúa River, N = Nacaome River.

(two specimens) and each of the three other species in the subgenus *Profundulus* ranged from 4.1 to 6.5% (Table 3).

## Discussion

*Profundulus portillorum* has the southernmost range of any species in the family; it is found in the Ulúa River in the Atlantic slope of Honduras and the Nacaome River in the Pacific slope of Honduras (Matamoros and Schaefer 2010). The Chamelecón River locality reported for *Profundulus kreiseri* represents a new drainage for the family. Most species of *Profundulus* have restricted distributional ranges (found only among a few adjacent river systems) and only one species has a widespread distributional range, *P. guatemalensis*. This species is the only *Profundulus* to cross the Motagua River Fault into nuclear Middle America, a region that extends from southern Guatemala to northern Nicaragua (Matamoros et al. 2012). The Motagua River Fault may be a biogeographic boundary for *Profundulus*. *Profundulus punctatus* and *P. labialis* also reach the Motagua River, but are not found south of it (Miller 1955; Miller et al. 2005; Matamoros and Schaefer 2010) and *P. portillorum* and *P. kreiseri* are restricted to nuclear Middle America but are not found north of the Motagua River. The combination of the tree topologies, node support, uncorrected pairwise divergences values and morphological comparisons between the new species and its congeners fully support the distinctiveness of *Profundulus kreiseri*.

*Profundulus kreiseri* has higher intraspecific genetic variation (0.016) than is found between some species (e.g., 0.010 in *P. labialis* versus *P. candalarius*). The low sequence divergence found between *P. labialis* and *P. candalarius* may be a reflection of a recent divergence. These two taxa are currently allopatric and can be differentiated based on morphological characters (e.g., fin ray counts, body depth). However, additional work may be needed to verify the taxonomic status of these taxa given the results from our molecular analysis. Intraspecific variation in *P. kreiseri* is also twice as high as what was recovered for the only other species for which multiple individuals were sampled in our study, *P. portillorum* (0.008). This variation in *P. kreiseri* may reflect a relatively long period of isolation between the populations in the Chamelecón and Ulúa rivers.

Our molecular phylogenetic analysis recovered two distinct clades corresponding to the nominal subgenera and placed *P. kreiseri* within the subgenus *Profundulus* as the sister taxon of *P. guatemalensis*. The caudal-fin scales of *P. kreiseri* do not extend beyond the anterior half of the fin (Fig. 2D), whereas they cover half or more of the caudal fin in other members of the subgenus *Profundulus* (e.g., *P. punctatus* and *P. guatemalensis*—Fig. 2E, F). Because the presence of squamation on at least half of the caudal fin is a defining character of the subgenus (Miller 1955), our recognition of *P. kreiseri* as a member of the subgenus *Profundulus* is based on the molecular data and the presence in *P. kreiseri* and other members of the subgenus of a dark humeral spot and scaled preorbital region. The new species exhibits none of the diagnostic features of the subgenus *Tlaloc*. In addition to the caudal squamation, species status of *Profundulus* (*P.*) *kreiseri* is warranted based on its pigmentation pattern and numbers of pectoral- and caudal-fin rays. A dichotomous key to all of the Central American species of *Profundulus* is presented below.

**Key to species of *Profundulus* from Central American**

- 1a Preorbital region usually naked, frequently with one or two isolated inconspicuous embedded scales; humeral spot absent ..... **2**
- 1b Preorbital region with at least three to four conspicuous (not deeply embedded under the skin) scales; humeral spot present ..... **4**
- 2a Lower jaw protruding beyond upper jaw..... *P. labialis*
- 2b Lower and upper jaws same length..... **3**
- 3a Pectoral-fin rays 16 – 19. Endemic to the Grijalva-Usumacinta River basin ..  
..... *P. candalarius*
- 3b Pectoral-fin rays 13 – 16. Endemic to Honduras..... *P. portillorum*
- 4a Body of adults with conspicuous brown spots (distinctly within the scales) in longitudinal rows on the midline from the midpoint of the body to the caudal fin; dorsal surface of head concave to nearly flat ..... *P. punctatus*
- 4b Body of young and adults lacking distinct brown spots (as described in 4a); dorsal surface of head convex (rounded) ..... **5**
- 5a Scales on the caudal fin covering at least the anterior half or more of the fin. Caudal-fin rays 19-23, very rarely 18 or 24; pectoral-fin rays 17-20, very rarely 16 or 21 ..... *P. guatemalensis*
- 5b Scales on the caudal-fin covering less than half of the fin. Caudal-fin rays 13-18, pectoral-fin rays 13–16. .... *P. kreiseri* sp. n.

**Comparative material.** *Profundulus candalarius*: UMMZ 1767317, n = 10, 23–44 mm SL, Guatemala, Huehuetenango, tributary of Río Lagartero in Ciénega Lagartero; UMMZ 2108276, n = 10, 41–66 mm standard length, LS, Mexico, Chiapas, Arroyo tributary to Río Comitán, 11.5 km east of Highway 190 on the road to Montebello National Park. *Profundulus guatemalensis*: UMMZ 1905421, n = 15, 43–62 mm SL, Guatemala, Escuintla, Río Marinala at Finca Peña Blanca 11 km north-east Escuintla; UMMZ 2191352, n = 4, 37–49 mm SL, Honduras, Río Copan bridge crossing on Ca 11, 26.4 km east of Copan.

*Profundulus punctatus*: UMMZ 1847303, n = 10, 42–51 mm SL, Mexico, Chiapas, Stream at Piedra Parada, 12.1 km west-north-west of Ocozocoautla; UMMZ 1941544, n = 4, 54–70 mm SL, Escuintla, Guatemala, Río Siguacan at Ca Highway 2, km 120, 8 km east of Río Bravo; UMMZ 1941605, n = 5, 55–66 mm SL, Escuintla, Guatemala, Río Aguna at CA 2, km 98, 15 km west-north-west.

*Profundulus hildebrandi* : UMMZ 1576348, 15, 46–103 mm SL, Mexico, Chiapas, Laguna de Maria Eugenia, San Cristobal de las Casas; UMMZ 1839149, n = 5, 33–47 mm SL, Mexico, Chiapas, Irrigation ditch of Laguna Maria Eugenia at Highway. 190, 2.4 km southwest of San Cristobal de las Casas. *Profundulus labialis*: UMMZ 16669811, n = 5, 50–71 mm SL, Guatemala, Rio Carchela c. 29.0 km north of Salama on road to Coban; UMMZ 17672610, n = 15, 43–64 mm SL, Guatemala, Huehuetenango, stream through pasture southwest of Jacaltenango.

*Profundulus portillorum*: USM 31597, n = 31, field number WAM07-03, Honduras, department of Comayagua, municipality of Potrerillos, in the town of Siguatepeque. Drainage: Ulúa. System: Ulúa: Río Calam. Quebrada de Potrerillos at Barrio San José, 14.53000°N, 87.84000°W, Collectors: Matamoros W.A. and H. Portillo; USM 31628, n = 21, field number WAM07-39, Honduras, department of Francisco Morazan, municipality of Lepaterique, Basin: Pacific. Drainage: Nacaome, System: Nacaome, Quebrada El Sapo, near the community of Lepaterique, 100 meters away from Catholic Church, 14.064275°N, 87.466850°W, Collectors: Matamoros W.A., A. Sanchez, E. Lopez and J. Hernandez.

*Profundulus kreiseri*: USM 39028, 9, field number WAM08-141, Honduras, department of Santa Barbara, Drainage: Ulúa, System: Ulúa, small creek that drains in to main river. 15.029520°N, 88.508°W. Collectors: W.A. Matamoros, F. Elvir and H. Vega; USM 39027, n = 3, same data as USM 39028.

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## References

- Chakrabarty P (2010) Genotypes: a concept to help integrate molecular systematics and traditional taxonomy. *Zootaxa* 2632: 67–68.
- Costa JEM (1998) Phylogeny and classification of the Cyprinodontiformes (Euteleostei: Atherinomorpha): a reappraisal. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS (Eds) *Phylogeny and Classification of Neotropical Fishes*. EDIPUCRS, Porto Alegre, 537–560.
- Doadrio I, Carmona JA, Martínez E, de Sostoa A (1999) Genetic variation and taxonomic analysis of the subgenus *Profundulus*. *Journal of Fish Biology* 55: 751–756. doi: 10.1111/j.1095-8649.1999.tb00715.x

- Doadrio I, Dominguez O (2004) Phylogenetic relationships within the fish family Goodeidae based on cytochrome *b* sequence data. *Molecular Phylogenetics and Evolution* 31: 416–430. doi: 10.1016/j.ympev.2003.08.022
- González-Díaz AA, Díaz-Pardo E, Soria-Barreto M, Rodiles-Hernández R (2005) Morphometric analysis of the fish included in the *Labialis* group, genus *Profundulus* (Cyprinodontiformes: Profundulidae), in Chiapas, Mexico. *Revista Mexicana de Biodiversidad* 76: 55–61.
- Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791. doi: 10.2307/2408678
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754–755. doi: 10.1093/bioinformatics/17.8.754
- Machordom A, Doadrio I (2001) Evidence of a Cenozoic Betic-Kabilian connection based of freshwater fish phylogeography (*Luciobarbus*, Cyprinidae). *Molecular Phylogenetics and Evolution* 18: 252–263. doi: 10.1006/mpev.2000.0876
- Matamoros WA, Schaefer JF (2010) A new species of *Profundulus* (Cyprinodontiformes: Profundulidae) from the Honduran central highlands. *Journal of Fish Biology* 76: 1498–1507. doi: 10.1111/j.1095-8649.2010.02596.x
- Matamoros WA, Schaefer JF, Kreiser BR (2009) Annotated checklist of the freshwater fishes of continental and insular Honduras. *Zootaxa* 2307: 1–38.
- Matamoros WA, Kreiser BR, Schaefer JF (2012) A delineation of Nuclear Middle America biogeographical provinces based on river basin faunistic similarities. *Reviews in Fish Biology and Fisheries* 22: 351–365. doi: 10.1007/s11160-011-9232-8
- Miller RR (1948) The cyprinodont fishes of the Death Valley system of eastern California and southwestern Nevada. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan* 68: 1–155.
- Miller RR (1955) A systematic review of the Middle American fishes of the genus *Profundulus*. *Miscellaneous Publications of the Museum of Zoology of the University of Michigan* 92: 1–64.
- Miller RR, Minckley WL, Norris SM (2005) *Freshwater Fishes of México*. The University of Chicago Press, Chicago, 652pp.
- Posada D (2008) jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* 25: 1253–1256. doi: 10.1093/molbev/msn083
- Swofford DL (2002) PAUP\* 4.0: Phylogenetic analysis using parsimony (\* and other methods). Ver. 4.b10. Sinauer Associates, Inc. Publishers, Massachusetts.
- Valencia-Díaz X, Espinosa-Pérez H (2011) Comparative analysis of three species populations of *Profundulus* (Teleostei: Cyprinodontiformes) using two genetic markers. *Mitochondrial DNA* 22: 19–21. doi: 10.3109/19401736.2010.539214
- Velázquez-Velázquez E, Schmitter-Soto JJ (2004) Conservation status of the San Cristobal pupfish *Profundulus hildebrandi* Miller (Teleostei: Profundulidae) in the face of urban growth in Chiapas, Mexico. *Aquatic Conservation: Marine and Freshwater* 14: 201–209. doi: 10.1002/aqc.605
- Velázquez-Velázquez E, Schmitter-Soto JJ, Domínguez-Cisneros S (2009) Threatened fishes of the world: *Profundulus hildebrandi* Miller, 1950 (Profundulidae). *Environmental Biology of Fishes* 84: 345–346. doi: 10.1007/s10641-008-9425-8

# New *Mecyclothorax* spp. (Coleoptera, Carabidae, Moriomorphini) define Mont Mauru, eastern Tahiti Nui, as a distinct area of endemism

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## Abstract

Seven species of *Mecyclothorax* Sharp precinctive to Mont Mauru, Tahiti, Society Islands are newly described: *M. tutei* sp. n., *M. tihotii* sp. n., *M. putaputa* sp. n., *M. toretore* sp. n., *M. anaana* sp. n., *M. pirihaio* sp. n., and *M. poro* sp. n. These seven constitute the first representative *Mecyclothorax* species recorded from Mauru, and their geographic restriction to this isolated massif defines it as a distinct area of endemism along the highly dissected eastern versant of the Tahiti Nui volcano. Each of the new species has a closest relative on another massif of Tahiti Nui, supporting speciation associated with vicariance caused by extensive erosional valley formation, especially the development of Papenoo Valley. Comparison of the known elevational distributions of the new discoveries on Mont Mauru to the elevational diversity profile of the comparatively well-sampled Mont Marau, northwest Tahiti Nui, suggests that numerous *Mecyclothorax* species remain to be discovered in higher-elevation habitats of Mont Mauru.

## Keywords

French Polynesia, allopatric speciation, biodiversity, biogeography

## Introduction

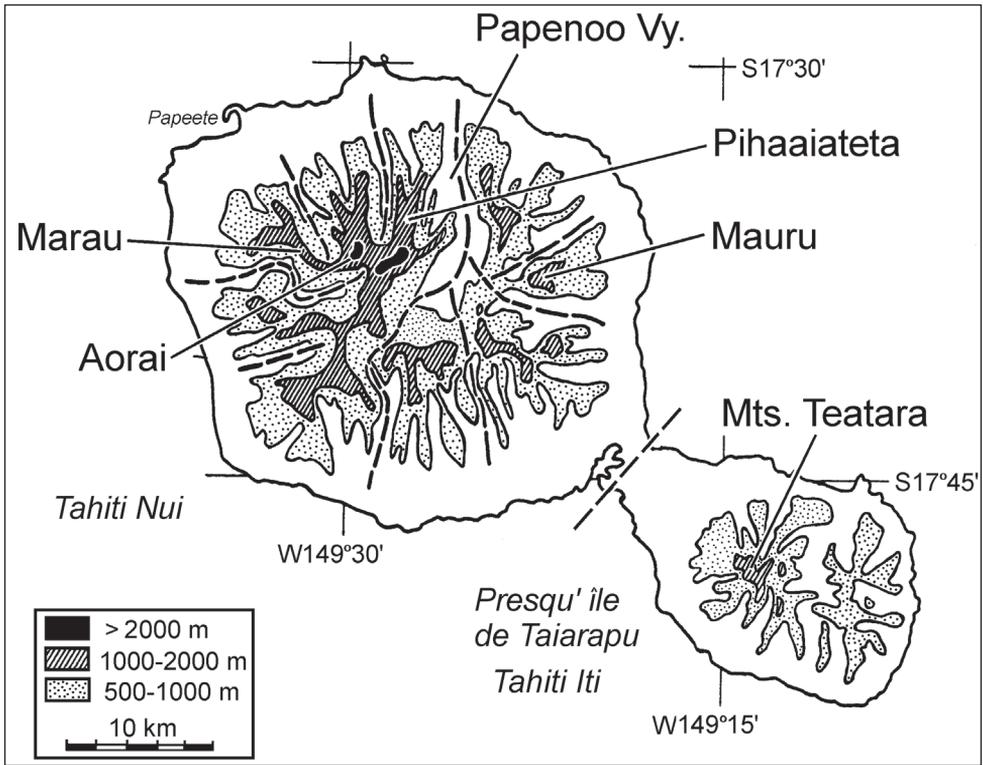
The island of Tahiti is remarkably dissected. The two volcanoes that comprise Tahiti—Tahiti Nui and Tahiti Iti—are estimated to have formed 1.75 and 1.0 Myr ago (Craig et al. 2001), and both have undergone extensive erosion leading to deep, broad valleys separating narrow ridgelike mountains with extremely steep slopes. At the center of Tahiti Nui, Mont Orohena stands 2,241 km tall less than 5 km from the 169 m elevation floor of Papenoo Valley. To Papenoo Valley's east lie a series of isolated massifs that comprise the dissected, windward and eastern versant of Tahiti Nui volcano. To its west range a set of interconnected ridge systems; Marau, Aorai, and Pihaaiaateta (Fig. 1), the latter culminating in Mont Orohena.

