

# A BLIND ABYSSAL CORAMBIDAE (MOLLUSCA, NUDIBRANCHIA) FROM THE NORWEGIAN SEA, WITH A REEVALUATION OF THE SYSTEMATICS OF THE FAMILY

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*Echinocorambe brattegardi* gen. et sp. nov. is described based on five eyeless specimens collected between 2538 and 3016 m depth in the Norwegian Sea. This new monotypic genus differs from other confamilial taxa in having the dorsum covered with long papillae and a radula formula n.3.1.3.n. The posterior notch in the notum and gill morphology, which have traditionally been used as generic characters in the family Corambidae, are considered to have little or no taxonomical value above species level. Instead of the currently described 11 nominal genera, we recognize as valid only *Corambe* and *Loy*, to which is now added *Echinocorambe*. *Loy* differs from *Corambe* in the asymmetrical lobes of the posterior notal notch and the presence of spicules in the notum. All other nominal genera are objective or subjective synonyms of these two.

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## INTRODUCTION

The family Corambidae comprises fewer than 20 species of onchidoridoid nudibranches (MARTYNOV, 1994b), living mostly in littoral and sublittoral temperate waters of the northern hemisphere. The species are small (usually 5-10 mm), cryptic when on their prey of encrusting bryozoans, and apparently quite elusive in their occurrence. In the present paper we describe the first known abyssal representative of the family, a new species from deep water in the Norwegian Sea. Based on a reevaluation of the characters used at supraspecific level, we then review the systematics of the family and propose a revised taxonomy.

## DESCRIPTION

Superfamily Onchidoridoidea GRAY, 1827  
Family Corambidae BERGH, 1871

*Echinocorambe* gen. nov.

**Diagnosis.** Body depressed, covered by numerous papillae and having a posterior median notch with symmetrical lobes. Notal spicules absent. Rhinophores conical

with transverse lamellae. Foot notched anteriorly, with two large oral tentacles. Posterior part of the foot forming a long tail. Rhinophoral pockets smooth. Gill or gills in ventral position, without lamellae. The anus opens at the base of the gill. Radula formula n.3.1.3.n. Lateral teeth with large inner and several smaller outer cusps.

**Type species.** *Echinocorambe brattegardi* sp. nov.

*Echinocorambe brattegardi* sp. nov.  
(Figs 1-2)

**Type material.** Holotype in Muséum National d'Histoire Naturelle, Paris (MNHN): Norwegian Sea, 65°29'N, 00°02'E, 21 July 1975, 3016 m depth [NORBI Expedition, stn DS04]. Paratypes: Norwegian Sea, 64°20'N, 01°40'E, 20 July 1975, 2538 m depth [NORBI Expedition, stn DS03], 3 specimens (MNHN), 1 specimen (Zoological Museum, University of Bergen). The accompanying mollusc fauna at these stations was (BOUCHET & WARÉN, 1979): *Katadesmia kolthoffi*, *Batharca frielei*, *Hyalopecten frigidus*, *Thyasira* sp., *Axinodon symmetros*, *Policordia jeffreysi*, *Cuspidaria centobi*, *Anatoma crispata*, *Skenea turgida*, *Anekes undulisculpta*, *Pseudosetia semipellucida*, *Mohnia danielsseni*, *M. mohni*, *Oenopota ovalis*, *Cylichna lemchei* and *Diaphana lactea*.

