# Family Dysideidae Gray, 1867

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Dysideidae Gray (Demospongiae, Dictyoceratida), including Spongelidae, consists of five valid genera, with approximately 43 species described worldwide. In Dysideidae spongin fibres making up the anastomosing skeleton are always concentrically stratified but to varying degrees. As in some members of the Thorectidae, this character is affected in development by the extent to which the sponge incorporates foreign debris into the fibres. Pith components, as optically distinct central regions of the fibres, are evident, except where fibres are packed with detritus. The choanocyte chambers are eurypylous, and the matrix contains only light collagen reinforcing. The sponges are histologically simple, with few secretory cell types present. The sponge texture is soft and compressible unless rendered brittle by interstitial detritus. Incorporation of debris into both fibres and matrix is frequent. The sponge surface is always conulose, but the size, shape and arrangement of conules ranges from very small, fine and even, to large and irregular, or tuberculate. Dysideid genera are distinguished by their general form, skeletal morphology and the presence of an intrafibre core of foreign debris.

Keywords: Porifera; Demospongiae; Ceractinomorpha; Dictyoceratida; Dysideidae; Dysidea; Pleraplysilla; Euryspongia; Lamellodysidea gen.nov.; Citronia gen. nov.

# **DEFINITION, DIAGNOSIS, SCOPE**

## Synonymy

Dysideidae Gray, 1867a; Bergquist, 1980b. Spongelidae Schulze, 1879; Lendenfeld, 1886a, 1888, 1889a; Row, 1911.

# Definition

Dictyoceratida with laminated skeletal fibres and eurypylous choanocyte chambers.

## Diagnosis

Dysideids are uniquely characterised within the Dictyoceratida by the presence of eurypylous choanocyte chambers. They also have concentrically laminated and pithed skeletal fibres (to varying degrees), cored fibres, and some species have a sand-armoured surface. The sponges are histologically simple, with few secretory cell types present in the mesohyl. These sponges are soft and compressible or pliable, unless rendered brittle by interstitial detritus. The sponge surface is always conulose, but the size, shape and arrangement of conules ranges from very small, fine and even, to large and irregular, or tuberculate. Members of the Dysideidae often develop a tangential network of cellular tracts which produce a lacy pattern on the surface. These tracts convey debris for incorporation into growing fibres. Dysideids have only light collagen deposition within the mesohyl.

# Scope

Five valid genera, *Dysidea*, *Pleraplysilla*, *Euryspongia*, *Lamellodysidea*, *Citronia*. This is a wide-ranging family, occurring in shallower continental shelf waters, from cold-temperate to tropical seas. A checklist of described dysideid species is available on the internet (Cook, 2001).

# History and biology

The family Dysideidae was proposed by Gray (1867a). Some authors, notably Lendenfeld (1887a, 1889a) used the name Spongelidae established by Schulze, 1879, but included some additional taxa (*Psammopemma*, *Phoriospongia* and *Sigmatella*) which are no longer considered to be Dictyoceratida. The family is now well established and recognised by authors, however, there have been varying opinions as to the ordinal assignment of Dysideidae itself, in Dictyoceratida or Dendroceratida (e.g., Bergquist, 1996, Vacelet *et al.*, 1989, respectively) (see below).

# Remarks

The Dysideidae is one of several dictyoceratid taxa that are particularly difficult to deal with taxonomically. Bergquist's (1996) treatment of the family left it with only two genera, one of which, Dysidea, has long been recognised as heterogeneous, and is certainly a difficult genus in which to clearly characterise distinct species (Vacelet, 1959; Bergquist, 1980b). The first step towards remedying this situation is to clarify the generic diagnoses, highlighting those characters that were clearly used by the author in their concept of the genus, but which have subsequently been overlooked. Those species that do not easily fit into the genus can then be reassessed, rather than simply leaving them in unsuitable genera. This applies to the two new genera described below, Lamellodysidea gen. nov. and Citronia gen.nov. The species now assigned to those new genera did not fit easily within their prior generic assignment. It is possible that other species within Dysidea and Euryspongia should also be reassigned to other taxa. With regard to the ordinal placement of the family the diagnosis of Dysideidae (above) contrasts with members of the order Dendroceratida, which have moderate to heavy mesohyl collagen deposition, diverse cell types in the mesohyl and a dramatically different fibre morphology that has more similarity to that of the Verongida than to any dictyoceratid species. The assignment of Dysideidae to Dictyoceratida is also supported by more recently published rDNA sequence data (Bergquist *et al.*, 1998), and these authors also provide a useful analysis of all morphometric features comparing Dysideidae and other sponge taxa lacking a mineral skeleton.