This paper presents the first descriptions of *Mecyclothorax* carabid beetles precinctive to one of the isolated eastern massifs; Mont Mauru (Fig. 1). All of the species discovered on Mauru are new to science. The novel aspects of Mauru's beetle fauna stem from the historical restriction of all prior carabid beetle sampling in Tahiti Nui to the interconnected western ridges. Perrault (1978a, 1978b, 1984, 1986, 1987, 1988, 1989) collected extensively on Marau, Aorai, and Pihaaiaateta, as well as in the mountains of Teatara, Presqu'île de Taiarapu, Tahiti Iti (Fig. 1). He found that even among the interconnected ridges of western Tahiti Nui, most species are restricted to a single ridge system (Perrault 1992). Given the extreme geographic isolation of Mont Mauru vis à vis the western sites sampled by Perrault, it should come as little surprise that Mont Mauru houses a fauna completely distinct from that of the western mountains. Nonetheless, sampling accomplished to date on Mont Mauru remains very limited, suggesting that our biological knowledge of this massif's *Mecyclothorax* diversity is dramatically incomplete. To make an initial estimate of the level of our ignorance, the elevational distributions of *Mecyclothorax* beetle species on Mauru are compared to those observed on Mont Marau, the best sampled and therefore apparently most diverse Tahitian mountain. By this estimate, somewhere between  $\frac{1}{4}$  to  $\frac{1}{2}$  of the *Mecyclothorax* fauna of Mauru has been discovered, lending support for further biological survey activities on this massif.

## Methods

### Taxonomic material

This study is based on 41 *Mecyclothorax* specimens—40 adults plus 1 larva—collected on Mont Mauru during September, 2006. Diagnoses of all new species were developed through comparison with type specimens of Tahitian *Mecyclothorax* species described by Perrault (1978a et seq.), as well as specimens representing 35 described species plus 20 additional new species, to be described subsequently, that were collected elsewhere in Tahiti during September, 2006. Paratype specimens of Perrault



**Figure 1.** Massifs of the Tahiti Nui and Tahiti Iti volcanos, Tahiti, Society Islands (redrawn and amended from Perrault, 1992). Massifs indicated were either sampled by Perrault (1978a et seq.) or during 2006 field work supporting the current study. Dashed lines indicate lowland valleys and associated headlands below 1000 m elevation that separate major massifs.

species were borrowed from the Naturhistorisches Museum, Basel (NHMB) and the Muséum national d'Histoire naturelle, Paris (MNHN). Specimens representing all *Mecyclothorax* species in the Georges G. Perrault collection of Tahitian Carabidae (MNHN) were photographed, 24-26 August 2006, at which time structural, setational, and microsculptural characters were noted for all described species held at Paris. These include specimens for species described by Britton (1938). The sum of these comparisons plus associated notes, along with Perrault's (1992) hypotheses of phylogenetic affinity, were used to formulate hypotheses of sister-group relationships for the new species described below.

Primary type specimens and associated allotypic paratypes of the new species, where available, are deposited in the MNHN and incorporated into the Perrault collection. Other institutional depositories include: Cornell University Insect Collection (CUIC); Essig Museum of Entomology Collection, University of California, Berkeley (EMEC); U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH).

## Laboratory techniques

This paper follows directly the laboratory protocols and anatomical terminology presented in Liebherr (2009, 2011). Those papers may be consulted for explanations of the terminology used below.

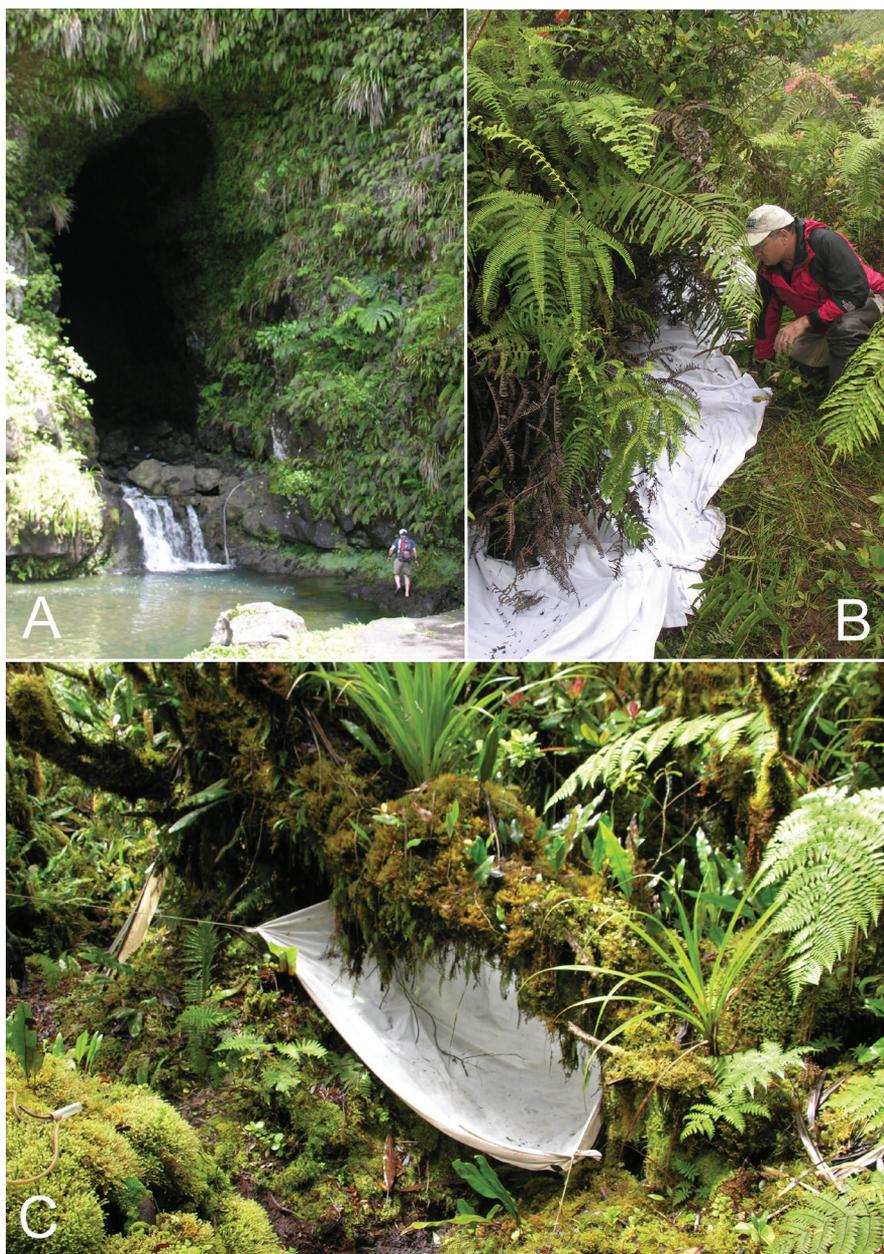
## Descriptive conventions

Various ratios of length and width are used to describe shapes of the head, pronotum and elytra. For the head these include the ocular ratio, the width across the outer surface of the compound eyes divided by the minimum width of the frons between the eyes, and the ocular lobe ratio, the diameter of the eye measured from above, divided by the distance from the front margin of the eye to the juncture of the ocular lobe and gena, measured from the same vantage point. Prothoracic dimensions presented as ratios include: MPW, maximum pronotal width; BPW, basal pronotal width, measured between the hind angles; APW, apical pronotal width measured between the two most anterior points at the pronotal front angles; and PL, pronotal length measured along the midline. Elytral dimensions include MEW, or maximum elytral width, and HuW, humeral width, measured between the most anteriorly positioned points, i.e. the humeral angles. Standardized body length comprises the sum of three values: 1, the length of the head from labral anterior margin to cervical ridge, the position of the ridge estimated from its lateral reaches when hidden medially under the pronotal margin; 2, median pronotal length; and 3, elytral length, distance from base of scutellum, where the surface dips ventrally, to apex of the longer elytron, measured along the suture.

When more than one individual was used to represent a ratio or range of ratios, the quantified number is followed by “(n = X)”, with X representing the number of individuals measured to make up the ratios. A maximum of five individuals were so measured for any species, with the largest individual, the smallest individual, and representatives of both sexes included in the sample of five. By this method the most disparate range of ratios was sought. The ratios are used only for descriptive purposes and are not statistically evaluated.

## Collecting localities

Entomological sampling of Mont Mauru, eastern Tahiti Nui, was facilitated by the private access road to the hydroelectric facilities of Électricité de Tahiti. The lowest elevation collecting site was along a northern tributary branch of the Faatautia River at a 30 m length of uncollapsed lava tube housing a highly variable stream (Fig. 2A). The lava tube was traversable at low water (18 September), with a small waterfall at its lower mouth bordered by a flat rocky terrace. At higher water (5 September), the flow



**Figure 2.** Habitats within which specimens of *Mecyclothorax* spp. were collected **A** Lava tube at 705 m elevation on Faatautia River drainage; holotype of *Mecyclothorax poro* collected by pyrethrin fogging vegetation growing on rocky bank between Dr. Curtis Ewing and climbing rope near edge of waterfall **B** Bank of *Dicranopteris* and *Blechnum* ferns at 1010 m elevation on Mont Mauru pylon trail; fern bank treated with pyrethrin fog by Dr. Dan Polhemus resulting in specimens of *M. anaana* and *M. pirihaio* **C** Pyrethrin fog sheet apparatus around moss-covered *Metrosideros* trunk in low stature, open-canopy, wet rain forest at 1060–1110 m elevation, Mont Mauru, by which specimens of *M. tibotii* and *M. putaputa* were collected; trees did not exceed 4m height, mossmats were as thick as 15 cm

covered the lava tube floor, flowing as high as the upper limit of the scoured rockface to the right of the terrace (Fig. 2A).

The hydroelectric facility transmits its electricity to Papeete by means of high tension lines strung on metal pylons, with four pylons traversing the southwestern portion of Mont Mauru from 850 m to 1060 m elevation. Access to habitats near the pylons is facilitated by the remnants of the original construction road, although erosion has eliminated portions of this track making it impassable for vehicles above 650 m elevation. Fern banks line old roadcuts (Fig. 2B), and open mesic forest with limited moss-mats on tree trunks is accessible from the trail. The fourth pylon at 1060 m elevation stands near the margin of low-stature wet montane forest, dominated by *Weinmannia* and *Metrosideros* trees that form an open canopy of stunted trees covered with thick mossmats (Fig. 2C). Abundant epiphytic growth occurs on older, decumbent nurse logs. This low wet forest was sampled up to 1110 m elevation, above which collecting was precluded by inclement weather.

Latitude and longitude readings were made at all collecting localities using a Garmin etrex® 12 channel GPS unit, with coordinates used to map the localities onto I.G.N. (1994). Distances between sites along elevational transects were then calculated and used to determine the elevational profiles of the collecting localities. Beetle distributions along elevational transects on Mont Mauru and Mont Marau were compared to obtain a comparative estimate of species distributions relative to elevation.

## Taxonomic treatment

### Identification Key to Adults of *Mecyclothorax* spp. known from Mont Mauru, Tahiti Nui

- |    |   |                           |
|----|---|---------------------------|
| 1  | Body size smaller, standardized body length 3.7–4.7 mm; pronotal hind angles projected, right to obtuse, lateral margins distinctly sinuate anterad hind angles (Figs 3B–C, 4).....   | 2                         |
| 1' | Body size larger, standardized body length 5.3 mm; pronotal hind angles rounded, a small jag present at basal seta, lateral margins indistinctly sinuate, nearly straight anterad hind angles except for jag (Fig. 3A) ....       | <i>M. tutei</i> sp. n.    |
| 2  | Two supraorbital setae present each side of frons (Fig. 3C).....  | 3                         |
| 2' | A single supraorbital seta present each side of frons, the anterior seta absent (Fig. 3B) .....   | <i>M. tibotii</i> sp. n.  |
| 3  | Pronotum with single seta each side just anterad midlength, hind angle glabrous (Fig. 4); elytral striae 1–4 smooth to minutely punctate in basal third, punctures if present not expanding strial breadth.....                   | 4                         |
| 3' | Pronotum with two setae along lateral margin each side, one just anterad midlength and the second at obtuse-rounded hind angle (Fig. 3C); elytral striae 1–4 punctate in basal half, the punctures expanding strial breadth ..... | <i>M. putaputa</i> sp. n. |

- 4 Elytra ellipsoid (Figs 4B, D) or oblong with sides subparallel (Fig. 4C); elytral stria 7 obsolete, striae 5–6 shallower than discal striae 1–4; two dorsal elytral setae each side in third interval, the anterior near basal quarter of length, the posterior near midlength or slightly behind ..... **5**
- 4' Elytra narrow, sides subparallel and humeri projected laterad (Fig. 4A); elytral striae 1–8 deep, complete laterally; a single dorsal elytral seta each side in third interval at 0.25× elytral length..... ***M. toretore* sp. n.**
- 5 Elytral striae 2–4 complete, smooth, deeply impressed in basal half, small punctures may be present in the deepest portion of stria, but punctures do not expand striae breadth (Figs 4C, D); discal elytral intervals with distinct transverse microsculpture, either transverse lines not connected into a mesh, or a well-developed transverse mesh..... **6**
- 5' Elytral striae 2–4 shallow, interrupted in basal half between punctures that expand striae breadth (Fig. 4B); discal elytral intervals glossy, without microsculpture..... ***M. anaana* sp. n.**
- 6 Pronotal hind angles obtuse rounded, not projected, the median base narrow, MPW/BPW = 1.83–1.90 (Fig. 4C) ..... ***M. pirihaio* sp. n.**
- 6' Pronotal hind angles nearly right, projected, the median base broader, MPW/BPW = 1.56 (Fig. 4D)..... ***M. poro* sp. n.**

### ***M. dannieae* species group**

**Diagnosis.** Perrault (1986) diagnosed this group by pronotal configuration—the base constricted and lateral margins not or only briefly sinuate anterad the setose, obtusely rounded hind angles—and smooth elytral striae. Of the 10 Tahitian species assigned to the group (Perrault 1992), 7 were described from Mont Aorai, 2 from Mont Marau, and 1 from Tairapu (Fig. 1).

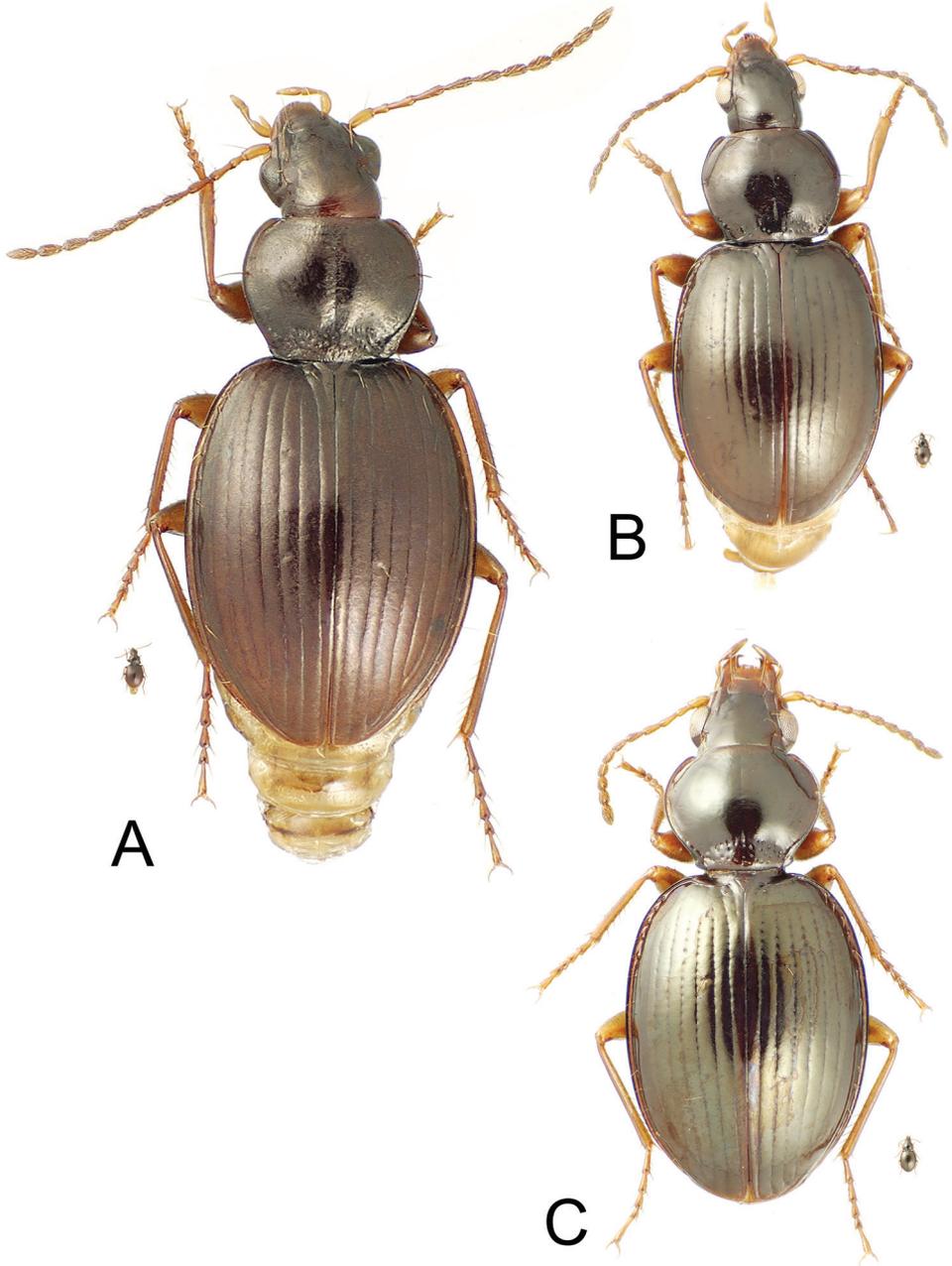
#### **1. *Mecyclothorax tutei* sp. n.**

urn:lsid:zoobank.org:act:3EA8F2C0-7762-4A3E-B007-0698D2C79170

[http://species-id.net/wiki/Mecyclothorax\\_tutei](http://species-id.net/wiki/Mecyclothorax_tutei)