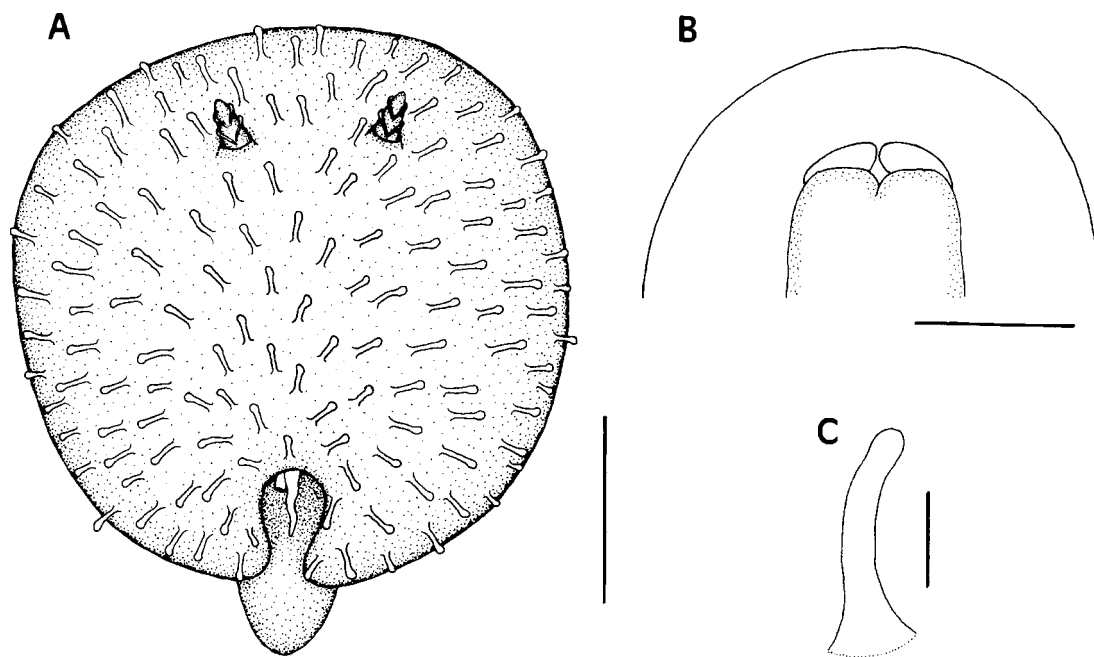


Fig. 1. *Echinocorambe brattegardi* sp. nov. (MNHN). A. dorsal view of the holotype (scale bar = 1 mm); B. ventral view of the anterior part of the foot (scale bar = 1 mm); C. detail of a dorsal papilla (scale bar = 0.05 mm).

**Description.** Preserved in alcohol, the slugs are whitish. The notum is flattened and has a posterior notch above the foot (Fig. 1A). Notal spicules are absent. The dorsum is covered by numerous simple, cylindrical papillae with a blunt apex (Fig. 1C), smaller in size near the edge of the notum. Where the anus ends, there is a single gill, projecting backwards under the notch. Branchial glands have not been observed. Rhinophores conical, with transverse lamellae. The rhinophoral pockets are simple, without peculiar closing processes. The foot is notched anteriorly (Fig. 1B); it is as broad as the border of the mantle, and extends posteriorly behind it, forming a long tail. There are two large tentacular lobes. There are no eyes.

The reproductive system is fully developed in 3 mm preserved length specimens, but it has not been dissected due to their small size. The penis is smooth, lacking hooks. Radula formula  $36 \times (4.3.1.3.4)$ , central tooth a cusp-less plate (Fig. 2). The 3 laterals have a large asymmetrical inner cusp and 3-4 smaller outer cusps. The first lateral has an additional denticle on the inside of the cusp. The 4 marginal have only one large inner cusp. The buccal bulb has two sessile pumps dorsally. The oesophagus and intestine are visible through the mantle as a dark brown mass. The digestive gland is pale

cream. The intestine has a large dilatation on its proximal region. The anus opens at the base of the single smooth gill.

Dimension: preserved length 3 mm.

**Etymology.** *Echinocorambe* is derived from the Latin *echinus*, a hedgehog, with reference to the papillate notum, and the suffix *-corambe*, type genus of the family. The specific name honours Dr. Torleiv Brattegard (University of Bergen), a companion of the second author during the NORBI Expedition, in recognition for his dedication to the zoological exploration of the northeastern Atlantic.

#### DISCUSSION

For over a century, the systematics of the family Corambidae has remained quite simple, with only two genera regarded as valid. *Corambe* BERGH, 1869 and *Doridella* VERRILL, 1870 (and its accepted synonym *Corambella* BALCH, 1899) were distinguished by, respectively, the presence and absence of a posterior notch on the notum (see MILLEN & NYBAKKEN 1991). In the last few years, however, two independent papers (MARTYNOV 1994a, SWENNEN & DEKKER 1995) have

