

## Zoanthids (Cnidaria: Hexacorallia: Zoantharia) from shallow waters of the southern Chilean fjord region, with descriptions of a new genus and two new species

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### Abstract

The taxonomy of the order Zoantharia (= Zoanthidea = Zoanthiniaria) is greatly hampered by the paucity of diagnostic morphological features. To facilitate discrimination between similar zoanthids, a combination of morphological and molecular analyses is applied here. The three most abundant zoanthid species in shallow waters of the southern Chilean fjord region are described. Comparison with other zoanthids using molecular markers reveals that two of them are new to science; these are described as *Mesozoanthus fossii* gen. n., sp. n. and *Epizoanthus fiordicus* sp. n. Their representatives grow on rocky substratum and do not live in symbiosis with demosponges. In the less abundant *M. fossii*, animals are greyish in colour and resemble members of *Parazoanthus* in growth form. Individual polyps can be up to 35 mm long. The more abundant *E. fiordicus* are also greyish; the polyps arise from thin stolons and reach only 12 mm in length. The third species studied is *Parazoanthus elongatus* McMurrich, 1904. For these three Chilean zoanthid species, in-situ photographs are presented as well as information on distribution, habitat and associated species. Establishment of the *Mesozoanthus* gen. n. is of particular importance to taxonomy in the chaotic suborder Macrocnemina.

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**Keywords:** *Mesozoanthus*; *Epizoanthus*; Chile; Taxonomy; Benthos; Fjords

### Introduction

The diversity of marine organisms in the southern Chilean fjord region (42–55°S) provides great potential

for taxonomic studies. However, the inhospitable geomorphological conditions and remote location make access very difficult. Thus, the benthic fauna of the region is poorly studied and the zoanthid fauna (order Zoantharia [= Zoanthidea = Zoanthiniaria]) is almost unknown. Among the seven currently valid zoanthid genera (representing five families), only *Isozoanthus* Carlgren has not been reported from the Pacific Ocean.

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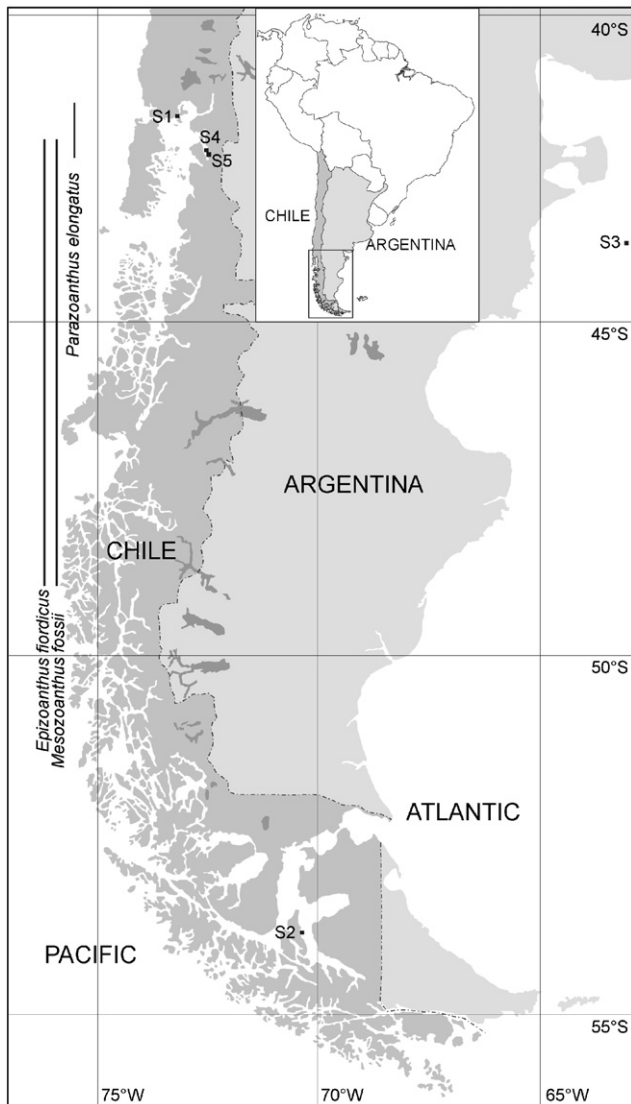
E-mail address: [fredsinniger@hotmail.com](mailto:fredsinniger@hotmail.com) (F. Sinniger).