Figs 3A, 8A

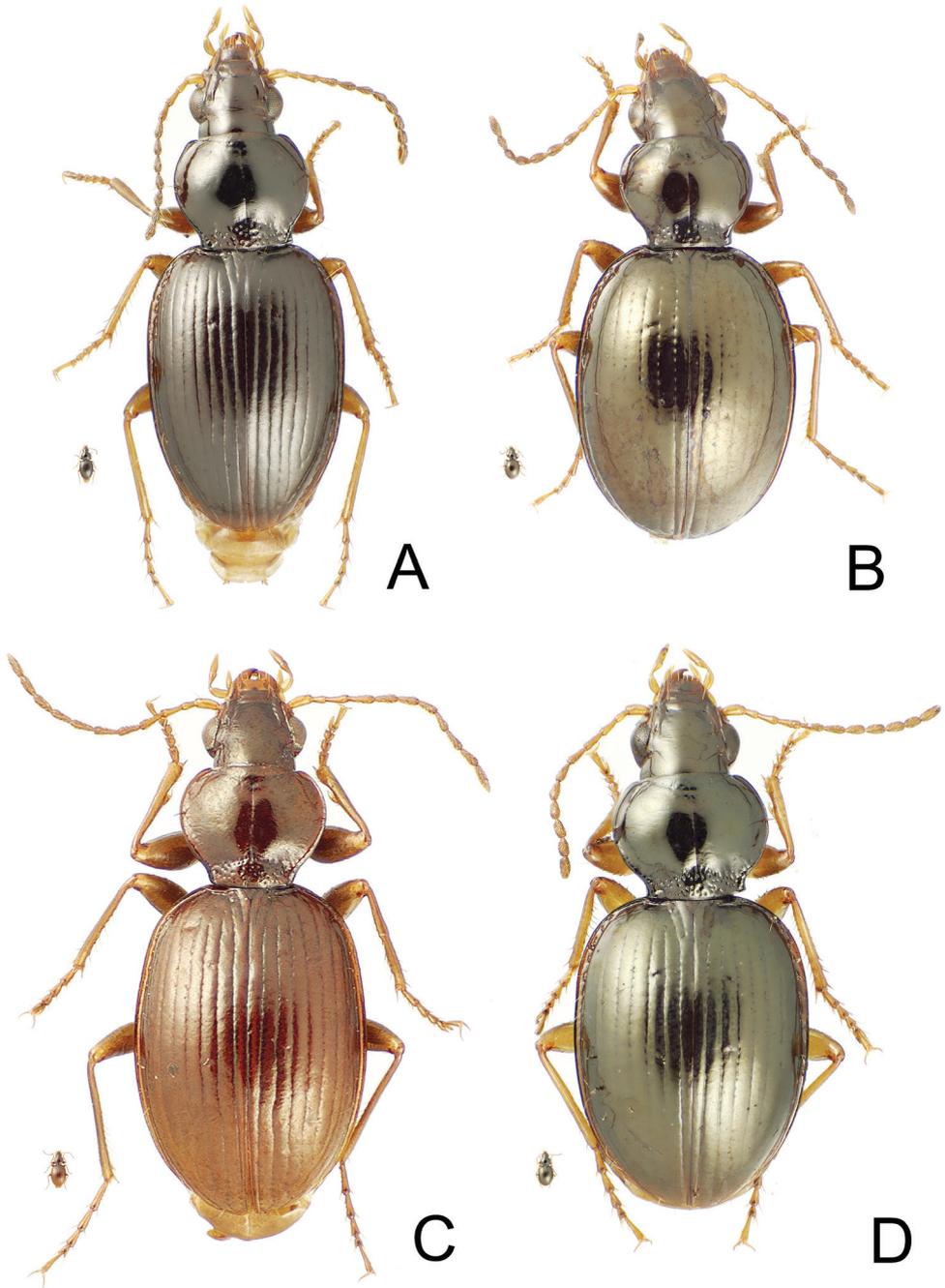
**Diagnosis.** Most similar to *M. cooki* Perrault, sharing: 1, moderately transverse pronotum, MPW/PL = 1.25; 2, straight to slightly sinuate pronotal lateral margin anterad obtusely rounded hind angle; 3, well-indicated parascutellar striole; 4, transverse-mesh elytral microsculpture; 5, two dorsal elytral setae; and 6, convex elytral intervals. Both species are characterized by a 2221 setal formula, however the pronotal hind angles are more rounded in *M. tutei* (Fig. 3A) and the pronotal base more constricted; MPW/BPW = 1.42 for *M. tutei*, versus 1.37 for *M. cooki*. Standardized body length is somewhat smaller in *M. tutei*; 5.3 mm versus 5.7 mm for *M. cooki*.



**Figure 3.** *Mecyclothorax* spp., dorsal view; small silhouette indicates actual size of beetle specimen at printed journal page size **A** *M. tutei* female holotype **B** *M. tibotii* male holotype **C** *M. putaputa* female paratype (CUIC)

**Description.** *Head capsule* with shallow frontal grooves, broad and obliquely wrinkled posteromedially near clypeus, transversely wrinkled medially on frons, with low rounded convexity laterally near antennal base, and thin carina mesad anterior supraor-

bital seta; vertex transversely depressed between posterior margin of eyes, depression visible in dorsal view; ocular lobe broadly convex, moderately protruded, meeting gena at  $> 135^\circ$  angle, juncture marked by narrow groove that is carinate behind; ocular ratio 1.46, ocular lobe ratio 0.78; labral anterior margin nearly straight, medially emarginated  $< 0.1 \times$  length; antennomeres 1–3 glabrous except for apical setae; antennae filiform, antennomere 8 length  $2.0 \times$  maximum breadth; mentum tooth sides defining an acute angle, apex tightly rounded. *Pronotum* moderately transverse,  $MPW/PL = 1.25$ , with narrower base,  $MPW/BPW = 1.42$ ; setose hind angles obtusely rounded, lateral margins briefly, indistinctly sinuate anterad minutely projected margin at seta, basal margin convexly rounded posterad seta causing jag in margin; median base distinctly depressed relative to disc,  $\sim 13$  punctures medially each side plus rugose wrinkles laterally; basal margin slightly convex between laterobasal depressions; median longitudinal impression broad, moderately deep with finely incised center, fine transverse wrinkles emanating laterally onto disc; anterior transverse impression very broad and shallow medially, crossed by numerous, distinct longitudinal wrinkles, finely incised and smooth in lateral half of breadth each side; anterior callosity as depressed as transverse impression medially, crossed by longitudinal wrinkles; front angles very slightly protruded, broadly rounded, closer together than hind angles,  $APW/BPW = 0.89$ ; lateral marginal depression narrow in apical half, edge upturned, broadened in basal half to broad, explanate margin laterad laterobasal depression; laterobasal depression broadly expanded from lateral depression, surface with small punctures mesally at disc, broadly raised lateral margin transversely wrinkled; proepisternum with 5 broad punctures along granulate hind margin, proepimeron with granulate hind margin; prosternal process broad, lateral margins broadly beaded, slightly depressed medially between procoxae. *Elytra* broadly ovoid, disc convex, upraised above scutellum, sides moderately sloped to  $75^\circ$  angle at marginal depression; basal groove distinctly arcuate forward to tightly rounded, proximate humeral angles,  $MEW/HuW = 2.39$ ; parascutellar seta present; parascutellar striole shallow, smooth, continuous; sutural interval convex, similar to striae 2–4 basally, narrower and more upraised apically; discal striae 2–6 broadly, moderately convex, smooth, slightly wavering along length; striae 1–8 of subequal depth at elytral apex, stria 2 slightly shallower, irregular; eighth interval upraised, bulging from apex to point laterad juncture of striae 5 + 6; two dorsal elytral setae in deep, evident depressions that extend only  $\frac{1}{2}$  width of interval 3, the setae at  $0.26\text{--}0.27 \times$  and  $0.54\text{--}0.57 \times$  elytral length; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 6; subapical sinuation very shallow, elongate, most impressed at posterior end of posterolateral setal series. *Mesepisternum* lined with about 24 punctures in 3–4 vertical rows; metepisternum short, width to length ratio 0.86; metepisternum separated from metepimeron by distinct suture. *Abdomen* with visible ventrites 1–5 irregularly wrinkled laterally, ventrites 4–6 with rounded lateral depressions; suture between visible ventrites 2 and 3 effaced laterally. *Legs* gracile, metatarsomeres elongate, metatarsomere 1 length  $0.215 \times$  metatarsal length; metatarsomere 4 emarginated apically, overall length  $1.4 \times$  median tarsomere length, apical setae present, subapical setae very short (or perhaps broken in the single type specimen); metatarsal dorsolateral sulci shallow, lateral, tarsomeres broadly convex medially. *Microsculpture* of head distinct, frons covered with a mixture of isodiametric



**Figure 4.** *Mecyclothorax* spp., dorsal view; small silhouette indicates actual size of beetle specimen at printed journal page size **A** *M. toretore* female holotype **B** *M. anaana* male paratype (CUIC) **C** *M. pirihaio* male paratype (CUIC) **D** *M. poro* female holotype

and transverse meshes; pronotal disc with shallow, evident transverse mesh, sculpticell breadth 2–4× length; pronotal median base with isodiametric mesh swirling among punctures; elytral disc covered with distinct transverse mesh microsculpture, sculpticell breadth 2–3× length, mixed with transverse lines; elytral apex with mixture of isodiametric and transverse mesh, the transverse sculpticells twice as broad as long; metasternum covered with transverse mesh; laterobasal abdominal ventrites covered with swirling isodiametric and transverse sculpticells. *Coloration* of head capsule rufobrunneous with piceous cast in frontal grooves; antennomeres 1–2 rufoflavous, 3–11 rufobrunneous; pronotal disc rufobrunneous, pronotal margins slightly paler on edge of disc, darker, rufopiceous on explanate lateral margins; proepipleuron rufoflavous anterad, rufobrunneous posterad, proepisternum brunneous; elytral disc rufobrunneous with silvery metallic reflection; sutural interval rufous basally, rufoflavous apically; elytral lateral marginal depression rufoflavous; elytral apex broadly, slightly paler, rufoflavous at apex; elytral epipleuron rufoflavous, metepisternum rufobrunneous; visible abdominal ventrites 1–3 rufobrunneous, 4–6 rufoflavous; metafemur rufoflavous; metatibia rufoflavous with brunneous cast.

**Female reproductive tract.** The unique female holotype was not dissected, although the gonocoxae were exposed allowing their preliminary characterization (Fig. 8A). Basal gonocoxite 1 broad apically, with apical fringe of 3–4 setae; apical gonocoxite 2 broad basally, stout, with tightly rounded apex, 2 lateral ensiform setae and 1 dorsal ensiform seta (visible through gonocoxite in ventral view (Fig. 8A), 2 apical nematiform setae in round pitlike depression.

**Holotype** female (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru cloud for. 1080 / m el. 20-IX-2006 lot 03 / 17°37.916'S, 149°22.318'W / pyrethrin fog fern frond / tangles C.P. Ewing // HOLOTYPE / Mecyclothorax / tutei / J.K. Liebherr 2012 (black-bordered red label).

**Etymology.** The species epithet honors Captain James Cook who named the Society Islands after the Royal Society, at whose behest he observed the 1769 transit of Venus from Tahiti. The epithet is his last name in Tahitian, Tute (Wahlroos 2002), treated as a latinized second declension noun in the genitive singular; *tutei*.

**Distribution and habitat.** The lone specimen of this species was found in tangles of living and dead fern fronds in low-stature wet montane *Weinmannia* and *Metrosideros* forest at 1080 m elevation. The beetle was collected from a beating sheet held under fronds that were sprayed with synthetic pyrethrin. The single specimen of *M. toretore* and a series of *M. pirihaio* were also found using this method at this elevation.

### ***M. altiusculus* species group**

**Diagnosis.** This species group comprises a disparate assemblage of taxa that Perrault (1988) suggested may need subdivision. The species treated below adheres to the original (Perrault 1986), less inclusive concept of the group, whereby the included taxa are assigned based on a pronotum that is basally constricted with straight to briefly sinuate basolateral margins and glabrous hind angles.

## 2. *Mecyclothorax tibotii* sp. n.

urn:lsid:zoobank.org:act:45EE710E-CF09-4BB5-86E9-EF1B0DBEC8F5

[http://species-id.net/wiki/Mecyclothorax\\_tibotii](http://species-id.net/wiki/Mecyclothorax_tibotii)

Figs 3B, 5A–B, 6A, 7A

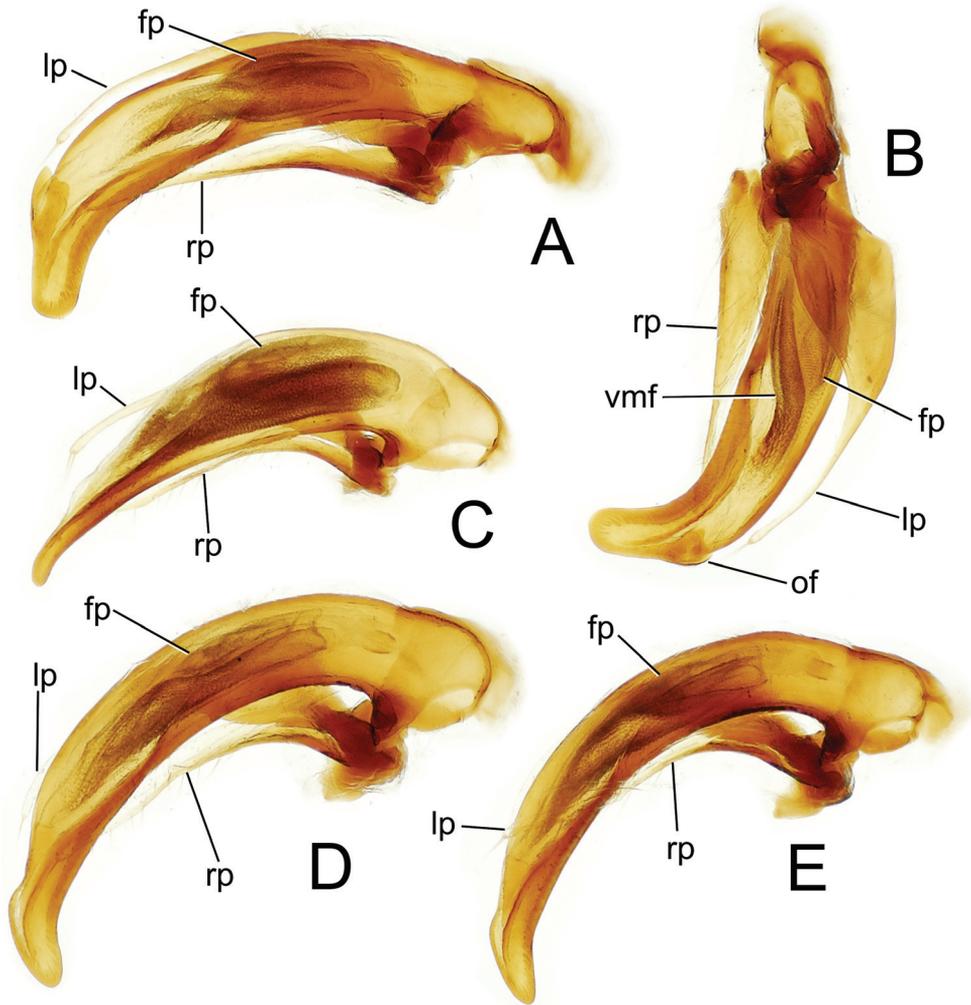
**Diagnosis.** Most similar to *M. ballioides* Perrault, based on: 1, glabrous, well-indicated pronotal hind angle and briefly sinuate basolateral pronotal margin (Fig. 3B); 2, presence of only the apical elytral seta, the subapical seta associated with the seventh stria absent. However, this species is characterized by presence of only the posterior supraorbital seta, resulting in a setal formula of 1121. The pronotal base is also much broader than in *M. ballioides*, with MPW/BPW = 1.33–1.36 (n = 2), versus 1.58–1.73 (n = 5) for *M. ballioides*. Standardized body length 4.1 mm.