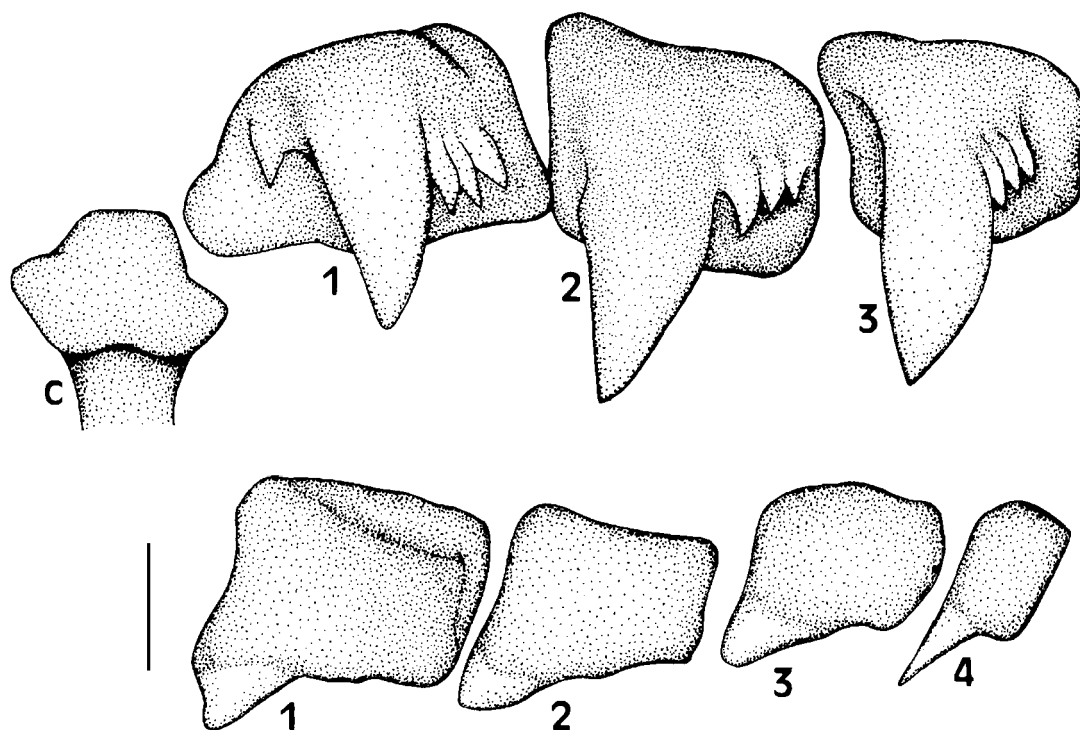


Fig. 2. *Echinocorambe brattegardi* sp. nov. (MNHN), radular teeth of a half row: lateral teeth above, marginal teeth down, c: central tooth. Scale bar = 10  $\mu$ m.

brought much new morphological information on the family, but have resulted in two uncoordinated classifications. MARTYNOV'S (1994a) classification recognizes 2 subfamilies, 5 genera and 5 subgenera. He speculated that the notch described by BERGH (1871) in the holotype of *Corambe sargassicola* BERGH, 1871 is the result of damage, and consequently *Corambe* (currently used for species with posterior notch) and *Doridella* (used for

species lacking notch) are subjective synonyms. Martynov's concept of *Corambe* includes three subgenera, *Corambe* s. s., *Corambella* and *Suhinia* MARTYNOV, 1994, based on differences in gills and rhinophore morphology. In addition, Martynov introduced for species with a natural notal notch the new genus *Quasicorambe* MARTYNOV, 1994, which he further subdivided into *Quasicorambe* s. s. and *Gulbinia*

Table 1. Nominal genera in the family Corambidae and radular formula of their type species.