Species number estimations are very difficult due to the taxonomical chaos in the order. Characters used to describe species have not been standardised; thus, many species names may eventually fall as junior synonyms. This concerns especially the tropical shallow-water zoanths, which show high colour variation and morphological plasticity. Few studies have focused on Chilean zoanths (Carlgren 1899, 1927; McMurrich 1904; Lwowsky 1913). Prior to the present study there were four zoanthid species described from Chile: *Epizoanthus patagonichus* Carlgren, 1899 from Calbuco (approx. 41°45'S, 73°06'W; S1 in Fig. 1; depth

20 fathoms (c. 36 m)); *Parazoanthus fuegiensis* Carlgren, 1899 from Dawson Island/Puerto Harris in the Straits of Magellan (approx. 53°50'S, 70°25'W; S2 in Fig. 1; intertidal); *P. elongatus* McMurrich, 1904 from Calbuco (S1 in Fig. 1); and *Epizoanthus balanorum* Lwowsky, 1913 from the “Chilean coast”. *Epizoanthus patagonichus* had been described originally from southern Argentina (44°14'S, 61°23'W; east of S3 in Fig. 1; depth 60 fathoms (c. 110 m)); several specimens found later at Calbuco were assigned to this species by McMurrich (1904). Calbuco and the Straits of Magellan constitute approximately the northern and southern limits of the Chilean fjord region, respectively (Fig. 1).

Between 1994 and 2007, Vreni Häussermann and Günter Försterra collected, examined and preserved shallow-water anthozoans from more than 170 sites along the Chilean coast from Arica (18°30'S, 70°19'W) to Fuerte Bulnes, Straits of Magellan (53°36'S, 70°56'W). Detailed descriptions of the sampling sites are given in Häussermann (2004a, b, 2005, in the respective electronic supplementary material) and in Häussermann and Försterra (2007). Among the numerous specimens collected, three species of zoanths have been identified from this region and ascribed to the suborder Macrocnemina. In the present study, we apply a combination of molecular methods and the analyses of *in vivo* morphological and ecological observations to elucidate phylogenetic relationships among these morphologically similar zoanths.

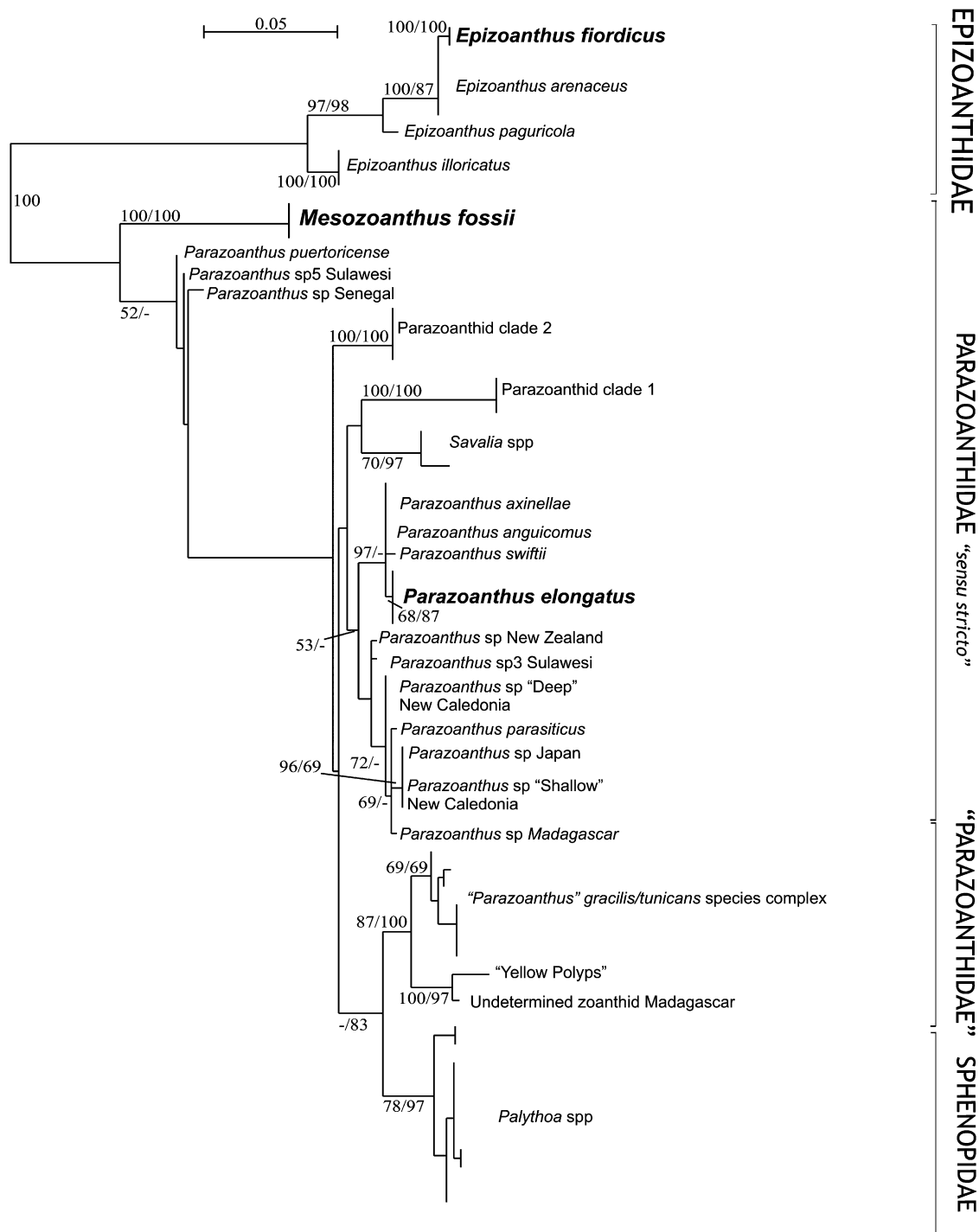
Molecular analyses have shown that taxonomic relationships within and between zoanthid genera inferred from morphological characters did not adequately represent the phylogeny (Sinniger et al. 2005). At the species level, Reimer et al. (2004) have demonstrated the usefulness of DNA data to clarifying relationships within morphologically variable clades. In accordance with the taxonomic studies on zoanths published recently (Reimer et al. 2007a, 2008), we compared the sampled species with other zoanths using the following molecular markers: mitochondrial 16S ribosomal DNA (mt 16S rDNA; Fig. 2), cytochrome oxidase subunit I (COI), and nuclear internal transcribed spacer of ribosomal DNA (ITS-rDNA). The results indicate one genus and two species new to science, which are established below as *Mesozoanthus fossii* gen. n., sp. n. and *Epizoanthus fiordicus* sp. n. The third of our study species is identified as *Parazoanthus elongatus*. For all three species, data on habitat, geographic and bathymetric distribution as well as on associated species are provided.