**Description.** *Head capsule* with sinuate frontal grooves that are closest at anterior margin of frons, and divergent laterally on clypeus and also posteriorly toward anterior margin of eye, frons smooth between grooves, a broad convexity laterad grooves from frontoclypeal suture to position immediately dorsad eye; neck convex; ocular lobe abruptly protruded behind, meeting gena at < 135° angle, a broad shallow groove at juncture of lobe and gena; ocular ratio 1.42–1.44 (n = 2); ocular lobe ratio 0.81–0.82 (n = 2); labral anterior margin nearly straight, slightly protruded at rounded lateral corners; antennomeres 1–3 glabrous except for apical setae; antennae submoniliform, antennomere 8 length 1.77× maximum breadth; mentum tooth sides defining an acute angle, apex broadly rounded. *Pronotum* moderately transverse, MPW/PL = 1.24 (n = 2), glabrous hind angles distinct, slightly obtuse, little projected; lateral margins convergent for very short distance anterad denticulate hind angles; median base slightly depressed relative to disc, sparsely punctate, about 10 small, deep, and isolated punctures each side; basal margin slightly, evenly convex between hind angles; median longitudinal impression finely incised, complete on disc, present as lenticular depression at front of median base; anterior transverse impression complete, shallow medially, finely incised in outer 2/3 of breadth each side; anterior callosity slightly convex, smooth; front angles not protruded, inner margin angulate at juncture with anterior transverse impression; front angles closer together than hind angles, APW/BPW = 0.81–0.82 (n = 2); lateral marginal depression very narrow, edge finely beaded laterally, broader with finely upturned edge at front angle, broad at hind angle, marginal bead arcuately filling surface at angle; laterobasal depression obsolete, posterolateral portion of pronotal disc sloped to meet thick marginal bead at hind angle; proepisternum with 5 distinct punctures along hind margin, proepimeron with indistinct punctures along hind margin; prosternal process broad, lateral margins broadly beaded, slightly depressed medially between procoxae. *Elytra* subquadrate, the humeri laterally extended, MEW/HuW = 1.83–1.93; elytral disc convex, sides distinctly sloped to vertical juncture with lateral depression; basal groove broadly, evenly curved to tightly rounded humerus; parascutellar seta present, situated near sutural stria; parascutellar striole shallow, 3-punctate, interrupted along length; sutural interval broad, slightly elevated on disc, narrower, more convex apically; discal striae 1–5 with elongate punctures in basal

$\frac{1}{3}$  –  $\frac{1}{2}$  of length, the punctures slightly expanding stria near base, striae 3–6 obsolete on elytral base and humerus; sutural stria fine and deep apically, stria 2 very shallow, broad, incomplete, striae 3–6 obsolete, and stria 7 broad and shallow apicad subapical sinuation; due to reduction of stria 7, interval 8 not subcarinate, but surface outwardly bulging, convex, vertically meeting stria 8; dorsal elytral setae in shallow impressions that span  $\frac{3}{4}$  of interval 3, setation unstable (see Variation section), the anterior seta at  $0.23\times$  elytral length, posterior seta at  $0.61\times$  length; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 6; elytral marginal depression moderately narrow, edge slightly upturned at humerus, margin beadlike from midlength to subapical sinuation; subapical sinuation shallow, nearly obsolete, elytral margin straight. *Mesepisternum* with 12 punctures in 2–3 vertical rows; metepisternum short, anterior and mesal margins of subequal length, width to length ratio 0.88; metepisternum separated from metepimeron by distinct suture; metathoracic flight wing an ovoid flap, the broadly rounded apex extended  $\frac{1}{2}$  distance to metanotal hind margin; wing vestigium with rudiments of R and M veins. *Abdomen* with visible ventrites 1–3 irregularly wrinkled laterally, ventrites 3–6 with rounded depressions laterally; suture between visible ventrites 2 and 3 effaced laterally. *Metatarsomere 4* slightly emarginated apically, overall length  $1.3\times$  median tarsomere length, both apical and subapical setae present; metatarsal dorsolateral sulci shallow and lateral, tarsomere median area slightly convex. *Microsculpture* reduced on head, frons glossy, neck with indistinct isodiametric sculpticells; pronotal disc glossy, indistinct transverse mesh with sculpticell breadth  $2\times$  length observable outside areas of reflected light; pronotal median base with swirling transverse mesh, sculpticell breadth  $2\times$  length among punctures; elytral disc covered with well-developed transverse lines connected only occasionally, surface subiridescent; elytral apex with transverse mesh, sculpticell breadth  $2\text{--}4\times$  length, mixed with transverse lines; metasternum covered with transverse mesh; laterobasal abdominal ventrites with swirling isodiametric and transverse sculpticells. *Coloration* of vertex rufous with a piceous cast; antennomere 1 flavous, antennomeres 2–3 rufoflavous, 4–11 rufobrunneous; pronotal disc dark rufous; pronotal margins concolorous with disc, lateral bead piceous, apex and base narrowly rufous; proepipleuron rufoflavous, proepisternum dark rufous; elytral disc dark rufous with silvery metallic reflection; sutural interval rufous basally, concolorous apically; elytral marginal depression rufoflavous apically; elytral epipleuron rufoflavous with a brunneous cast, metepisternum rufobrunneous; abdomen rufobrunneous medially, darker with piceous cast laterally; apical  $\frac{1}{3}$  of visible ventrite 6 rufoflavous; metafemur rufoflavous; metatibia rufoflavous with brunneous cast.

**Variation.** Although this species is characterized by the presence of two dorsal elytral setae, the two known specimens vary in this regard. The male holotype exhibits only an anterior seta on the left elytron, and only a posterior seta on the right. The female allotype has both anterior and posterior setae present on the left elytron, but only the anterior seta on the right side.

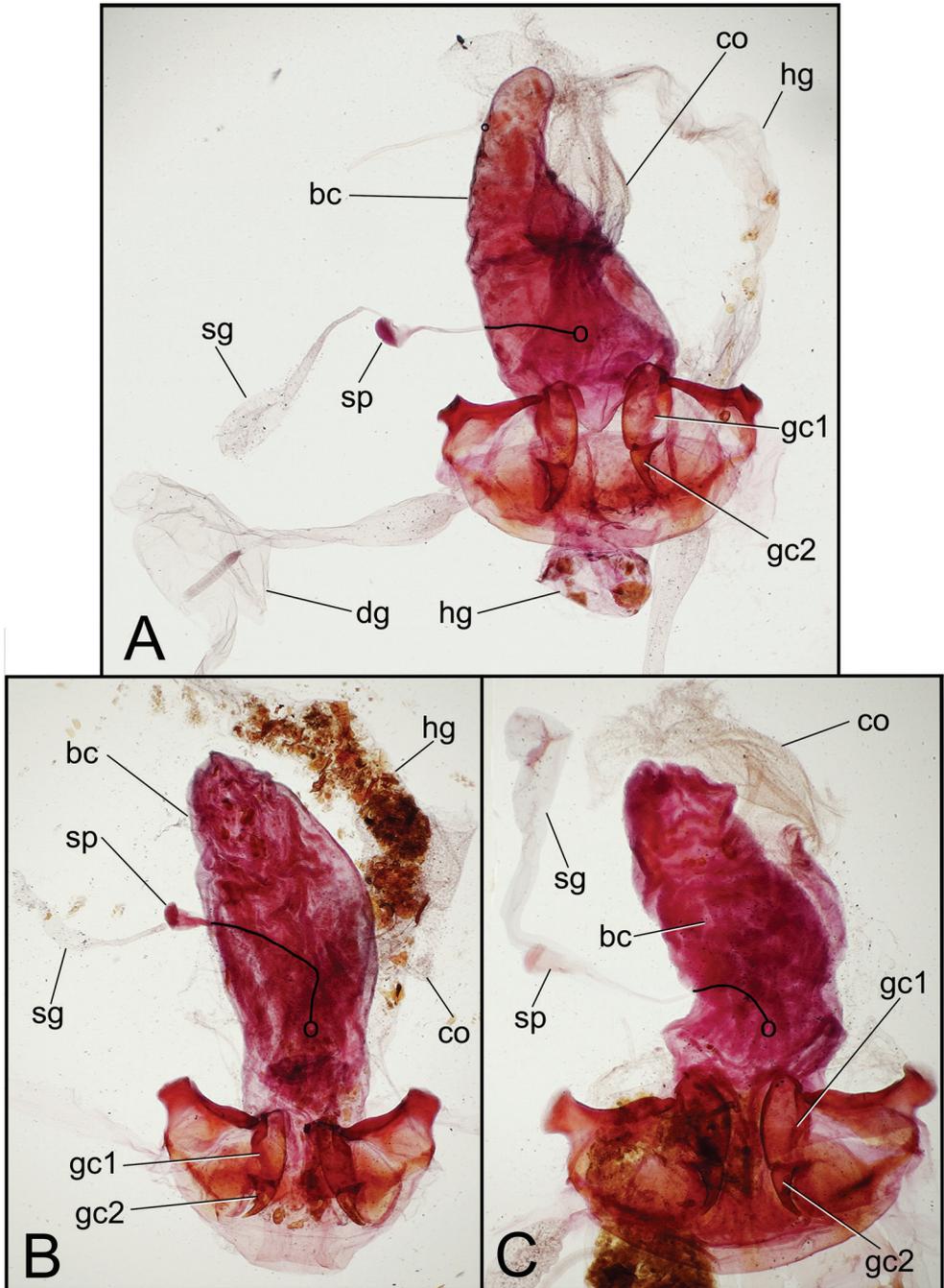
**Male genitalia.** Aedeagal median lobe narrow and straight basally, right lateral view (Fig. 5A), curved downward apicad articulatory projection of parameres, apex broadly rounded, a large ostial flap at apical margin of ostial opening (Fig. 5A); median



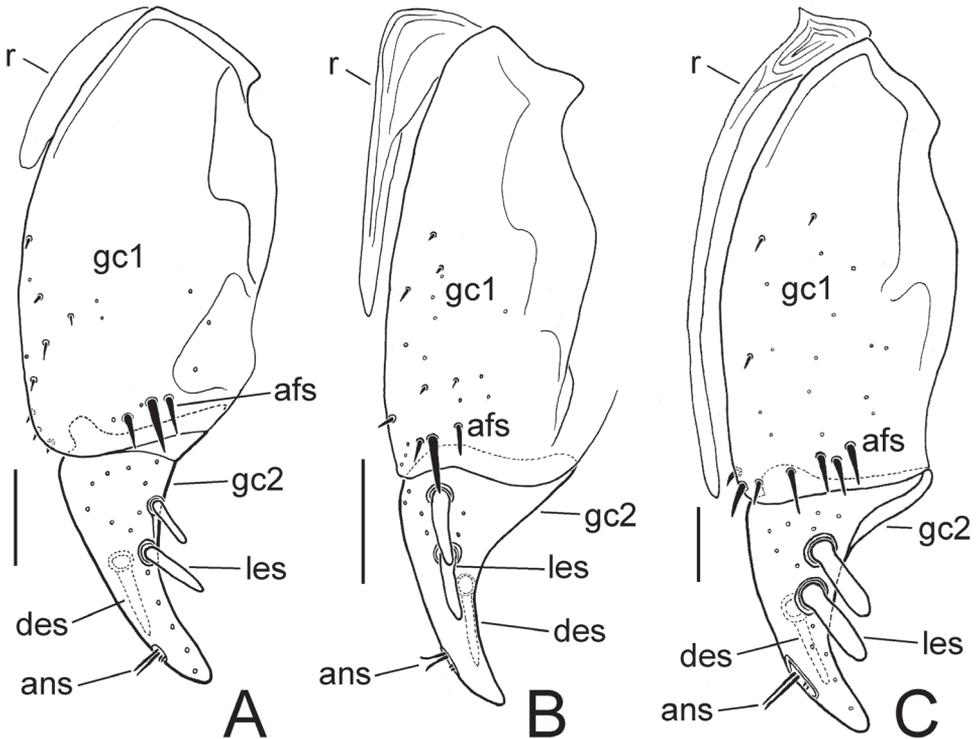
**Figure 5.** Male aedeagal median lobe and associated parameres, *Mecyclothorax* spp.; all figures to same scale **A** *M. tibotii*, right lateral view **B** *M. tibotii*, euventral view **C** *M. anaana*, right lateral view **D** *M. pirihaio*, male dissection 1, right lateral view **E** *M. pirihaio*, male dissection 2, right lateral view Abbreviations: **fp** flagellar plate **lp** left paramere **of** ostial flap **rp** right paramere **vmf** ventral microtrichial field.

lobe curved to the right apically in euventral view (Fig. 5B), the axis of apex nearly perpendicular to axis of median lobe base; internal sac with well-developed ventral microtrichial field but without distinct spicules; flagellar plate moderately large, length  $\frac{1}{3}$  distance from parameral articulation to distal surface of apex; parameres extended  $0.82\times$  distance from parameral articulation to distal surface of apex.

**Female reproductive tract.** Bursa copulatrix broad basally, narrowed to apical third that extends as a narrow projection (Fig. 6A); bursal membrane thin, unwrinkled under microslide cover slip; spermatheca broadest in apical half, length  $0.2\times$  length of spermathecal duct, duct joined to dorsal wall of bursa dorsad the basally broad common oviduct;



**Figure 6.** Female reproductive tract dissections, *Mecyclothorax* spp., ventral view; figures to same scale **A** *M. tibotii* **B** *M. anaana* **C** *M. pirihaio* Abbreviations: **bc** bursa copulatrix **co** common oviduct **dg** defensive fland reservoir **gc1** basal gonocoxite 1 **gc2** apical gonocoxite 2 **hg** rectum of hindgut **sg** spermathecal gland **sp** spermatheca. Position of spermathecal duct and juncture of duct with dorsal wall of bursa indicated by black line and terminal circle, respectively



**Figure 7.** Female left gonocoxite, *Mecyclothorax* spp., ventral view **A** *M. tihotii* **B** *M. anaana* **C** *M. pirihae*. Abbreviations: **afs** apical fringe setae **ans** apical nematiform setae **des** dorsal ensiform seta **gc1** basal gonocoxite 1 **gc2** apical gonocoxite 2 **les** lateral ensiform setae **r** ramus.

spermathecal gland with orbicular reservoir, the reservoir about  $\frac{1}{2}$  length of duct which enters at base of spermatheca; membranous ramus at base of basal gonocoxite of usual length for *Mecyclothorax* spp. (e.g., Liebherr 2011, 2012), extended about  $\frac{1}{3}$  length of basal coxite (Fig. 7A); basal gonocoxite 1 with 3 apical fringe setae, medial surfaces from dorsal to ventral with about 8 very small setae; apical gonocoxite 2 narrow, apex subacuminate, with 2 lateral ensiform setae, the basal seta shorter and narrower than apical seta, 1 dorsal ensiform seta, and 2 short apical nematiform setae in small pitlike depression.

**Holotype** male (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru trail at pylon 4 / el. 1060 m 5-IX-2006 lot 01 / 17°38.055'S, 149°22.146'W / pyr. fog mossy *Metrosideros* / & *Melicope* J.K. Liebherr // HOLOTYPE / *Mecyclothorax tihotii* / J.K. Liebherr 2012 (black-bordered red label).

**Allotype** female (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru trail at pylon 4 / el. 1060 m 5-IX-2006 lot 02 / 17°38.055'S, 149°22.146'W / beating flowering *Myrsine* & / *Metrosideros* J.K. Liebherr // ALLOTYPE... (same labeling as holotype).

**Etymology.** Based on the extreme similarity of this species to *M. ballioides*, by which Georges Perrault honored Professor George E. Ball, the species epithet *tihotii*—Tahitian for George (Wahlroos 2002)—is used. The epithet treats Tihoti, George, as a latinized second declension noun in the genitive singular.

**Distribution and habitat.** The holotype was collected in a pyrethrin fog sample of moss-covered *Metrosideros* trunks (e.g., Fig. 2C) that served as nursery logs for *Melicope* plants. This specimen plus the holotype of *M. putaputa* comprised the entirety of carabid beetles from that sampled trunk. The female allotype was collected by beating *Myrsine* and mossy vegetation in the same area of low-stature forest, the allotype syntopic with two specimens of *M. anaana*.

### *M. viridis* species group

**Diagnosis.** Member taxa of this species group are diagnosed by a pronotum with base narrower than maximal breadth near midlength, and lateral margins distinctly sinuate immediately anterad the projected, setose hind angles. The elytra are convex and ellipsoid (Fig. 3C). This is the sixth species described in the group. Of the others, two each are recorded from Mont Marau and Mont Aorai (Perrault 1986), and one is known from Mont Tohica, Moorea (Liebherr 2012).