# **Previous reviews**

Vacelet, 1959; de Laubenfels, 1948; Bergquist, 1980b; Bergquist, 1996; Bergquist *et al.*, 1998.

# **KEY TO GENERA**

(1) Primary and secondary fibres cored with foreign debris	
Primary fibres cored, secondary fibres clear	
(2) Skeleton regular, with primary fibres perpendicular to surface	
Skeleton irregular, without clear distinction into primary and secondary fibres	Lamellodysidea
(3) Encrusting, massive or branching, very soft and collapsible	Euryspongia
Lamellate or vasiform, dense, soft and pliable	Citronia
(4) Sponge thin, encrusting, fragile, with secondary fibre skeleton sparse or absent	Pleraplysilla
Sponge massive, with secondary fibre skeleton well developed	Dysidea

## DYSIDEA JOHNSTON, 1842

# Synonymy

[Duseideia] Johnston, 1842. [Dysidia] Agassiz, 1846. Spongelia Nardo, 1847a. [Dyseideia] Lieberkühn, 1859 (all nomina nuda). Spongelia Schmidt, 1862. Aulena Lendenfeld, 1885. Halmopsis Lendenfeld, 1886a. [Duseidea] Delage, 1899 (nomen imperfectum). Haastia Lendenfeld, 1888. Dysidea de Laubenfels, 1953a (nomen correctum); Vacelet, 1959; Bergquist, 1980b. Collospongelia Hernández, 1923.

# Type species

*Spongia fragilis* Montagu, 1818 (by subsequent designation; Burton, 1934a).

# Definition

Dysideidae in which all fibres are filled with detritus.

## Diagnosis

Thickly encrusting, massive or branching growth form, often with a marked conulose surface and a distinct net or weblike surface pattern, interconnecting between conules. Species with heavy intra-mesohyl detritus are not conulose. The skeleton consists of a regular, usually rectangular arrangement of concentrically laminated primary and secondary fibres, with primary fibres oriented perpendicular to the sponge surface. All fibres are axially to fully cored (Fig. 1B–E), although this may be in the form of scattered fragments rather than a dense core. Primary fibres are also pithed though this is usually obscured by the coring material. The sponge is soft and compressible, sometimes made fragile by large amounts of sand etc. incorporated into the sponge tissue. There is only light collagen deposition in the mesohyl, and the sponges are histologically simple, with few secretory cell types present.

#### **Previous reviews**

Burton, 1934a; de Laubenfels, 1948; Vacelet, 1959; Boury-Esnault *et al.*, 1990; Bergquist, 1996.

# **Description of type species**

Dysidea fragilis (Montagu) (Fig. 1A-E).

Synonymy. Spongia fragilis Montagu, 1818: 114, pl. 16 figs 1–2. Spongelia pallescens elastica Schulze, 1878b: 150, 154,



Fig. 1. Dysidea and Pleraplysilla. A–E, Dysidea. A, D. fragilis, specimen in situ, Portrush, Northern Ireland (photo B. Picton). B–E, examples of fibre skeletons in Dysidea species, as interpreted by Burton, 1934a. B, neotype of D. fragilis, BMNH 1930.7.3.447. C, BMNH 1930.7.3.442. D, BMNH 1930.7.3.440. E, BMNH 1930.7.3.446. F–H, Pleraplysilla. F, Pspinifera, specimen in situ, 30 m Mediterranean (photo R. Pronzato). G, P. minchini, specimen in situ, 3 m, Mediterranean (photo R. Pronzato). H, diagrammatic representation of skeleton (redrawn from Van Soest, 1978).

pl. 5 figs 4, 7, pl. 6 figs 3, 5–7, pl. 7 figs 1–5, pl. 8 figs 8–11. Spongelia elastica crassa Dendy, 1905: 205, pl. 14 fig. 4. Spongelia oculata Burton, 1929a: 448, pl. 4 fig. 7. Dysidea fragilis Burton, 1934a: 582, figs 18–33, pl. 2 figs 2–11; de Laubenfels, 1948: 137, pl. 23 fig. 42; de Laubenfels, 1953a: 515; Vacelet, 1959: 67–68; Bergquist, 1980b; Hooper & Wiedenmayer, 1994: 192 (see Burton, 1934a for more detailed synonymy).