Nominal genera	Radular formula	Type species
<i>Corambe</i> BERGH, 1869	n x (n.1.0.1.n)	<i>Corambe sargassicola</i> BERGH, 1871
<i>Doridella</i> VERRILL, 1870	n x (n.1.0.1.n)	<i>Doridella obscura</i> VERRILL, 1870
<i>Corambella</i> BALCH, 1899	n x (n.1.0.1.n)	<i>Corambella depressa</i> BALCH, 1899
<i>Suhinia</i> MARTYNOV, 1994	n x (n.1.0.1.n)	<i>Corambella steinbergae</i> LANCE, 1962
<i>Quasicorambe</i> MARTYNOV, 1994	n x (n.1.0.1.n)	<i>Corambe testudinaria</i> FISCHER, 1889
<i>Gulbinia</i> MARTYNOV, 1994	n x (n.1.0.1.n)	<i>Corambe pacifica</i> MACFARLAND & O'DONOGHUE, 1929
<i>Loy</i> MARTYNOV, 1994	n x (n.1.1.0.1.1.n)	<i>Loy meyeri</i> MARTYNOV, 1994
<i>Proloy</i> MARTYNOV, 1994	n x (n.1.1.0.1.1.n)	<i>Proloy millenae</i> MARTYNOV, 1994
<i>Psammodoris</i> MARTYNOV, 1994	n x (n.1.0.1.n)	<i>Corambe thompsoni</i> MILLEN & NYBAKKEN, 1991
<i>Neocorambe</i> SWENNEN & DEKKER, 1995	n x (n.1.0.1.n)	<i>Corambe testudinaria</i> FISCHER, 1889
<i>Paracorambe</i> SWENNEN & DEKKER, 1995	n x (n.1.0.1.n)	<i>Corambella steinbergae</i> LANCE, 1962
<i>Echinocorambe</i> gen. nov.	n x (n.3.1.3.n)	<i>Echinocorambe brattegardi</i> sp. nov.

MARTYNOV, 1994, based on gill morphology. He included *Corambe* and *Quasicorambe* in the subfamily Corambinae, characterised by the bilateral symmetry of the posterior part of the notum and the absence of spicules. The subfamily Loyinae MARTYNOV, 1994 is characterised by the asymmetry of the notum and the presence of dermal spicules. This subfamily includes the genera *Loy* MARTYNOV, 1994, *Proloy* MARTYNOV, 1994 and *Psammodoris* MARTYNOV, 1994, distinguished by the morphology of the radula, the disposition of the gills and the presence of a posterior notch. The following year and uninformed of Martynov's paper, SWENNEN & DEKKER (1995) discussed the genera of the Corambidae, based on the morphology of the rhinophores and gills and the posterior notch of the notum. From their examination of the holotype of *C. sargassicola*, they concluded that it does not have a natural notch, thus confirming MARTYNOV's (1994a) hypothesis and classification of *Doridella* as a synonym of *Corambe*. In addition, SWENNEN & DEKKER (1995) described the new genera *Neocorambe* SWENNEN & DEKKER, 1995 and *Paracorambe* SWENNEN & DEKKER, 1995, both with narrow gills, characterized respectively by longitudinally lamellate rhinophores and a posterior

notal notch, and smooth rhinophores and absence of notal notch.

The ventral position of the gill and anus and the presence of a posterior notal notch clearly place *Echinocorambe* in the family Corambidae. However, the notum with numerous papillae and the radula morphology with formula n.3.1.3.n and lateral teeth with large inner and 3-4 smaller outer cusps, separate *Echinocorambe* from all other corambid genera, which share a smooth dorsum and a radula morphology with formula n.1.0.1.n or n.1.1.0.1.1.n, with a single denticulated cusp on the lateral teeth. The rhinophores with transverse lamellae further separate *Echinocorambe* from other corambids which have either smooth or axially lamellar rhinophores.

The family Corambidae thus currently includes 2 subfamilies and 12 nominal genera (Table 1). However, of these, *Quasicorambe* and *Neocorambe* are based on the same type species, *Corambe testudinaria* FISCHER, 1889, and are thus objective synonyms. The same holds for *Suhinia* and *Paracorambe*, both based on *Corambella steinbergae* LANCE, 1962. On the other hand, the genera *Corambe*, *Doridella* and *Corambella* are subjective synonyms (SWENNEN & DEKKER 1995).

Table 2. Corambid genera and outgroup (*Adalaria*): character status and matrix of data. Data for *Neocorambe* and *Paracorambe*, objective synonyms of, respectively, *Quasicorambe* and *Suhinia*, are not repeated. Subjective synonyms are included.

Character status

0 = ancestral, 1-2 = derived states.

1.

Gill position: 0, dorsal; 1, ventral (over the anus); 2, ventral (each side of the anus).

2.

Gills shape: 0, plume-like; 1, plate-like.

3.

Notal spicules: 0, present; 1, absent.

4.

Posterior end of the body: 0, symmetrical; 1, asymmetrical.

5.

Posterior notch: 0, absent; 1, present; 2, secondarily absent.

6.

Rhinophores: 0, transverse lamellae; 1, longitudinal lamellae; 2, smooth.

7.

Central radular tooth: 0, present; 1, absent.

8.

Lateral radular teeth: 0, one; 1, two; 2, three.