### 3. *Mecyclothorax putaputa* sp. n.

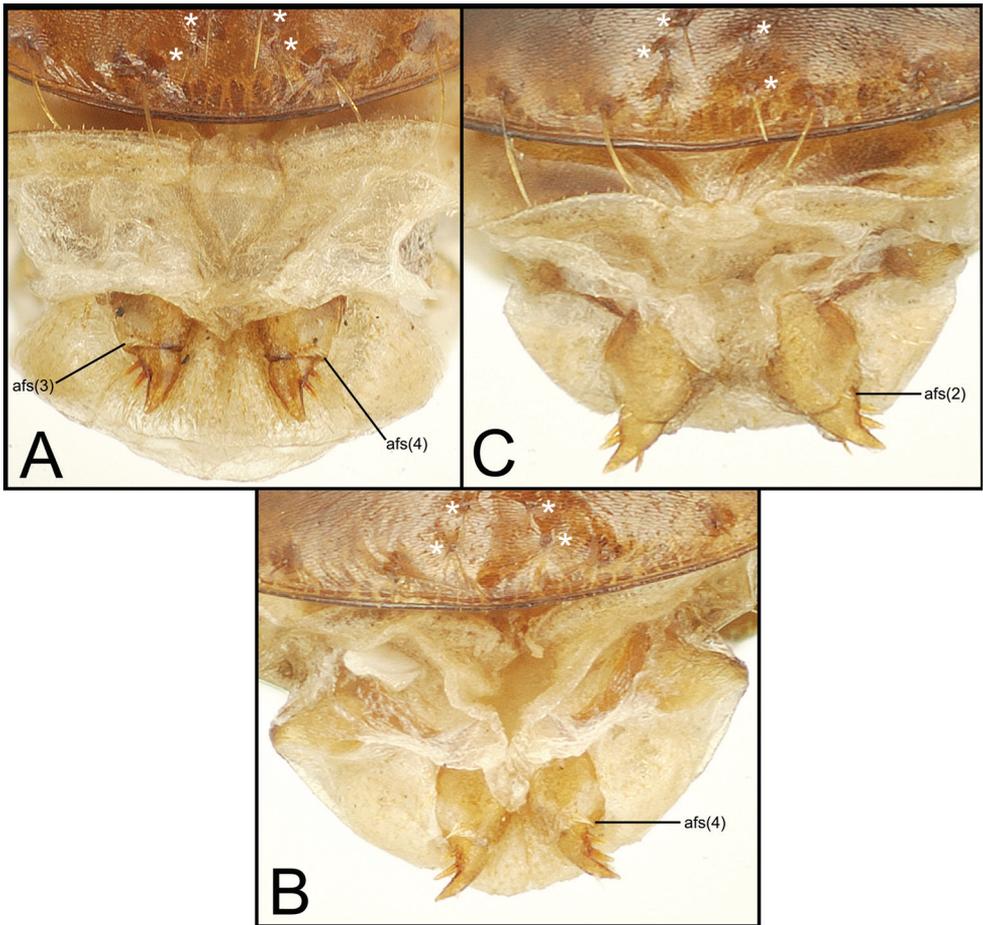
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[http://species-id.net/wiki/Mecyclothorax\\_putaputa](http://species-id.net/wiki/Mecyclothorax_putaputa)

Figs 3C, 8B

**Diagnosis.** This species shares well-developed microsculpture on head, pronotum and elytra with *M. castaneus* Perrault, the sculpticells a mixture of isodiametric and transverse on frons, transverse on pronotal disc, and of dense transverse lines on the elytral intervals. The discal elytral striae are distinctly punctate in this species, with the punctures in the basal third of striae 1–4 expanding the breadth of the striae, a character shared with *M. mapo* Liebherr of Moorea. However *M. mapo* differs by transverse-mesh elytral microsculpture and obsolete microsculpture on head and pronotum. This species differs from both *M. castaneus* and *M. mapo* by the obtuse-rounded pronotal hind angles, versus right and sharp hind angles in those two species. Whereas the two type specimens of *M. castaneus* (Perrault, 1986) variably exhibit one or two dorsal elytral setae (one the more common condition), the two specimens of this new species plus those of *M. mapo* are uniformly bisetose; setal formula 2221. Beetles of this species exhibit standardized body length 4.3–4.5 mm versus 3.8–4.1 mm for *M. castaneus*. The type series of *M. mapo* includes individuals with body length ranging 3.8–4.4 mm.

**Description.** *Head capsule* with frontal grooves subparallel mesad anterior supraorbital setae, convergent anteriorly, deep and broad at frontoclypeal suture, thin carina present mesad anterior supraorbital seta; neck convex between eye hind margins; ocular lobe little protruded, meeting gena at 150° angle, a shallow and narrow groove at juncture; ocular ratio 1.57 (n = 2), ocular lobe ratio 0.87–0.89; labral



**Figure 8.** Exposed gonocoxae and apical visible ventrite of *Mecyclothorax* holotype females, ventral view; four setae comprising median setal patch on female apical visible ventrite indicated by asterisks; number of apical fringe setae (afs) of basal gonocoxite 1 indicated in parentheses **A** *M. tutei* **B** *M. putaputa* **C** *M. toretore*

anterior margin angularly emarginated medially, impressed  $\frac{1}{8}$  length; antennomeres 1–3 glabrous except for apical setae, minute pore sensilla visible in translucent cuticle of shafts; antennae submoniliform, antennomere 8 length 1.67× maximal breadth; mentum tooth sides defining an acute angle, apex tightly rounded. *Pronotum* quadrisetose, moderately transverse, constricted basally, MPW/PL = 1.18–1.24 (n = 2), MPW/BPW = 1.52–1.60; hind angles obtuse, set forward from base by convex basal margin; lateral margins subparallel just laterad hind setae, then divergent immediately anterad setal sockets; median base slightly depressed relative to disc, margin with disc lined with 5 large punctures each side, about 14 smaller punctures each side on base; median longitudinal impression finely incised, shallow with fine transverse wrinkles, present as lenticular depression at front of median base; anterior transverse impression shallow, broad medially, fine longitudinal wrinkles present behind impression on disc, impression distinctly incised in outer half of breadth

each side; anterior callosity slightly convex, smooth; front angles slightly protruded, tightly rounded, distance between front angles subequal to distance between hind angles, APW/BPW = 0.97–1.0 (n = 2); lateral marginal depression very narrow at midlength, slightly broader at front angle, marginal bead and depression slightly broader along sinuate basolateral margin and basally posterad laterobasal depression; laterobasal depression a narrowly expanded continuation of lateral marginal depression, 2–3 punctures along mesal margin with disc; proepisternum with 5 distinct punctures along hind margin, the punctures separated by small carinae; prosternal process broad, broadly beaded laterally, median area convex between lateral beads. *Elytra* ellipsoid, moderately convex, disc little upraised above scutellum, sides sloped to near vertical juncture with marginal depression; basal groove narrowly curved to tightly rounded humerus, the humeri close together, MEW/HuW = 2.22–2.28 (n = 2); parascutellar seta present, situated just mesad sutural stria; parascutellar striole 4–5-punctate, striole interrupted or very shallow between punctures; sutural interval as broad and convex as intervals 2–4 basally, narrower and upraised to sutural juncture apically; discal striae 1–4 moderately impressed, minutely punctate, striae 5–6 shallow but evident on disc, stria 7 obsolete, interrupted in basal half, striae 2–6 very shallow but traceable to basal groove on humerus; striae 1, 2, and 7 deepest at elytral apex, striae 3–4 shallow, broad, and striae 5–6 very shallow but traceable; eighth interval carinate at apex of stria 3, more broadly subcarinate, convex laterally apicad stria 4; two dorsal elytral setae set in evident impressions that cross ½ width of interval 3, setal positions at 0.23–0.25× and 0.58–0.60× elytral length; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 6; elytral marginal depression moderately narrow at humerus, but edge upturned, depression broadest laterad anterior setal series, narrowed with beaded margin to subapical situation; subapical situation abrupt, deep, short. *Mesepisternum* with 9 punctures in 1–2 vertical rows; metepisternum slightly elongate, width to length ratio 0.79; metepisternum separated from metepimeron by distinct suture; metathoracic flight wing a trapezoidal flap, the apex extended just beyond metanotal hind margin; wing vestigium with rudiments of R and M veins, the vein remnants darker tan versus the ivory wing membrane. *Abdomen* with visible ventrites 1–5 irregularly wrinkled laterally, ventrites 3–6 with rounded depressions laterally; suture between visible ventrites 2 and 3 effaced laterally. *Legs* moderately gracile, metatarsomere 1 length 0.204× metatibial length; metatarsomere 4 moderately, broadly triangular apically, overall length 1.43× median tarsomere length; metatarsomere 4 with apical and subapical setae; metatarsal dorsolateral sulci shallow and lateral, tarsomere median surface broadly convex. *Microsculpture* of head well developed, frons with transverse mesh of sculpticell breadth 3–4× length, neck with transverse mesh 2× broad as long; pronotal disc with evident transverse mesh, sculpticell breadth 2–4× length, mixed with transverse lines; pronotal median base covered with swirling transverse mesh among punctures; elytral disc with evident transverse lines loosely joined into a mesh, the surface subiridescent; elytral apex with transverse mesh, sculpticell breadth 2–4× length; metasternum covered with distinct transverse mesh; laterobasal abdominal ventrites

with swirling isodiametric and transverse sculpticells. *Coloration* of head rufous with a piceous cast, clypeus rufoflavous; antennomeres 1–2 flavous, 3–11 darker, with smoky cast; pronotal disc rufous, margins of disc narrowly rufoflavous, marginal bead rufo-piceous; proepipleuron rufoflavous with brunneous cast, proepisternum rufo-brunneous; elytral disc rufous with silvery metallic reflection; sutural interval slightly paler basally, concolorous on disc, rufoflavous apically; elytral margins concolorous at humerus, narrowly rufoflavous in depth of lateral marginal depression; elytral apex beyond subapical sinuation graded to rufoflavous; elytral epipleuron rufoflavous with brunneous cast, metepisternum rufo-brunneous; visible abdominal ventrites 1–6 rufo-brunneous, ventrites 1–3 with piceous cast laterally, apical  $\frac{1}{4}$  of apical ventrite 6 paler, rufoflavous; metafemur flavous with brunneous cast; metatibia flavous, carina associated with longitudinal setal series darker, rufo-brunneous.

**Female reproductive tract.** The unique female holotype was not dissected, although the gonocoxae were exposed allowing their preliminary characterization (Fig. 8B). Basal gonocoxite 1 narrowed apically to narrow, scimitar-like apical gonocoxite 2; basal gonocoxite 1 with apical fringe of 4 setae; apical gonocoxite 2 narrow basally, curved, apex acuminate, with 2 lateral ensiform setae, the basal lateral seta much smaller than the apical seta, and 1 dorsal ensiform seta (visible through gonocoxite in ventral view); apical gonocoxite with 2 apical nematiform setae in pitlike depression. Initially, the female paratype was dissected, although the specimen apparently suffered trauma in the killing jar, as only the base of each basal gonocoxite 1 jaggedly remained attached to laterotergite IX. The internal reproductive tract was also damaged, however the following characters could be determined: bursa copulatrix ovoid with length twice breadth when compressed on microslide, apex with slight constriction defining an ill-defined apical lobe; spermatheca orbicular, spermathecal length about  $\frac{1}{4}$  length of spermathecal duct; spermathecal gland entering base of spermatheca, the duct subequal in length to apical gland reservoir.

**Holotype** female (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru trail at pylon 4 / el. 1060 m 5-IX-2006 lot 01 / 17°38.055'S, 149°22.146'W / pyr. fog mossy *Metrosideros* / & *Melicope* J.K. Liebherr // 1 // HOLOTYPE / Mecyclothorax / putaputa / J.K. Liebherr 2012 (black-bordered red label).

**Paratype** female. SOCIETY ISLANDS: Tahiti Nui; Mauru, above pylon 4, cloud forest, 17°38.05'S, 149°22.15'W, 1060 m el., beating vegetation, 19-ix-2006 lot 01, Liebherr (CUIC, 1).

**Etymology.** The species epithet, *putaputa*, is Tahitian for punctured (Wahlroos 2002), signifying the distinctly punctate discal elytral striae. The epithet is to be treated at a noun in apposition.

**Distribution and habitat.** The two specimens of this species were found at 1060 and 1100 m elevation, in low-stature *Weinmannia* and *Metrosideros* forest. One specimen was collected in a pyrethrin fog sample from moss growing on a *Metrosideros* trunk, the second by beating vegetation along the margins of openings in the forest. *M. tibotii* and *M. anaana* were the two species found syntopically in these situations (Fig. 2C).

### *M. globosus* species group

**Diagnosis.** Members of this group are characterized by the narrow pronotum with narrow lateral marginal depression, and the lateral pronotal margin elongately sinuate anterad the glabrous hind angle (Fig. 4). Perrault (1989) revised 19 species of the group, with Liebherr (2012) describing 2 more from Mont Tohiea, Moorea.

#### 4. *Mecyclothorax toretore* sp. n.

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[http://species-id.net/wiki/Mecyclothorax\\_toretore](http://species-id.net/wiki/Mecyclothorax_toretore)

Figs 4A, 8C

**Diagnosis.** This species shares fully striate elytra and transversely-lined elytral microsculpture with *M. fuscus* Perrault. Both species are also characterized by presence of only the anterior dorsal elytral seta and only the apical elytral seta; setal formula 2111. However, this species differs by: 1, the very narrow elytra with subparallel lateral margins versus more ovoid elytra in *M. fuscus*; and 2, the laterally extended humeri resulting in a MEW/HuW ratio of 1.89 in this species, versus MEW/HuW = 1.97 for *M. fuscus*. The pronotal hind angles are also profoundly margined in this species (Fig. 4A), with the lateral and basal marginal beads defining a U-shaped pronotal laterobasal depression. Conversely, the hind angles are upraised but without a distinctly beaded margin in *M. fuscus*. Standardized body length is 4.2 mm for this species versus 4.0 mm for *M. fuscus*.

**Description.** *Head capsule* with linear, slightly convergent frontal grooves, broad and shallow at frontoclypeal suture, terminated posteriorly mesad thin carina inside anterior supraorbital seta; neck slightly depressed between two pairs of supraorbital setae, depression visible dorsally (Fig. 4A); ocular lobe moderately protruded, hind margin joining gena at 135° angle, juncture marked by narrow, shallow groove; ocular ratio 1.34, ocular lobe ratio 0.88; labral anterior margin nearly straight, emarginated  $< 0.1 \times$  length; antennomeres 1–3 glabrous except for apical setae, pore sensilla visible in the translucent cuticle; antennae elongate, filiform, antennomere 8 length  $2.29 \times$  maximal breadth; mentum tooth sides defining acute angle, apex narrowly rounded. *Pronotum* subquadrate, MPW/PL = 1.14, base constricted with distinctly sinuate lateral margins anterad sharply projected, nearly right hind angles, MPW/BPW = 1.46; median base moderately depressed relative to disc, 14–16 regular punctures each side; basal margin slightly convex between laterobasal depressions; median longitudinal impression very fine and shallow on disc, indistinct transverse wrinkles emanating onto disc anteriorly, lenticular depression at front of median base; anterior transverse impression very broad, very shallow medially, impression incised in outer half of breadth each side; anterior callosity slightly convex, crossed with numerous fine longitudinal wrinkles; front angles slightly protruded, broadly rounded laterally; front angles closer together than hind angles, APW/BPW = 0.90; lateral marginal depression very narrow laterally,

slightly wider at front angle, margin beaded throughout, bead broad at sinuate basolateral margin; surface of U-shaped laterobasal depression sparsely lined with minute micropunctures; prosternal process distinctly beaded laterally between procoxae, medially convex between beads. *Elytra* narrowly subparallel, MEW/HuW = 1.89; disc slightly convex toward apical  $\frac{1}{3}$  of suture, sloped toward sides but ninth interval visible in dorsal view; basal groove broadly curved to point basad stria 5, then distinctly curved anterad to angulate humerus; parascutellar seta present, situated near sutural stria; parascutellar striole 4–5-punctate, striole shallow between shallow punctures; sutural interval broadly upraised to suture basally, narrower with similar convexity apically, therefore appearing more callouslike; striae 1–6 minutely punctate in basal  $\frac{1}{3}$ , punctures associated with strial irregularities, striae 5–6 obsolete basally; intervals 2–5 moderately convex on disc; striae 1–4 plus 7 deep apically, striae 5–6 shallow but traceable; eighth interval broadly convex from midpoint of posterior lateral setal series to apex; 1 dorsal elytral seta situated at  $0.26\times$  elytral length, seta situated in deep, evident depression that spans  $\frac{3}{4}$  width of interval 3; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 5; elytral marginal depression narrow, margin little upturned at humerus, margin slightly explanate outside anterior lateral setal series, beadlike in posterior half; subapical sinuation broad, shallow. *Mesepisternum* with about 16 punctures in 2–3 vertical rows; metepisternum slightly elongate, width to length ratio 0.79; metepisternum separated from metepimeron by distinct suture. *Abdomen* with visible ventrites 1–3 irregularly wrinkled laterally, ventrites 3–6 with rounded depressions laterally; suture between visible ventrites 2 and 3 complete. *Legs* somewhat foreshortened, metatarsomere 1 length  $0.17\times$  metatibial length; metatarsomere 4 slightly emarginated apically, overall length  $1.2\times$  median tarsomere length; metatarsomere 4 with apical and subapical setae; metatarsal dorsolateral sulci shallow and lateral, tarsomere median surface broadly convex. *Microsculpture* of head an indistinct transverse mesh, sculpticell breadth 2–3 $\times$  length, surface glossy; pronotal disc with transverse mesh, sculpticell breadth 2–4 $\times$  length, mixed with transverse lines; pronotal median base with shallow transverse mesh, sculpticell breadth  $2\times$  length among the punctures; elytral disc with well-developed transverse lines, only occasional cross-connections, surface subiridescent; elytral apex with a mixture of transverse mesh, sculpticell breadth 2–4 $\times$  length, and transverse lines; metasternum with distinct transverse mesh; laterobasal abdominal ventrites with swirling isodiametric and transverse sculpticells. *Coloration* of head capsule dark rufous, clypeus rufoflavous; antennomeres 1–2 rufoflavous, antennomere 3 slightly darker, 4–11 rufobrunneous; pronotal disc dark rufous; pronotal margins and median base paler, rufous; proepipleuron rufoflavous, proepisternum dark rufous; elytral disc dark rufous with piceous cast in apical  $\frac{1}{3}$ ; sutural interval rufous basally, pale rufous apically; elytral marginal depression concolorous with disc at humerus, lateral marginal depression paler, rufoflavous laterally and apically; elytral epipleuron rufoflavous dorsally, more brunneous ventrally, metepisternum rufobrunneous; abdomen rufobrunneous medially, visible ventrites 1–3 with piceous cast laterally; apical  $\frac{1}{4}$  of apical visible abdominal ventrite paler, rufoflavous; metafemur flavous; metatibia flavous with darker carina associated with longitudinal setal series.