*Material examined.* Neotype: BMNH 1830.7.3.447 (slide BMNH 1925.11.1.1034, fragment and slide SDCC/RF007).

**Description (from Ackers et al., 1992).** Form variable, ranging from cushions to massive-lobose, and with a conulose surface. This sponge is usually whitish or grey, though when packed with sand, the sand colour will dominate. The conules may be lighter in colour than the sponge surface. The consistency is variable, depending on the abundance of incorporated sand, but is usually soft, elastic, and tough. The skeletal fibre reticulum consists of ascending primary and connective secondary fibres, partially to fully packed with foreign debris.

**Remarks.** Within the Dysideidae the genus *Dysidea* is readily recognisable. Some *Dysidea* specimens may be confused with *Euryspongia*, because of occasional intermittent coring of secondary fibres (comparable to the uncored secondary fibres of *Euryspongia*), but the secondary fibres of *Dysidea* are usually regular and though they may branch, the secondary reticulum does not form the more developed reticulum seen in *Euryspongia*. The type species, *D. fragilis* Montagu, is often referred to as cosmopolitan, but this assumption is almost certainly wrong. Resolution requires an in-depth study of type material and fresh specimens, from around the world. Twenty seven nominal species are known.

De Laubenfels (1936a: 30) placed *Collospongelia* Hernández, 1923 in Dysideidae allegedly because it resembled *Dysidea*, but he stated he was 'most uncertain' about the assignment. The type material of this genus has not been re-examined but it is described as conulose, with cored fibres and somewhat reduced skeleton, and it is included here in synonymy tentatively until the type material is revisited.

# Distribution

Devon (type locality), England, Arctic, Atlantic coasts of Europe and Mediterranean (see remarks).

## PLERAPLYSILLA TOPSENT, 1905

#### Synonymy

Pleraplysilla Topsent, 1905b; Bergquist, 1980b.

## Type species

*Spongelia spinifera* Schulze, 1878b (by subsequent designation; Vacelet, 1959).

# Definition

Encrusting Dysideidae with cored fibres, and a secondary skeleton that, where present, is weak.

#### Diagnosis

These sponges are encrusting, some flat against the substratum (Fig. 1G), some producing upright fingers (Fig. 1F), with a maximum thickness of 20 mm. They are spreading, sparsely conulose, and whitish to pale yellow or mid-brown. The sponge is delicate, soft, with a slippery texture. The fibre skeleton is sparse. Fibres arising from basal plates (Fig. 1H) are cored with foreign debris, and taper toward the surface where they extend into short conules. A secondary fibre reticulum is developed in one species but is concentrated towards the base of the 5 mm thick sponge (Maldonado & Uriz, 1999).

## **Previous reviews**

Topsent, 1905b; Dendy, 1905; de Laubenfels, 1948; Vacelet, 1959; Bergquist, 1980b; Maldonado & Uriz, 1999.

# **Description of type species**

Pleraplysilla spinifera (Schulze) (Fig. 1F).

*Synonymy. Spongelia spinifera* Schulze, 1878b: 152, pl. 5 fig. 6, pl. 6 figs 8–10; *Pleraplysilla minchini* Topsent, 1905b: 184; *Pleraplysilla spinifera* Vacelet, 1959: 64; Bergquist, 1980b: 484; Hooper & Wiedenmayer 1994: 153.

*Material examined.* Holotype: Missing. Other material. Specimen of *P. spinifera* – preserved material from Mediterranean (coll. J. Vacelet). Holotype of *P. minchini*: slide from type series (MNHN).

**Description (from Vacelet, 1959).** The species is encrusting, up to 2 mm thick, with colour ranging from white to yellowish, to light brown. The consistency is very soft and fragile, with a sticky texture. The surface is elevated into sharp conules, up to 8 mm high with fibres often protruding, but is otherwise not reinforced. Oscules 0.8-1.0 mm in diameter are scattered. The skeleton is in the form of dendritic fibres, more or less ramified according to the thickness of the specimen. No anastomosing or fusion between adjacent fibres has been observed. Fibres are attached to the substratum by plaques of spongin, space 2-3 mm apart. All fibres are centrally cored, clearly stratified, and tapering, from 400  $\mu$ m at the base to 60  $\mu$ m at the surface. Most of the fibre reduction occurs in the fibre bark, while the axial detritus and pith core remains largely constant in diameter.