9.

Marginal radular teeth: 0, more than ten; 1, less than ten.

10.

Dorsal tubercles: 0, present; 1, absent.

Matrix of data

	1	2	3	4	5	6	7	8	9	10
<i>Adalaria</i>	0	0	0	0	0	0	0	0	0	0
<i>Echinocorambe</i>	1	0	0	0	1	0	0	2	1	0
<i>Corambe</i>	2	1	1	0	2	1	1	0	1	1
<i>Doridella</i>	2	1	1	0	2	1	1	0	1	1
<i>Corambella</i>	2	1	1	0	2	1	1	0	1	1
<i>Suhinia</i>	2	0	1	0	2	2	1	0	1	1
<i>Quasicorambe</i>	2	0	1	0	1	1	1	0	1	1
<i>Gulbinia</i>	1	0	1	0	1	1	1	0	1	1
<i>Loy</i>	1	0	0	1	2	2	1	1	1	1
<i>Proloy</i>	1	0	0	1	1	2	1	1	1	1
<i>Psammodoris</i>	1	0	0	1	1	2	1	0	1	1

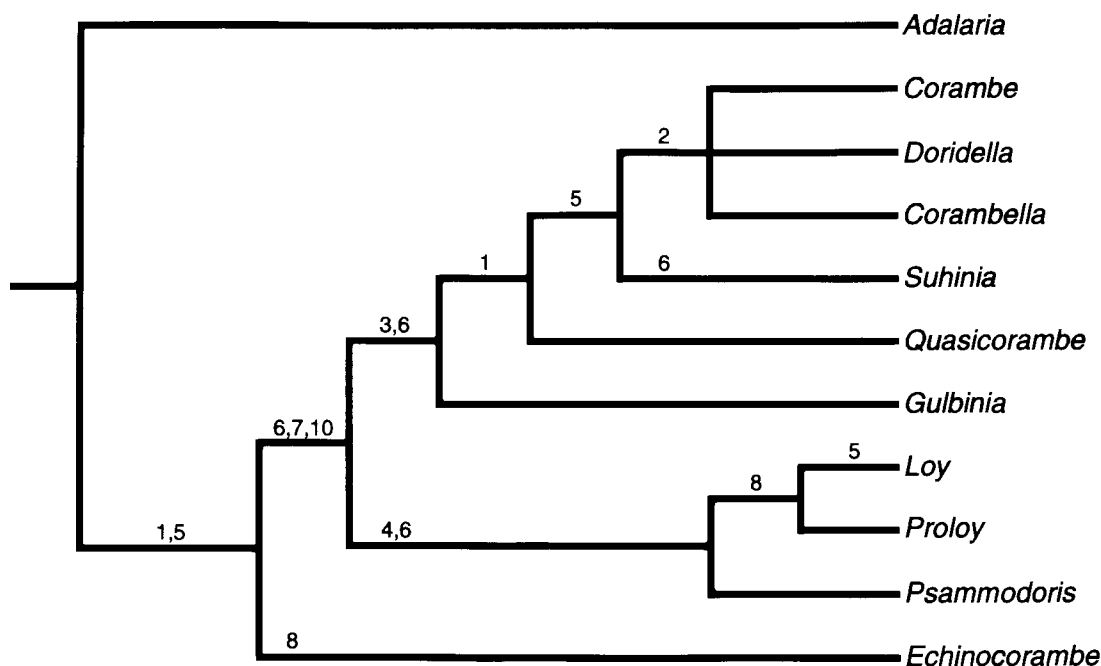


Fig. 3. Phylogeny of the family Corambidae. Numbers refer to the characters discussed in the text and as listed in Table 2.

To reevaluate the systematics of the family, we have considered the suite of morphological characters available, and character states were extracted from the literature (MARTYNOV 1994a, SWENNEN & DEKKER 1995) and from our own observations (*Echinocorambe*). The genus *Adalaria* BERGH, 1878 (family Onchidorididae) has been chosen as the outgroup because it is more plesiomorphic than other onchidorid genera, which have 5 (*Acanthodoris* GRAY, 1850) or only one (*Onchidoris* BLAINVILLE, 1816 and other genera) marginal teeth per radula half-row; *Adalaria* has 10 or more. Character states extracted from the literature (THOMPSON & BROWN 1984) for *Adalaria* have been used to determine the polarity of characters in Corambidae. Ten characters were considered (Table 2):