**Fig. 1.** Map of the southern South American distribution of shallow-water zoanths. Vertical bars indicate known ranges, dots indicate type localities as follows: S1 (Calbuco) = *Parazoanthus elongatus*, S2 = *P. fuegiensis*, S3 (representing true locality at 44°14'S, 61°23'W, outside of map) = *Epizoanthus patagonichus*, S4 = *E. fiordicus* sp. n., S5 = *Mesozoanthus fossii* gen. n., sp. n.

## Material and methods

Seventeen specimens were examined and photographed in situ during scuba dives in the coastal waters



**Fig. 2.** Maximum likelihood tree based on sequences of mitochondrial 16S ribosomal DNA and cytochrome oxidase subunit I; bootstrap support values (16S/COI) shown at nodes. Chilean zoanthids indicated in boldface. Previous studies showed that the species grouped under "Parazoanthidae" are closer to brachycnemid zoanthids than to other Parazoanthidae.

of northern and central Chile (down to a depth of 25 m) and in the fjords of southern Chile (to depths of 35–40 m). The distance between adjacent sites was less than 200 km. For morphological and molecular studies, specimens were preserved in 10% formalin-seawater and in 96% ethanol, respectively (cf. Häussermann 2004a, b).

Each colony sampled was identified by the location, depth, date, and name of the collector. Samples were split to be fixed in formalin or ethanol, and in some cases split again (each subsample contains a few polyps) to be deposited in different institutions (i.e. *E. fiordicus* paratypes ZSM 20080022, ZSM 20080023, RMNH

Coel. 38798, and RMNH Coel. 38799 are fragments of the same original colony). Further preparation of the formalin-seawater samples included decalcification by chelation, and dissolution of siliceous material by digestion during 30 min in 5% hydrofluoric acid. Mesenterial arrangements were observed on hand-made cross sections. For cnidae preparations, squash preparations of small amounts of tissue from two preserved specimens per species were examined, photographed, and measured using a light microscope (1000 $\times$ , oil immersion). Cnidae nomenclature follows England (1991). For histological examinations, specimens were embedded in paraffin, sectioned at 8 $\mu$ m intervals, and stained with Masson's trichrome. Due to the combination of remaining incrustations and aggressive treatment (HF), histological sections were successful for *Parazoanthus elongatus* only. The nomenclature of morphological characters follows Ryland and Lancaster (2004), except for the use here of 'mesenteria' instead of 'septa'.