**Remarks.** Following Vacelet (1959), and accepting the synonymy of *P. minchini* with *P. spinifera*, the genus includes five valid species. This genus is never common, is always thin, and is difficult to detach from the substratum. Consequently good specimens and histological preparations are rare. However, the figures provided (Fig. 1F–G) suggest a good morphological basis for separating the two species, in which case *P. minchini* Topsent, 1905b, would become the designated type, by monotypy. Further study of both species is required to clarify this point.

Bergquist (1996) pointed to the doubts about the correct familial assignment for *Pleraplysilla*, whether Darwinellidae or Dysideidae, as the degree of pith development in the fibres was not of the extent and type seen in the dendroceratids. Certainly it was present, but it lacked what is now recognised as the clearly disjunct boundary in relation to bark seen in dendroceratids. The presence of coring material in the fibres also obscures pith structure in many cases. A feature which has proven constant for all *Dysidea* species studied (presently around 10), is that their secondary metabolite chemistry is characteristic, including a range of sesquiterpenes. This chemistry has been recorded for *P. spinifera* from the vicinity of Naples. In contrast, Dendroceratida possess a range of diterpenoid metabolites.

A recent report (Maldonado & Uriz, 1999) of a new species of *Pleraplysilla* from the western Mediterranean, *P. reticulata*, with a weakly developed, but clearly reticulate secondary skeleton, provides further support for inclusion of *Pleraplysilla* within the Dysideidae.

Following the identification of a novel type of secretory cell, the spumous cell in *P. spinifera* (Donadey & Vacelet, 1977), it was thought that this may signify, from a histological perspective, affinity of *Pleraplysilla* with Dendroceratida where similar cells have been noted in *Darwinella* and *Dendrilla*, however, they are absent from *Chelonaplysilla* and *Dictyodendrilla* (Bergquist, 1996). Presence or absence of spumous cells cannot unfortunately be used to confirm the familial affinity of *Pleraplysilla*.

Recent 28 s rDNA sequence evidence (unpublished data) also places the genus with Dysideidae, which supports the chemical and morphological evidence.

## Distribution

The sponge is reliably recorded from the English channel, Portugal, western Mediterranean and the Adriatic (Lesina, the type locality). Records from Australia (Lendenfeld, 1889a) are almost certainly erroneous.

## EURYSPONGIA ROW, 1911

## Synonymy

Euryspongia Row, 1911; Bergquist, 1980b.

## Type species

Euryspongia lactea Row, 1911 (by monotypy).

# Definition

Dysideidae in which the primary fibres are cored and the secondaries are clear of debris. Secondary fibres form a well-developed reticulum, which has been likened to the development seen in *Spongia*.

## Diagnosis

Encrusting, massive or branching growth form, often with a strongly conulose surface (e.g., Fig. 2B). The surface is marked by a delicate superficial tissue and sand network extending between conules and pore areas. The skeleton consists of laminated primary and secondary fibres. Only primary fibres are axially to fully cored, whereas secondary fibres are uncored. The primary network is regular, the secondary is irregular, branching and well-developed (Fig. 2C). Primary and secondary fibres are pithed, although this is often obscured by coring material in primary fibres at least. The sponge is typically very soft and compressible, to the point of being collapsible; sometimes made fragile by large amounts of foreign material incorporated into the sponge tissue.

#### **Previous reviews**

Bergquist, 1980b, 1996.

# **Description of type species**

Euryspongia lactea Row (Fig. 2A-C).

*Synonymy. Euryspongia lactea* Row, 1911: 366, pl. 39 fig. 23, pl. 41 figs 27–28, Bergquist, 1980b: 482.