**Female reproductive tract.**— The unique female holotype was not dissected, although the gonocoxae were exposed allowing their preliminary characterization (Fig. 8C). Basal gonocoxite 1 with angulate apical margin, the margin angled toward base along lateral half of apical gonocoxite 2; basal gonocoxite with apical fringe of 2 setae; apical gonocoxite 2 distinctly convergent in basal half of length, apical half more narrowly convergent to subacuminate tip, with 2 lateral ensiform setae and 1 dorsal ensiform seta that extends medially—and is thus visible in ventral view—and 2 apical nematiform setae.

**Holotype** female (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru cloud for. 1080 / m el. 20-IX-2006 lot 03 / 17°37.916'S, 149°22.318'W / pyrethrin fog fern frond / tangles C.P. Ewing // HOLOTYPE / Mecyclothorax / toretore / J.K. Liebherr 2012 (black-bordered red label).

**Etymology.** The Tahitian word toretore means striped, as in striped cloth (Wahlroos 2002). The word's use as the species epithet signifies the deep, distinct elytral striae, and is to be used as a noun in apposition.

**Distribution and habitat.** The lone specimen of this species was found in the highest, wettest rain forest sampled—1080–1100 m elevation—during a tropical rain-storm, the use of a hand-held pyrethrin fog canister over a beating sheet the sole collecting method of any utility under those conditions. That the beetle plus those of *M. tutei* and *M. pirihaio* were found in dead fern tangles during this storm suggests that the beetles had moved into such tight quarters due to the rain. Neither *M. tutei* nor *M. toretore* were collected during drier conditions in this elevational band of forest even though extensive beating of vegetation had been undertaken over the course of three days.

### 5. *Mecyclothorax anaana* sp. n.

urn:lsid:zoobank.org:act:71CD8BDF-267A-4AFC-A753-CA92AE48966C

[http://species-id.net/wiki/Mecyclothorax\\_anaana](http://species-id.net/wiki/Mecyclothorax_anaana)

Figs 4B, 5C, 6B, 7B

**Diagnosis.** This species is closest to *M. hemisphaericus* Perrault, sharing much reduced dorsal microsculpture, very shallow elytral striae and flat elytral intervals, and two supraorbital setae. However this species deviates from *M. hemisphaericus* by the presence of two dorsal elytral setae; setal formula 2121 versus 2111 for *M. hemisphaericus*. Standardized body length ranges 3.7–4.2 mm in this species versus 3.5–3.9 mm for *M. hemisphaericus* (n = 2, NHMB). The male aedeagus differs also, with the apex of the median lobe narrowly extended and downturned in this species (Fig. 5C) versus expanded both dorsally and ventrally, and no more downturned than the more basal portion of the shaft in *M. hemisphaericus* (Perrault 1989, fig. 11).

**Description.** *Head capsule* with linear, slightly convergent frontal grooves, deep and broad at frontoclypeal suture, narrowly terminated mesad thin carina inside anterior supraorbital seta; frons and neck convex; ocular lobe moderately protruded, posteriorly meeting gena at > 135° angle; eyes small with outer surface more convex

than curvature of lobe, hind portion of lobe meeting gena at shallow groove with low carina behind; ocular ratio 1.41–1.46 ( $n = 5$ ), ocular lobe ratio 0.77–0.81 ( $n = 5$ ); labral anterior margin nearly straight, emarginated  $< 0.1 \times$  length; antennomeres 1–3 glabrous except for apical setae; antennae submoniliform, antennomere 8 length  $1.85 \times$  maximal breadth; mentum tooth sides defining acute angle, apex narrowly rounded. *Pronotum* cordate, basolateral margin constrictedly sinuate, base narrow, MPW/BPW = 1.55–1.65 ( $n = 5$ ), overall shape appearing only slightly transverse, although MPW/PL = 1.16–1.23 ( $n = 5$ ); glabrous hind angle sharply projected, nearly right, basal margin of angle convex; median base moderately depressed relative to disc, surface smooth, glossy, 9–10 deep, isolated punctures each side; basal margin slightly convex between hind angles; median longitudinal impression very shallow, finely incised, present as lenticular depression at front of median base; anterior transverse impression broad and shallow to obsolete medially, incised in outer half of breadth each side; anterior callosity flat, depressed medially, basal half may be crossed by indistinct longitudinal wrinkles; front angles slightly protruded, narrowly rounded; apical pronotal width greater than narrow base, APW/BPW = 1.09–1.13 ( $n = 5$ ); lateral marginal depression very narrow at midlength, slightly wider at front angle, margin beaded throughout, bead slightly broader outside laterobasal depression; laterobasal depression linear, bordered laterally by broad marginal bead, medially by linear depression or punctures at edge of median base; proepisternum with 5–6 distinct punctures along hind margin, propimeron with 5 punctures along hind margin; prosternal process narrow, broadly beaded laterally, narrowly depressed medially between procoxae. *Elytra* ellipsoid, disc very convex, upraised above scutellum, sides sloped to vertical juncture with marginal depression; elytral suture implacably fused in one individual examined for assessment of metathoracic flight wing configuration; basal groove tightly arcuate, anteriorly extended to angulate humerus; humeri proximate, MEW/HuW = 2.26–2.35 ( $n = 5$ ); parascutellar seta present, situated near sutural stria; parascutellar striole 3-punctate, interrupted between punctures; sutural interval slightly more convex than lateral intervals yet depressed at sutural juncture, narrower in apical half and more convex due to deeper sutural stria at elytral apex; elytral striae 2–3 only slightly convex on disc, 4–5 nearly flat; stria punctures separated by shallowly depressed striae 1 and 2, completely isolated by interruptions of striae 3–5; stria 1 and 7 deep at elytral apex, 2–4 very shallow, difficult to trace, 5–6 obsolete; eighth interval abruptly upraised laterad stria 7 apicad subapical situation, the elytral apex mesad the seventh striae circularly depressed, enhancing carina of eighth interval; two dorsal elytral setae situated in deep but very small depressions that span  $< \frac{1}{4}$  width of interval 3, setae positioned at  $0.25\text{--}0.26 \times$  and  $0.52\text{--}0.61 \times$  elytral length; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 6; elytral marginal depression moderately broad from angulate humerus posteriorly, margin upraised laterally, beaded in apical  $\frac{1}{3}$ ; subapical sinuation shallow but evident, internal plica visible in dorsoposterior view. *Mesepisternum* with 14 punctures in 2–3 vertical rows; metepisternum slightly elongate, width/length ratio 0.81; metepisternum separated from metepimeron by distinct suture; metathoracic flight wing an ovoid, broadly rounded flap with apex extended  $\frac{1}{2}$  distance to

metanotal hind margin; only a vestige of the M vein evident as a melanic line in the membrane of the wing vestigium. *Abdomen* with visible ventrites 1–5 irregularly wrinkled laterally, ventrites 3–6 with rounded depressions laterally; suture between visible ventrites 2 and 3 effaced laterally. *Legs* moderately gracile, tarsomeres short, metatarsomere 1 length  $0.19\times$  metatibial length; metatarsomere 4 broad, moderately emarginated, overall length  $1.2\times$  median tarsomere length; metatarsomere 4 with apical and subapical setae; metatarsal dorsolateral sulci shallow and lateral, tarsomere broadly convex medially. *Microsculpture* of head shallow to obsolete, surface glossy or with indistinct transverse mesh, sculpticell breadth  $2\text{--}3\times$  length; pronotal disc with indistinct transverse mesh, sculpticell breadth  $2\text{--}3\times$  length, microsculpture visible outside field of reflected light, surface glossy; pronotal median base glossy, indistinct transverse sculpticells visible among punctures; elytral disc glossy, indistinct transverse mesh laterally; elytral apex with indistinct transverse mesh, sculpticell breadth  $2\text{--}3\times$  length; metasternum glossy, shallow indistinct transverse mesh medially; laterobasal abdominal ventrites with shallow, swirling isodiametric and transverse sculpticells. *Coloration* of frons rufous with a piceous cast, clypeus rufous; antennomeres 1–2 flavous, 3–4 rufoflavous, 5–11 rufobrunneous; pronotal disc dark rufous, margins concolorous; proepipleuron rufoflavous, proepisternum rufobrunneous; elytral disc dark rufous; sutural interval rufous basally, rufoflavous apically; elytral margins concolorous at humerus, deepest portion of lateral depression rufoflavous laterally; elytral epipleuron rufoflavous with brunneous cast, metepisternum rufobrunneous; abdominal visible ventrites 1–3 rufobrunneous, 4–6 rufoflavous, apical  $1/6$  of apical visible ventrite paler, flavous; metafemur flavous with brunneous cast; metatibia flavous with darker carina associated with longitudinal setal series.

**Male genitalia.** ( $n = 1$ ). Aedeagal median lobe broad basally and narrowed in apical half to finely protruded apex with downturned tip (Fig. 5C); median lobe straight in euventral view; internal sac with broad melanic ventral microtrichial field but without spicules; flagellar plate large, length  $0.46\times$  distance from parameral articulation to distal surface of downturned tip; paramere extended  $0.83\times$  distance from parameral articulation to tip.

**Female reproductive tract.** ( $n = 1$ ). Bursa copulatrix columnar, broadest near midlength, length  $2.3\times$  maximal breadth when compressed on microslide (Fig. 6B); bursal walls moderately thickened, wrinkled, and variably stained with Chlorazol Black; spermatheca obovate, broadest near apex, reservoir length about  $1/4$  length of spermathecal duct that joins dorsal bursal wall dorsad bursal juncture with common oviduct; spermathecal gland with elongate reservoir, reservoir length subequal to spermathecal gland duct length; membranous ramus mesad basal gonocoxite 1 long, apex extended beyond midlength of basal gonocoxite (Fig. 7B); basal gonocoxite 1 with apical fringe of 3–4 setae—3 on left side, 3 plus 1 isolated apicolateral seta on right side—and only several small setae along medial surface; apical gonocoxite 2 broad basally, narrowed in apical half to subacuminate apex; apical gonocoxite with 2 subequal lateral ensiform setae that are situated on the ventral surface, 1 dorsal ensiform seta, and 2 apical nematiform setae.

**Holotype** male (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru trail nr. pylon 3 / el. 1010 m 6-IX-2006 lot 01 / 17°38.094'S, 149°22.073'W / pyr. fog live/dead *Blechnum* / fern fronds J.K. Liebherr // HOLOTYPE / Mecyclothorax / anaana / J.K. Liebherr 2012 (black-bordered red label).

**Allotype** female (MNHN) with same date-locality label // 5 // ALLOTYPE ... labeled as holotype.

**Other paratypes.** SOCIETY ISLANDS: Tahiti Nui; Mauru, above pylon 4, 17°38.06'S, 149°22.15'W, 1100 m el., beating *Myrsinel*/mossy vegetation, 05-ix-2006 lot 02, Liebherr, (CUIC, 2); pylon trail, 17°38.08'S, 149°22.07'W, 960–1010 m el., beating ferns, 06-ix-2006 lot 02, Liebherr (CUIC, 1; NMNH, 1); above pylon 4, cloud forest, 17°38.05'S, 149°22.15'W, 1060 m el., beating vegetation, 19-ix-2006 lot 01, Liebherr (CUIC, 2); 17°37.90'S, 149°22.34'W, 1100 m el., beating *Weinmannial Myrsinel/Melicope*, 20-ix-2006 lot 01, Liebherr (CUIC, 2).

**Etymology.** The Tahitian word anaana means bright, shining, or brilliant (Wahlroos 2002), and is used to describe the glossy dorsal body surface of beetles of this species. As a Tahitian word the epithet is to be treated as a noun in apposition.

**Distribution and habitat.** This species has been found from 960–1110 m elevation, with beetles living arboreally on a variety of plants; *Weinmannia*, *Myrsine*, *Melicope*, and ferns. Two individuals were collected in a pyrethrin fog sample made along a bank of live and dead *Blechnum* and *Dicranopteris* ferns (Fig. 2B)

## 6. *Mecyclothorax pirihaio* sp. n.

urn:lsid:zoobank.org:act:D3C0062F-AFBF-424D-A709-6A0B5C9414E6

[http://species-id.net/wiki/Mecyclothorax\\_pirihaio](http://species-id.net/wiki/Mecyclothorax_pirihaio)

Figs 4C, 5D–E, 6C, 7C

**Diagnosis.** This species and *M. spinosus* Perrault share the characteristics of: 1, two supraorbital setae and two dorsal elytral setae, therefore a setal formula of 2121; 2, deep, smooth and complete elytral striae 1–8; 3, regular transverse-mesh elytral microsculpture and feeble transverse microsculpture on the pronotal disc; and 4, sparsely punctate pronotal median base, the punctures small and separated by glossy areas with indistinct microsculpture. However the species can be easily distinguished by the pronotal hind angles, which are obtuse-rounded in this species (Fig. 4C) versus acute and distinctly projected in *M. spinosus* (Perrault 1989: fig. 22). The pronotal median base is also narrower in this species, MPW/BPW = 1.83–1.90 (n = 5), versus 1.59–1.63 (n = 2) in *M. spinosus*. The male aedeagal median lobe apex is also dramatically different: downturned with a slight ventral projection in this species (Figs 5D–E), versus dorsally spinose in *M. spinosus* (Perrault 1989: fig. 13). Finally, individuals of this species are larger; standardized body length 4.2–5.0 mm, versus 4.1 mm for *M. spinosus*.