1. Position of gill. – The presence of ventral gills is the most important distinctive feature of the family Corambidae, separating it from other families of Onchidoridoidea, which have dorsal gills. Ventral gills have been considered an autoapomorphy through pedomorphosis (MARTYNOV, 1994b).
2. Type of gills. – There are two different gill types, broad (plate-like) and narrow (plume-like). The latter is considered plesiomorphic.
3. Notal spicules. – In several genera of Corambidae the dorsum bears numerous spicules whereas in other genera the dorsum is soft. The presence of dorsal spicules is considered plesiomorphic.
4. Posterior part of notum. – The posterior part of the notum may be symmetrical or asymmetrical. MARTYNOV (1994b) considered that this latter is apomorphic through pedomorphosis.
5. Posterior notch. – A posterior notal notch is known only in Corambidae, but some taxa lack it. According to MARTYNOV (1994b), in *Proloy* the lobes of the notch are secondarily fused, and in *Suhinia* and *Corambe* the notch may secondarily disappear. The presence of the notch (even when the lobes are fused or it has secondarily disappeared) is considered apomorphic because this character is absent in *Adalaria*.
6. Rhinophores. – In the Onchidoridoidea, smooth or longitudinally lamellar rhinophores are known only in Corambidae. *Echinocorambe*, as well as other Onchidoridoidea, have transversal lamellae and this is considered the plesiomorphic condition.
7. Central radular tooth. – Most genera of Corambidae lack a central tooth, whereas *Echinocorambe* and most species of *Adalaria* have one. A central tooth is considered plesiomorphic.

8. Lateral radular teeth. – In *Echinocorambe* there are three lateral teeth, whereas *Loy* and *Proloy* have two, and other nominal corambid genera have only one. In *Adalaria* there is only one and this is considered the plesiomorphic condition.
9. Marginal teeth. – The presence of numerous marginal teeth is considered plesiomorphic. Species of *Adalaria* have 10 or more.
10. Dorsal tubercles. – Species of *Adalaria* and *Echinocorambe* have the dorsum covered with numerous tubercles. Other Corambidae have a smooth dorsum, and this is considered the apomorphic condition.

A single tree (Fig. 3) was obtained based on an analysis of the characters listed in Table 2 using PAUP version 3.1 (SWOFFORD 1993). This tree has a length of 16 steps and a consistency index of 0.88. Is the taxonomy of the family Corambidae introduced by MARTYNOV (1994a) supported by the present analysis? *Echinocorambe* emerges as the sister group, characterized by having three lateral radular teeth, to the rest of the family Corambidae, which is further separated in two distinct well-supported clades. One clade, formed by the genera *Loy*, *Proloy* and *Psammodoris* (subfamily Loyinae Martynov, 1994), is supported by two apomorphies, the asymmetrical posterior part of the notum and the rhinophores lacking transverse lamellae; another clade, comprising *Corambe* (with the subgenera *Corambe*, *Corambella* and *Suhinia*) and *Quasicorambe* (with *Quasicorambe* and *Gulbinia*), is supported by two apomorphies, the absence of spicules and the rhinophores lacking transverse lamellae.

The question of how many further subdivisions should be recognized in a classification of the Corambidae is a subjective matter. The family comprises currently only 17 nominal species and as many as 6 genera are monotypic. If the character presence/absence of a notal notch is given generic importance, one alternative view is to segregate, as did MARTYNOV (1994a), Corambinae into a monophyletic genus *Corambe* (including *Corambella* and *Suhinia*) and a paraphyletic genus *Quasicorambe* (including *Gulbinia*), and Loyinae into three monotypic genera. If, however, one considers that the notal notch is a plesiomorphic character within Corambidae, that has been lost at least twice in the family, too much importance should perhaps not be given to that single character. The result would be a classification with only 3 genera: *Echinocorambe* gen. nov. (1 species), *Loy* MARTYNOV, 1994 (= *Proloy* = *Psammodoris*; 3 species) and *Corambe* BERGH, 1869 (= *Doridella* = *Corambella* = *Paracorambe* = *Suhinia* = *Quasicorambe* = *Neocorambe* = *Gulbinia*; 13 species). Unless the family is, in the future, found to be much more diverse than is currently appreciated, we think that the latter classification is sufficient to express the diversification that has taken place.

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