# Material examined. Holotype: BMNH 1912.2.1.81.

**Description (from Row, 1911).** Irregular, sub-spherical cushions, growing probably on mud. The surface is covered with conuli, 1-2 mm high, and crowded together very closely, 2-3 mm apart. Conules are frequently connected by low ridges. Primary fibres project from the conules, and are simple or branched. Oscules are numerous, variable in size (3–100 mm in diameter), and are scattered at irregular intervals over the sponge surface; minute pores occur between the conule ridges. The colour of the sponge is milky white, due to the large quantities of white-grey mud that the sponge has ingested or incorporated. The sponge is soft and easily compressible, but quite tough. Primary fibres are cored, run radially and are 80  $\mu$ m in diameter. Secondary fibres are very delicate and variable in diameter ranging between 14 to 30  $\mu$ m. They form an irregular, branching reticulation, and are uncored.

**Remarks.** The key characters that distinguish *Euryspongia* from other dysideid genera are the soft consistency and the development of the secondary fibre reticulum, which according to Row (1911) "approaches very closely indeed to the genus *Euspongia* (now *Spongia*), the only difference being in the eurypylous chambers." It is suspected that some species have been assigned to *Euryspongia* which do not wholly conform to Row's concept, and should be re-visited. It was this realisation that resulted in the proposal of a new genus, *Citronia*, for a species previously described as a species of *Euryspongia*. Seven nominal species are known.

## Distribution

Suez (type locality), Red Sea, West Indies, Indo-West Pacific Ocean, New Zealand, Australia.

#### LAMELLODYSIDEA GEN. NOV.

#### Type species

Spongelia herbacea Keller, 1889.

# Definition

Massive, lamellate to digitate dysideids, with a thin, encrusting basal plate. The skeleton is irregular, without clear distinction between primary and secondary fibres. All skeletal fibres are cored with foreign material.

#### Diagnosis

Lamellate to digitate sponges, arising from a thin, encrusting basal plate. The surface is finely conulose, and in lamellate specimens the conules tend to be aligned in parallel rows, from the base to distal edges. The unorganised skeletal reticulum is comprised of cored fibres, without clear distinction into primary ascending fibres and secondary connecting fibres. Typically there are dense populations of cyanobacteria inhabiting the mesohyl. These sponges are soft and compressible, though specimens with significant deposits of interstitial detritus are firmer, and they have a slimy texture.

#### **Description of type species**

Lamellodysidea herbacea (Keller) (Fig. 2D-H).



Fig. 2. Euryspongia, Lamellodysidea and Citronia. A, Euryspongia lactea, holotype, BMNH 1912.2.1.81. B, E. delicatula, holotype, QMG304693, in situ New Caledonia (photo P. Laboute). C, E. lactea, fibre skeleton (from Row, 1911). D–H, Lamellodysidea herbacea. D, specimen in situ, New Caledonia (photo P. Laboute). E–G, whole specimens (from Bergquist, 1965). H, cross-section of base (SDCC/RF015). I, L. chlorea, cross-section of base (from Bergquist, 1965). J–K, Citronia vasiformis. J, holotype, QMG304694. K, fibre skeleton.

Synonymy. Spongelia herbacea Keller, 1889: 336, pl. 20 fig. 1; Dysideopsis palmata Topsent, 1897a: 482, pl. 20 fig. 25; Spongelia delicatula Row, 1911: 364; Phyllospongia cordifolia Row, 1911: 378; Dysideopsis topsenti Hentschel, 1912: 439; Dysidea herbacea; Burton, 1934a: 593; Bergquist, 1965: 140, figs 7a–c; Hooper & Wiedenmayer, 1994: 192; Phyllospongia complex de Laubenfels, 1954: pl. 18 fig. 8, pl. 3 fig. 6. Not Dysidea herbacea de Laubenfels, 1954: 38.

*Material examined.* Syntypes: ZMUZ 123 968, 123 879. Other material. Holotype of *Dysideopsis palmata*: MNHG C-12/77. Holotype of *Spongelia delicatula*: BMNH 1937.8.30. Holotype of *Phyllospongia complex*: USNM 23110. Authors collections, including: SDCC/RF015 (*herbacea*); SDCC/RF087 (*herbacea*).