**Description.** *Head capsule* with slightly convergent frontal grooves, triangularly depressed posterad frontoclypeal suture, the apex directed medially onto frons, terminated narrowly mesad thin carina immediately inside dorsal supraorbital seta, frons

crossed by numerous fine transverse wrinkles emanating from groove; frons and vertex convex medially, neck not depressed; ocular lobe moderately protruded, joined to gena at broad, shallow groove; ocular ratio 1.47–1.51, ocular lobe ratio 0.81–0.89; labral anterior margin angularly emarginated medially  $\frac{1}{8}$ × length; antennomeres 1–3 glabrous except for apical setae, minute pore sensilla visible across surface; antennae elongate filiform, eighth segment length 2.25× maximal breadth; mentum tooth sides defining acute angle, apex rounded. *Pronotum* extremely constricted basally, moderately transverse, MPW/PL = 1.17–1.25 (n = 5); lateral margin slightly to distinctly sinuate anterad obtuse, rounded, glabrous hind angle; median base moderately depressed relative to disc, margin with disc lined with 4–5 small, circular punctures, 12–13 smaller punctures posteriorly across each side of base; basal margin slightly convex between laterobasal depressions, margin posterad depression slightly expanded posteriorly inside hind angle; median longitudinal impression finely incised, shallow, present as lenticular depression at front of median base; anterior transverse impression broad, shallow, unmarginated anteriorly in middle of disc, finely incised in outer half of breadth each side; anterior callosity slightly convex, depressed relative to disc, crossed with fine longitudinal wrinkles; front angles slightly protruded, rounded; distance between front angles visibly greater than basal width, APW/BPW = 1.10–1.20 (n = 5); lateral marginal depression very narrow at midlength, slightly wider at front angle, bead broader along sinuate basolateral margin; laterobasal depression narrow, sinuously defined laterally by broadened marginal bead, medially by punctate edge of median base; proepisternum with 5–6 distinct punctures along hind margin, about 5 punctures along hind margin of proepimeron; prosternal process broadly margined laterally, narrowly depressed medially between procoxae. *Elytra* oblong, sides subparallel at midlength, disc flat near suture; basal groove well developed, curved anterolaterally to angulate humerus; humeri proximate, MEW/HuW = 2.42–2.56 (n = 5); parascutellar seta present, situated in middle of sutural stria; parascutellar striole 4–5-punctate, continuous; sutural interval and lateral intervals of similar convexity basally, sutural interval narrower and convexly upraised to meet at suture apically; all striae evident in basal half, striae 1–6 moderately deep, minutely punctate at stria depth, stria 7 shallower but complete, nearly smooth; all striae complete at apex, sutural stria deep and fine, stria 7 deep and broad, the eighth interval convexly subcarinate apicad the subapical sinuation; dorsal elytral setae in evident depressions that cross half to the entire width of interval 3, setae positioned at 0.21–0.24× and 0.54–0.59× elytral length; apical elytral seta present, subapical seta absent in most individuals, rarely present unilaterally; lateral elytral setae 7 + 6; elytral marginal depression narrow at humerus but margin upraised, margin upraised laterally, more beadlike as depression narrows to subapical sinuation; subapical sinuation very shallow, elytral margin straight. *Mesepisternum* with 11 punctures in 1–2 vertical rows; metepisternum elongate, width to length ratio 0.68; metepisternum separated from metepimeron by distinct suture; metathoracic flight wing a triangular flap with inner and posterior margins of equal length, apex of longer lateral margin extended 0.8× distance to hind margin of metanotum; rudiments of R and M veins visible, not melanic, the same coloration as vestigium membrane. *Abdomen* with visible ventrites

1–5 irregularly wrinkled laterally, ventrites 3–6 with round depressions laterally; suture between visible ventrites 2 and 3 effaced laterally. *Legs* gracile, metatarsomere 1 length 0.24× metatibial length; metatarsomere 4 emarginated apically, overall length 1.4× median tarsomere length; metatarsomere 4 with apical and subapical setae; metatarsal dorsolateral sulci broad and shallow, tarsomere dorsal surface medially subcarinate. *Microsculpture* of head an indistinct transverse mesh, sculpticell breadth 2–3× length, sculpticells most visible just outside area of reflected light; pronotal disc with transverse mesh, sculpticell breadth 3–4× length, mixed with glossy patches; pronotal median base glossy, indistinct isodiametric sculpticells visible along edge of reflected light; elytral disc with regular transverse mesh, sculpticell breadth 3–5× length; elytral apex with shallow transverse mesh, sculpticell breadth 2–4× length; metasternum glossy, elongate transverse mesh visible in part; laterobasal abdominal ventrites with shallow, swirling isodiametric and transverse sculpticells. *Coloration* of head rufobrunneous, piceous cast in frontal grooves, clypeus rufoflavous; antennomere 1 flavous, antennomeres 2–11 rufoflavous; pronotal disc brunneous, margins slightly paler; proepipleuron rufoflavous, proepisternum rufobrunneous; elytral disc brunneous with silvery metallic reflection; sutural interval pale rufous basally, rufoflavous apically; elytral margin concolorous with disc at humerus, deepest part of lateral depression rufoflavous in apical half; elytral epipleuron rufoflavous, metepisternum rufobrunneous; visible abdominal ventrites 1–3 rufobrunneous, ventrites 4–6 rufoflavous; apical half of apical abdominal ventrite flavous; metafemur flavous with brunneous cast; metatibia flavous, carina associated with longitudinal setal series darker, brunneous.

**Male genitalia.** (n = 2). Aedeagal median lobe evenly curved and of subequal diameter from basal bulb to ostial opening, apex with rounded dorsal projection at base, the downturned tip rounded to tightly rounded (Figs 5D, E); median lobe straight in euventral view; internal sac with broad ventral microtrichial field but without spicules; flagellar plate of moderate size, length 0.35× distance from parameral articulation to distal face of apex; parameres extended 0.83× distance from parameral articulation to apex.

**Female reproductive tract.** (n = 1). Bursa copulatrix shape columnar, length 2.5× maximal breadth compressed on microslide (Fig. 6C), membranous surface wrinkled and unevenly stained with Chlorazol Black; spermatheca obovate, broadest near apex, reservoir about 0.25× length of spermathecal duct that enters dorsal wall of bursa dorsal the basally broad common oviduct; membranous ramus mesad basal gonocoxite 1 very long, extended as a fold in dorsal vagina wall to apex of basal gonocoxite 1 (Figs 6C, 7C); basal gonocoxite 1 with 4 apical fringe setae along middle of coxite apex, plus 3 smaller setae near apicomedial angle (Fig. 7C); 2–3 very small setae in medial half of basal gonocoxite; apical gonocoxite 2 broad basally, base broadly extended laterally, with 2 subequal lateral ensiform setae, 1 narrower dorsal ensiform seta, and 2 moderately elongate apical nematiform seta.

**Holotype** male (MNHN) labeled: French Polynesia: Tahiti Nui / Mt. Mauru trail nr. pylon 3 / el. 1010 m 5-IX-2006 lot 03 / 17°38.094'S, 149°22.073'W / beating *Blechnum* fern / fronds J.K. Liebherr // HOLOTYPE / Mecyclothorax / pirihaio / J.K. Liebherr 2012 (black-bordered red label).

**Allotype** female (MNHN) labeled as holotype except for allotype designation.

**Other paratypes.** SOCIETY ISLANDS: Tahiti Nui; Mauru, pylon 3 to 4, 1010 m el., 17°38.08'S, 149°22.07'W, beating *Blechnum* fern, 05-ix-2006 lot 03, Liebherr (CUIC, 1), pyrethrin fog *Dicranopteris/Blechnum*, 06-ix-2006 lot 01, Liebherr (CUIC, 2; NMNH 1); pylon trail, 960-1010 m el., 17°38.08'S, 149°22.07'W, beating ferns, 06-ix-2006 lot 02, Liebherr (CUIC, 3; NMNH, 1); 880–960 m el., 17°38.05'S, 149°21.66'W, beating ferns, 06-ix-2006 lot 03, Liebherr (CUIC, 2); above pylon 4, cloud forest, 1100-1110 m el., 17°37.90'S, 149°22.34'W, beating *Weinmannia/Myrsine/Melicope*, 20-ix-2006 lot 01, Liebherr (CUIC, 2), 1080 m el., 17°37.92'S, 149°22.32'W, pyrethrin fog fern frond tangles, 20-ix-2006 lot 02, Liebherr (CUIC, 1), 20-ix-2006 lot 03, Ewing (EMEC, 6).

**Etymology.** The Tahitian word *pirihao*, meaning narrow, constricted, or close (Wahlroos 2002), is used to signify the basally constricted pronotum characterizing this species. As Tahitian, the species epithet *pirihao* is to be used as a noun in apposition.

**Distribution and habitat.** This is the most commonly encountered, and most broadly distributed species within the elevational range so far sampled on Mauru, having been collected in habitats at 880–1110 m elevation. However, 20 of the 22 specimens were collected in association with ferns of either the genus *Blechnum* or *Dicranopteris*, and only 2 were associated with flowering plants; a mixed beating sample from *Weinmannia*, *Myrsine*, and *Melicope*.

### 7. *Mecyclothorax poro* sp. n.

urn:lsid:zoobank.org:act:5474B951-8E36-4480-B240-7CBF0EA7836E

[http://species-id.net/wiki/Mecyclothorax\\_poro](http://species-id.net/wiki/Mecyclothorax_poro)

Fig. 4D

**Diagnosis.** This species shares with *M. angulosus* Perrault the distinctly constricted lateral pronotal margins anterad right, projected hind angles. Both species are also characterized by two supraorbital setae and two dorsal elytral setae, and therefore a setal formula of 2121. Both also display dense transverse-line elytral microsculpture loosely joined in a mesh, the microsculpture resulting in an aeneous reflection. The pronotal median base is more distinctly punctate in *M. angulosus*, and the cuticle between the punctures is covered with indistinct transverse microsculpture, versus the smooth areas between punctures observed in this new species (Fig. 4D). Elytral stria 6 is shallow and nearly smooth near the elytral midlength in this species, versus deeper and punctate—nearly as deep as striae 1–5—in *M. angulosus*. Also, elytral striae 2–6 are obsolete basally in this species, versus deep and continuously depressed to their juncture with the elytral basal groove in *M. angulosus*. Standardized body length in this species is 4.4 mm, larger than *M. angulosus* at 4.0 mm ( $n = 2$ ; MNHN holotype male plus CUIC female).

**Description.** *Head capsule* with broad, shallow frontal grooves that extend medially as depressed triangles that nearly meet along midline posterad frontoclypeal

suture, grooves terminated posteriorly mesad broad carina inside supraorbital seta, fine transverse wrinkles emanating from grooves onto frons; frons and vertex convex, neck not depressed; ocular lobe moderately protruded, meeting gena at  $> 135^\circ$  angle, juncture marked by narrow, shallow groove; ocular ratio 1.45, ocular lobe ratio 0.76; labral anterior margin moderately emarginated medially to  $1/7$  length; antennomeres 1–3 glabrous except for apical setae, minute pore sensilla visible in translucent cuticle of shafts; antennae submoniliform, antennomere 8 length  $1.67\times$  maximal breadth; mentum tooth with sides subparallel, apex rounded. *Pronotum* transversely cordate, MPW/PL = 1.25, base narrow, MPW/BPW = 1.56; lateral margins convergent for short distance anterad protruded, nearly right and glabrous hind angles; median base moderately depressed relative to disc, margin with disc lined with 7–8 elongate punctures, 10–12 more small, isolated punctures each side; basal margin distinctly convex between laterobasal depressions; median longitudinal impression shallow, very finely incised; anterior transverse impression shallow but continuous medially, smooth, deeper and more definite in outer  $3/4$  of breadth each side; anterior callosity slightly convex, smooth; front angles not protruded, broadly rounded posteriorly; apical pronotal width equal to basal width; lateral marginal depression narrow, slightly broadened from lateral seta to front angle, narrowest posterad lateral seta; laterobasal depression a broadened continuation of lateral depression, surface irregularly punctured, bordered laterally and basally by broad upraised bead; proepisternum with 5 distinct punctures along hind margin, proepimeron with granulate groove along hind margin; prosternal process broad, margins broadly beaded, distinctly depressed medially between procoxae. *Elytra* ellipsoid, disc moderately convex, upraised above scutellum, sides approaching vertical at juncture with lateral depression; basal groove gently arcuate laterad scutellar striole, anteriorly curved to meet subangulate humerus; humeral angles proximate, MEW/HuW = 2.24; parascutellar seta present, situated near sutural stria; parascutellar striole 5-punctate, shallow but continuous between punctures; sutural interval of similar convexity to intervals 2–5 near base, but each side upraised at sutural juncture, narrowed and more convex, callouslike apically; striae 1–4 minutely punctate in basal  $1/3$  of length, punctures slightly expanding striae, striae 5–6 broader and shallower on disc, striae 1–6 absent near basal groove and humerus; sutural stria fine, deep at apex, striae 2 and 3 broader and shallower, 4–6 obsolete, difficult to trace, and stria 7 interrupted, deepest at short depressed strial remnant associated with apical elytral seta; eighth interval convex, although not carinate medially due to reduction of stria 7; two dorsal elytral setae in deep, evident impressions that span  $1/2$  width of third interval, setae positioned at  $0.24\text{--}0.27\times$  and  $0.51\text{--}0.52\times$  elytral length; apical elytral seta present, subapical seta absent; lateral elytral setae 7 + 6; elytral marginal depression moderately broad to subangulate humerus, margin upraised laterad humerus, depression broadest along anterior lateral setal series, narrowed with margin beaded along posterior setal series; subapical situation broad, shallow, internal plica visible in dorsal view. *Mesepisternum* with 16 punctures in 2–3 vertical rows; metepisternum slightly elongate, width to length ratio 0.78; metepisternum separated from met-

epimeron by distinct suture. *Abdomen* with visible ventrites 1–4 irregularly wrinkled laterally, ventrites 4–6 with rounded depressions laterally; suture between visible ventrites 2 and 3 effaced laterally. *Legs* robust, metatarsomere 1 length 0.18× metatibial length; metatarsomeres broad, tarsomere 4 broadly triangular, overall length 1.4× median tarsomere length; metatarsomere 4 apical and subapical setae present; metatarsal dorsolateral sulci shallow and lateral, median surface broadly convex. *Microsculpture* of head indistinct, transverse mesh with sculpticell breadth 2–3× length on glossy surface; pronotal disc with indistinct transverse mesh, sculpticell breadth 2–4× length visible outside areas of reflected light; pronotal median base with indistinct transverse mesh, sculpticell breadth 2× length among punctures; elytral disc covered with transverse lines irregularly joined into a loose mesh, the surface with aeneous reflection; elytral apex with transverse mesh, sculpticell breadth 2–4× length; metasternum with transverse mesh; laterobasal abdominal ventrites covered with swirling isodiametric and transverse sculpticells. *Coloration* of head capsule piceous, clypeus rufous; antennomeres 1–2 rufoflavous, 3–11 rufobrunneous; pronotal disc dark rufous with piceous cast, median base, anterior callosity and edges of disc rufous, lateral marginal bead piceous; proepipleuron rufoflavous, proepisternum dark rufous; elytral disc dark rufous; sutural interval rufous basally, rufoflavous apically; elytral marginal depression rufous basally, rufoflavous apically; elytral apex beyond subapical situation rufoflavous; elytral epipleuron rufoflavous dorsally, rufobrunneous ventrally, metepisternum rufobrunneous; visible abdominal ventrites 1–6 rufobrunneous laterally, with piceous cloud medially; apical abdominal ventrite graded to flavous margin in apical third; metafemur flavous; metatibia flavous with brunneous cast.

**Female reproductive tract.** The unique female holotype was not dissected, nor were its external genitalia visible for examination.

**Holotype.** French Polynesia: Tahiti Nui / Mt. Mauru lava tube / el. 705 m 18-IX-2006 lot 01 / 17°38.017'S, 149°21.284'W / pyr. fog moss/liverworts / along stream J.K. Liebherr // HOLOTYPE / Mecyclothorax / poro / J.K. Liebherr 2012 (black-bordered red label).

**Larva.** One larval specimen was collected 18-ix-2006 by use of pyrethrin fog on a moss-covered boulder at the upper mouth of the lava tube, 725 m elevation. Complete description of the larva will be presented subsequently, but identification as *Mecyclothorax* sp. is possible based on its intrinsic characters assessed within the context of the disharmonic carabid fauna of Tahiti. Using Emden (1942), the specimen keys to couplets 28 and 29 whereupon it violates the key, exhibiting various attributes agreeing with each couplet half. In accordance with couplet 28, *Patrobini*, the larva exhibits: 1, maxillary palpomere 2 longer and stouter than palpomere 3; 2, inner lobe, or lacinia of maxilla absent. In accord with couplet 29, *Pterostichini*, *Drimostomina* etc., it exhibits: 1, mandible with unisetose penicillus; 2, antennomere 2 shorter than 1 or 3; 3, nasale broadly and indistinctly produced.

The larval labium includes a bisetose ligula, with the setae LA1, LA2, LA3, LA4, and the ligular setal pair LA6 present, and the setae at position LA5 absent (Bous-

quet and Larochelle 1984). The second pair of ligular setae—termed LA7 by Arndt (1998)—that are observed in Patrobini are not present. Also absent are the paired ligular pores homologized by Arndt with LA7. The configuration of bisetose ligula with pores substituting for LA7 is a synapomorphy for the subfamily Harpalinae (Arndt 1998). Thus the larval ligula deviates from Patrobini by the absence of LA7, but also deviates from members of subfamily Harpalinae by absence of two pores accompanying the LA6 setae on the ligula. In sum, the larva appears to represent a grade of development between Patrobini and Harpalinae. The only candidates present in Tahiti that represent that phylogenetic level would be in the genus *Mecyclothorax* of the Moriormorphini. Corroborating this hypothesis, the larva shares characters with that of *Melisodera picipennis* Westwood, an Australian moriormorphine (Moore 1964). These characters include, among others: 1, a medially emarginated nasale; 2, cervical keel; 3, mandibular penicillus; 4, absence of a maxillary inner lobe; 5, bisetose ligula; 6, legs with two claws; and 7, urogomphi with short setose nodes.

The larva exhibits a 0.9 mm head width measured across the head capsule behind the stemmata, and a body length of 5.1 mm measured from the anterior margin of the nasale to the urogomphal tips (measurements made on a cleared larva). Based on these dimensions and the adult body length of 4.4 mm, the larva is considered to represent the third instar.

Given that *M. poro* was the only other *Mecyclothorax* species collected at this site, the larva is tentatively identified as that species based on geographic association. Of course, larval and adult individuals could have been deposited at this site during high water, but *M. poro* was not found at any other site suggesting this is its native habitat. Moreover, larvae and one adult of *Metacolpodes eremita* (Fairmaire) (Carabidae: Platynini) were also found together on moss-covered boulders at the lower entrance to the lava tube (Fig. 2A), suggesting that a resident streamside carabid community resides and breeds at this site.

**Etymology.** Among several meanings, the Tahitian word *poro* means corner or angle (Wahlroos 2002), and its use for the species epithet signifies the acute, projected hind pronotal angles characterizing this species. As Tahitian, the epithet is to be used as a noun in apposition.

**Distribution and habitat.** The adult and presumed larva of this species were collected at 705–725 m elevation, from moss and liverwort covered rocks along a stream running through a lava tube “tunnel”; the uncollapsed portion of a very large lava tube (Fig. 2A). This is the lowest elevation record for any *Mecyclothorax* species in Tahiti. For both the adult and larva, individuals were discovered through use of pyrethrin fog on the moss and liverworts, demonstrating that the individuals inhabited the depths of that vegetation. The rock face inhabited by the adult was wet, as the mouth of the lava tube was in shade for much of the day, and the site of adult collection was within a meter of the water’s edge. The larva was found on a boulder in the middle of the streambed at the upper end of the lava tube where the moss was quite dry to the touch.

**Table 1.** *Mecyclothorax* spp. described from Mont Mauru, putative adelphotaxa, and distributional ranges of putative adelphotaxa (Fig. 1).

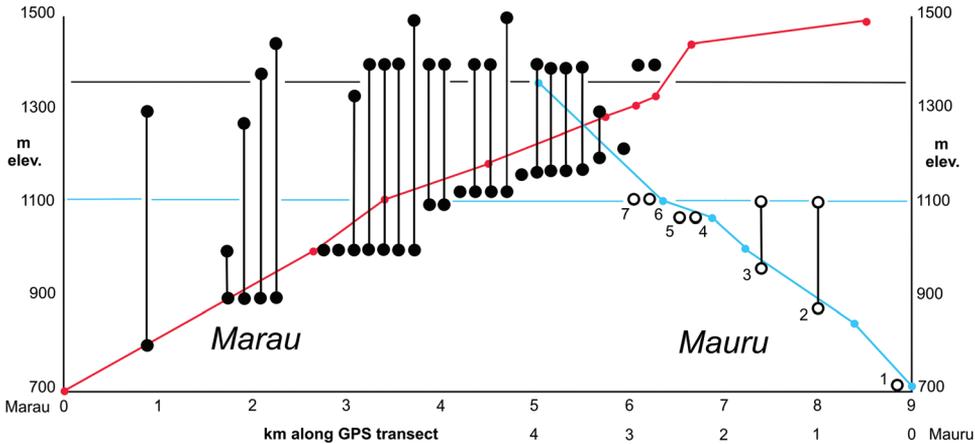
Mont Mauru species	Putative adelphotaxon	Range of adelphotaxon
<i>M. tutei</i>	<i>M. cooki</i>	Aorai
<i>M. tihotii</i>	<i>M. ballioides</i>	Marau
<i>M. putaputa</i>	<i>M. castaneus</i> or <i>M. mapo</i>	Marau or Moorea
<i>M. toretore</i>	<i>M. fuscus</i>	Aorai
<i>M. anaana</i>	<i>M. hemisphaericus</i>	Marau
<i>M. pirihaio</i>	<i>M. spinosus</i>	Pihaaiateta
<i>M. poro</i>	<i>M. angulosus</i>	Aorai

## Discussion

The presence of seven precinctive *Mecyclothorax* species on Mont Mauru amply defines this isolated massif as a distinct area of endemism. All of the seven species from Mauru have putative adelphotaxa on one of the western mountains or, in one instance, possibly on the island of Moorea (Table 1). Thus corroborating Perrault's (1992, table 10.2) general findings, the presently known Mauru fauna has not diversified via autochthonous speciation within the massif, but instead has come about through more broadly based allopatric speciation implicating the various major massifs.

Mauru is isolated from the western mountains—Marau, Aorai, and Pihaaiateta—by the broad and deep Papenoo Valley. This present-day erosional depression within which the Papenoo River reaches the sea after having breached the Tahiti Nui caldera wall has been configured via successive phases of erosion, secondary volcanism, secondary erosion, and late-stage marine incursion. Secondary volcanic products emplaced within the valley are dated 440,000 years old (Becker et al. 1974). These flows and the original valley floor stood at 200–250 m elevation, an elevation that would fragment distributional ranges of all extant *Mecyclothorax* species. Thus it would appear that the Papenoo Valley has served as a formidable vicariant barrier between Mauru and the western mountains for at least 400,000 yr. Given the hypothesized species duration of 200–300 Kyr for *Mecyclothorax* species on West Maui (Liebherr 2011), the Papenoo Valley has been in place long enough to have facilitated allopatric speciation between the *Mecyclothorax* of Mauru and those of the various western mountains. Whether *Mecyclothorax* populations on Mauru have been isolated long enough from those on Mont Urufa to the south or Mont Aramaoro to the north, thereby allowing speciation to proceed among the isolated eastern massifs, must await biotic surveys of those peaks.

Discovery of seven *Mecyclothorax* species on Mauru elevates the number of *Mecyclothorax* described from Tahiti to 74 species (Perrault 1978a, 1978b, 1984, 1986, 1987, 1988, 1989). This radiation is by far the most diverse species assemblage documented for Tahiti (Nishida 2008); a testament to the value of intense field work complemented by comprehensive revisionary taxonomy (Perrault 1992). That an assemblage of predatory insects should be the most speciose members of an



**Figure 9.** Elevational distributions of species found on Mont Marau, northwest Tahiti Nui (●) and Mont Mauru, eastern Tahiti Nui (○); elevational ranges indicated by vertical “barbells.” Sloping red line connects GPS-associated collecting localities along Marau summit road recorded during 2006 collecting activities. Sloping blue line connects GPS-associated localities along pylon trail ascending Mauru. Kilometer marks for these transects reflect direct map distances. Horizontal blue line indicates maximal 1110 m elevation achieved during 2006 collecting activities on Mauru. Horizontal black line indicates summit elevation of Mauru. Species from Mauru include: 1 *M. poro* 2 *M. pirihae* 3 *M. anaana* 4 *M. tutei* 5 *M. toretore* 6 *M. tihotii* 7 *M. putaputa*.

isolated oceanic insect fauna may seem surprising at first glimpse. However such a result points to several aspects of community organization on such islands that make them fundamentally different from mainland communities. Firstly, botanical diversity is relatively low on isolated Pacific archipelagos (Mueller-Dombois and Fosberg 1998), removing the foundation for substantial diversification based on host plant specialization. Second, the predatory lifestyle ties the diversifying radiation to a relatively stable source of food comprising a taxonomically varied suite of food items, thereby lowering the risk of populations suffering extinction in any fragment of a primordial geographic range. Switching from a phytophagous to a predatory way of life is cited as one evolutionary attribute of island radiations (Gillespie and Roderick 2002). Experiencing enhanced survival as a ready-made predator in a disharmonic island fauna is more straightforward, not requiring an evolutionary change in life style. Climatic stability and geographic isolation characteristic of isolated oceanic islands conspire to select for reduced dispersal capability (Southwood 1977). In the instance of *Mecyclothorax*, this selected for vestigialization of metathoracic flight wings early in the radiation, with the end-result being 100% brachypterous taxa in the present-day Tahitian fauna. Moreover, given the holometabolous life cycle and small, terrestrially bound larvae of *Mecyclothorax*, long-distance dispersal does not occur in any life stage. Finally, *Mecyclothorax* species add small body size to this scenario, with individuals being able to reproduce within very limited ecological circumstances using minimal ecological resources.

The seven new taxa that establish Mont Mauru as a unique biogeographic entity were collected from habitats ranging 705–1110 m elevation. Yet the summit of Mauru stands at 1361 m elevation, begging the question of how much diversity remains to be discovered in the upper reaches of the mountain. An initial estimate of this undiscovered diversity can be made by comparing the elevationally limited samples from Mauru to those from the best sampled Tahitian mountain, Mont Marau (Fig. 1). Historically, Perrault (1992) based his taxonomic findings on 1388 specimens, 1103 from Tahiti Nui, of which over half—629—were collected on Marau. During the 2006 survey, 268 of the 539 specimens collected in Tahiti were found on Marau (unpubl. data). The aggregate Marau collections include 27 species, 21 of which were treated by Perrault (1992, table 10.2; *M. muriauxioides* Perrault will be synonymized in the future) and 6 more that remain to be described (unpubl. data). Of these species, 14 have been collected in habitats below 1100 m elevation, the elevational band sampled on Mauru that netted 7 species (Fig. 9). An additional 11 species have been collected on Marau from 1100–1360 m elevation, with two species known only from 1400 m near the summit of the mountain. Thus, assuming the faunas of these two mountains contain vicariant representatives of a primordial Tahiti Nui fauna, and that extinction associated with relative areal extent of the mountains or climatic differences associated with rainfall and aspect are not significant factors, we have sampled perhaps half of the Mauru *Mecyclothorax* fauna present below 1110 m elevation, and only a third to a fourth of the entire fauna on this massif. The only way to test this estimate is to redouble sampling efforts on the upper reaches of Mauru. Such findings will provide a baseline for characterizing the eastern Tahiti Nui fauna, allowing subsequent collections from neighboring massifs to answer questions about overall levels of diversity and speciation rates for the diverse Tahitian *Mecyclothorax* radiation.

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## References

- Arndt E (1998) Phylogenetic investigation of Carabidae (Coleoptera) using larval characters. In: Ball GE, Casale A, Vigna Taglianti V (Eds) Phylogeny and classification of Caraboidea (Coleoptera: Adephaga). Proceedings of a symposium (28 August, 1996, Florence, Italy). 20 International Congress of Entomology, Atti Museo Regionale di Scienze Naturali (Museo Regionale di Scienze Naturali–Torino, Torino), 171–190.
- Becker M, Brousee R, Guille G, Bellon H (1974) Phases d'érosion—comblement de la vallée de la Papenoo et volcanisme subrécent à Tahiti, en relation avec l'évolution des îles de la Société (Pacifique Sud). *Marine Geology* 16: M71–M77. doi: 10.1016/0025-3227(74)90064-4
- Bousquet Y, Goulet H (1984) Notation on primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology* 62: 573–588. doi: 10.1139/z84-085
- Britton EB (1938) Carabidae of the Society Islands and Rapa (Coleoptera). *Occasional Papers of Bernice P. Bishop Museum* 14: 103–110.
- Craig DA, Currie DC, Joy DA (2001) Geographical history of the central–western Pacific black fly subgenus *Inseliellum* (Diptera: Simuliidae: *Simulium*) based on a reconstructed phylogeny of the species, hot–spot archipelagoes and hydrological considerations. *Journal of Biogeography* 28: 1101–1127. doi: 10.1046/j.1365-2699.2001.00619.x
- Emden FI van (1942) A key to the genera of larval Carabidae (Col.). *Transactions of the Royal Entomological Society of London* 92: 1–99. doi: 10.1111/j.1365-2311.1942.tb03318.x
- Gillespie RG, Roderick GK (2002) Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* 47: 595–632. doi: 10.1146/annurev.ento.47.091201.145244
- IGN [Institut Géographique National] (1994) Tahiti, Archipel de la Société, Carte Touristique au 1:100,000. Paris.
- Liebherr JK (2009) Taxonomic revision of the *Mecyclothorax* beetles (Coleoptera: Carabidae) of Oahu: epithets as epitaphs for an endangered fauna? *Systematic Entomology* 34: 649–687. doi: 10.1111/j.1365-3113.2009.00477.x
- Liebherr JK (2011) The *Mecyclothorax* beetles (Coleoptera: Carabidae: Moriomorphini) of West Maui, Hawaii: taxonomy, biogeography, and conservation. *Deutsche Entomologische Zeitschrift* 58: 15–76. doi: 10.1002/mmnd.201100005
- Liebherr J (2012) The first precinctive Carabidae from Moorea, Society Islands: new *Mecyclothorax* spp. (Coleoptera) from the summit of Mont Tohiewa. *ZooKeys* 224: 37–80. doi: 10.3897/zookeys.224.3675
- Moore BP (1964) Australian larval Carabidae of the subfamilies Broscinae, Psydrinae and Pseudomorphinae (Coleoptera). *Pacific Insects* 6: 242–246.
- Mueller-Dombois D, Fosberg FR (1998) *Vegetation of the Tropical Pacific Islands*. New York, NY, Springer Verlag, xvii + 733 pp.
- Nishida GM (2008) Checklists: French Polynesia (27). *Essig Museum of Entomology, Berkeley Natural History Museums, University of California, Berkeley*. [Accessed 7 August 2012: <http://essigdb.berkeley.edu/checklists/MooreaList.doc>]
- Perrault GG (1978a) La faune des Carabidae de Tahiti II. genre *Mecyclothorax* (Sharp). *Nouvelle Revue d'Entomologie* 8: 27–36.

- Perrault GG (1978b) La faune des Carabidae de Tahiti II. genre *Mecyclothorax* (Sharp). Nouvelle Revue d'Entomologie 8: 133–162.
- Perrault GG (1984) La faune des Carabidae de Tahiti VI. révision du genre *Mecyclothorax* (Sharp) (Psydrini). 1. le groupe de *M. muriauxi* Perrault (Coleoptera). Nouvelle Revue d'Entomologie (NS) 1: 19–31.
- Perrault GG (1986). La faune des Carabidae de Tahiti VII. révision du genre *Mecyclothorax* (Sharp) (Psydrini). 2. les groupes de *M. striatopunctatus* n. sp., *M. dannieae* Perrault, *M. marginatus* Perrault et *M. viridis* Perrault (Coleoptera). Nouvelle Revue d'Entomologie (NS) 3: 439–455.
- Perrault GG (1987) Microendemisme et speciation du genre *Mecyclothorax* (Coleoptera – Carabidae Psydrini) à Tahiti. Bulletin de la Société Zoologique de France 112: 419–427.
- Perrault GG (1988) La faune des Carabidae de Tahiti. VIII. révision du genre *Mecyclothorax* Sharp (Psydrini) 3. les groupes de *M. altiusculus* Britton et de *M. gourvesi* Perrault (Coleoptera). Nouvelle Revue d'Entomologie (NS) 5: 229–245.
- Perrault GG (1989) La faune des Carabidae de Tahiti: IX. révision du genre *Mecyclothorax* (Sharp) (Psydrini) 4. le groupe de *M. globosus* Britton (Coleoptera). Nouvelle Revue d'Entomologie (NS) 6: 57–70.
- Perrault GG (1992) Endemism and biogeography among Tahitian *Mecyclothorax* species (Coleoptera: Carabidae: Psydrini). In: Noonan GR, Ball GE, Stork NE (Eds) The Biogeography of Ground Beetles of Mountains and Islands. Intercept, Ltd., Andover, Hampshire, UK, 201–215.
- Southwood TRE (1977) Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337–365. doi: 10.2307/3817
- Wahlroos S (2002) English–Tahitian Tahitian–English Dictionary. The Mā`ohi Heritage Press, Honolulu, Hawai`i, xxvi + 684 pp.



# Corrigenda: Sereno PC (2012) Taxonomy, morphology, masticatory function and phylogeny of heterodontosaurid dinosaurs. ZooKeys 226: 1–225

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The International Code of Zoological Nomenclature (ICZN 1999) mandates that the gender of a Greek or Latin stem composing a species name must match the gender of a stem in any generic name with which it is combined (Article 31.2). Should there exist gender mismatch at the time a new binomen is proposed, the original authorship and citation are maintained but the name must be corrected (Article 34.2). Thus “*Pegomastax africanus*” is here corrected to *Pegomastax africana*, which is derived from Greek (*pegos*, strong; *mastax* [f.], jaw), unknown sources (“Africa”), and Latin (*-ana* [f.], pertaining to).

## References

ICZN (Ed) (1999) International Code of Zoological Nomenclature. The International Trust for Zoological Nomenclature. <http://iczn.org/code>