**Description (from Bergquist, 1965, 1995).** This species is variable in form, from simple spreading mats with digitate or lamellate extensions to complex, soft, often interlocking lamellae. The surface is finely conulose, with individual conules up to 0.4 mm high, and with a tendency to be aligned in vertical rows, giving a slightly striated appearance. A layer of foreign material is

present in the dermis, that may extend into the body of the sponge. The skeleton is an open network of fibres, that does not show any clear distinction between primary and secondary elements. All fibres are cored with sand grains of variable size. Fibres are 50–153  $\mu$ m in diameter. Choanocyte chambers are abundant, oval, eurypylous and 54–120 × 28–82  $\mu$ m. Colour ranges from greygreen to green, reflecting the abundance of cyanobacteria that typically occur within the sponge.

**Remarks.** This group of lamello-digitate sponges, characterised by *L. herbacea*, has been split from *Dysidea* because of the consistent presence of an encrusting basal plate, and the lack of orientation of the skeleton, with respect to the surface. The name *Dysidea herbacea* has been widely applied to lamello-digitate sponges throughout the Indo-Pacific. However, it is likely that this species has been confused with other species, particularly *L. chlorea* (de Laubenfels) (Bergquist, 1995). Currently there are two recognised species of *Lamellodysidea*, the type species *L. herbacea* (Keller, 1889) and *L. chlorea* (de Laubenfels, 1954). *Lamellodysidea* might be superficially confused with *Lendenfeldia*  (Thorectidae), but the genera differ significantly in their respective fibre structure, coring patterns of fibres and choanocyte chambers.

# Distribution

Suakin (type locality), Red Sea, Palau, Papua New Guinea, New Caledonia. Other records are uncertain due to likely identification errors.

## Etymology

*Lamellodysidea* simply reflects the lamellate form, but otherwise similar to *Dysidea*.

#### CITRONIA GEN. NOV.

#### Type species

Euryspongia vasiformis Bergquist, 1995.

#### Definition

Dysideidae with cored primary fibres and uncored secondary fibres. Consistency is soft, but dense and pliable.

#### Diagnosis

Lamellate to caliculate or vasiform sponges, arising from a narrow basal stalk. The walls of the lamellae or vase are thin, up to 8 mm thick. The surface is conulose, with small, flush oscules on both inner and outer surface, and covered by a fine, web-like pattern. The fibre skeleton comprises laminated primary and secondary fibres. Primary fibres are simple, cored with foreign debris, and may be slightly fascicular near the surface. The primary fibre skeleton is irregular, in that fibres can be seen running parallel to the surface, before converging towards surface conules. Secondary fibres are branching and uncored. The consistency is dense and pliable, not flimsy and collapsible as seen in *Euryspongia* species. There is only one described species.

# **Previous review**

Bergquist, 1995.

# **Description of type species**

Citronia vasiformis (Bergquist) (Fig. 2J–K). Synonymy. Euryspongia vasiformis Bergquist, 1995. Material examined. Holotype: QMG304694; paratype: ORSTOM R1282 – Baie des Citrons, Noumea, New Caledonia.

**Description (from Bergquist, 1995).** An irregular, thinwalled, vasiform sponge, 16 cm high, up to 10 cm in diameter, with walls 4–8 mm thick. The surfaces are covered with closely-spaced, sharp conules, 1–2 mm high, each supported by a single primary fibre. Oscules are small, flush with the surface and scattered on both interior and exterior surfaces of the sponge. The consistency is soft, flexible and easily torn. The skeleton comprises lightly cored primary fibres, that can be slightly fascicular near the surface, and a loose, open reticulum of uncored secondary fibres. Primary fibres are often arranged parallel to the surface before converging toward the conules. Primary fibres are 80–200  $\mu$ m in diameter, and secondary fibres are 40–120  $\mu$ m in diameter. Only a superficial band of collagen is present. Choanocyte chambers are eurypylous, oval, and 60–90  $\mu$ m in maximum dimension.

**Remarks.** This genus is created to accommodate a species that would traditionally have been assigned to *Euryspongia*, based on skeletal characters. However, if the original diagnosis of *Euryspongia* (Row, 1911) is considered closely, it is apparent that one of the key features of that genus appears to have been ignored, namely the density of the secondary fibre reticulum. Clearly, *C. vasiformis* is a dysideid, but the original generic assignment was somewhat hasty. This new genus accommodates *vasiformis*, and removes any ambiguity surrounding the diagnosis of *Euryspongia*. Currently monotypic.

#### Distribution

New Caledonia (type locality).

#### Etymology

Named for the type locality, Baie des Citrons, New Caledonia.