DNA extractions, PCR and sequencing were performed as described in Sinniger et al. (2005). The universal primers LCO1490 and HCO2198 (Folmer et al. 1994) were used to amplify COI. For mt 16S rDNA we used the primers 16Sant1a and 16SbmoH described in Sinniger et al. (2005); for ITS-1, ITS-2 and 5.8S rDNA we used the primers ZoanF and ZoanR (Reimer et al. 2007b). Novel sequences have been deposited in GenBank (for accession numbers see Table 1). The sequences obtained were manually aligned in BioEdit (Hall 1999) and analysed phylogenetically by applying the maximum likelihood (ML) method in PhyML (Guindon and Gascuel 2003). All ML analyses were performed with GTR nucleotide substitution matrix, a gamma 1 invariant model with eight categories, estimated  $\alpha$ -parameter, and estimated frequencies of amino acids. Only zoanthid outgroups were used in order to maximise informative sites in the alignments. Sinniger et al. (2005) have shown the clearly basal position of *Epizoanthus* in phylogenetic trees of Zoantharia, using an actiniarian outgroup.

*Abbreviations used:* GF = Günter Försterra, VH = Verena Häussermann; MNHG = Natural History Museum of Geneva (Switzerland), RMNH = Naturalis (Leiden, The Netherlands), ZSM = Zoologische Staatssammlung Munich (Germany).

## Taxonomic section

### Suborder Macrocnemina Haddon & Shackleton, 1891

#### Diagnosis

Characterised by a complete fifth pair of mesenteries.

### Family Epizoanthidae Delage & Hérouard, 1901

#### Diagnosis

Characterised by a simple mesogloea sphincter muscle. Comprises the genera *Epizoanthus* Gray and *Palaeozoanthus* Carlgren. Polyps usually strongly encrusted with sand particles. Species found on rocky substrata or gastropod shells often inhabited by pagurids; some cases of free-living species reported (*E. lindhali*, *E. vagus*). In colonial species, polyps linked by stolons or, in pagurid-associated species, by a continuous coenenchyme. No symbioses with *Symbiodinium* zooxanthellae.

### *Epizoanthus* Gray, 1867

#### Type species

*Epizoanthus papillosus* Johnston, 1842. According to some authors (e.g. Ryland 2000), *E. incrustatus* Dueben & Koren, 1847 is a synonym denoting the same species.

#### Diagnosis

Generally as for the family. Distinct from *Palaeozoanthus* by non-fertile micromesenteries.

### *Epizoanthus fiordicus* sp. n.

#### Etymology

The specific epithet refers to the species having been found in the inner fjords of the southern Chilean fjord region; it is to be treated as an adjective for the purposes of nomenclature.

#### Material examined

*Holotype.* Chile, Comau Fjord, Pta Llonco (42°20.634'S, 72°27.429'W), 15 m, 12.02.2004, leg. VH and GF; MNHG INVE54341 (in 96% ethanol and 10% formalin).

*Paratypes.* Chile, Bernardo Area, Estero Farquhar (48°29'18.7"S, 74°12'25.7"W), 28 m, 29.03.2005, leg. VH and GF; MNHG INVE54342 (96% ethanol). Chile, Canal Messier, Estero Caldclough (48°21'37"S, 74°26'13"W), 34 m, 28.03.2005, leg. VH and GF; ZSM 20080022 and RMNH Coel. 38798 (96% ethanol), ZSM 20080023 and RMNH Coel. 38799 (10% formalin).

*Sequences.* For GenBank accession numbers of sequences obtained from type specimens, see Table 1.

#### Description

*Size.* Living polyps with oral disc diameter up to 8 mm; column diameter up to 5 mm; height up to 12 mm; proximal part of polyp slightly broader than distal part. Preserved polyps with column diameter up to 5 mm; height up to 5 mm; distal tip of contracted polyp usually rounded.

**Table 1.** Sources of specimens used, and GenBank accession numbers of corresponding gene sequences.

Sample name	Locality	Depth (m)	Collector/donor	COI	mt 16S rRNA	ITS-rDNA
<i>Epizoanthus illoricatus</i>	New Caledonia	35	F. Sinniger	EU591613	EU591597	–
<i>Epizoanthus illoricatus</i>	New Caledonia	58	F. Sinniger	EU591614	EU591598	EU591540
<i>Epizoanthus illoricatus</i>	Sulawesi, Indonesia	22	M. Boyer	AB247349	AY995929	EU591541
<i>Epizoanthus paguricola</i>	NW Mediterranean Sea	130	H. Zibrowius	AB247347	AY995928	EU591539
<i>Epizoanthus fiordicus</i>	Chile	15	V. Häussermann	EF672674	EF687813	–
<i>Epizoanthus fiordicus</i>	Chile	28	V. Häussermann	EF672675	EF687814	–
<i>Epizoanthus arenaceus</i> “Marseille”	NW Mediterranean Sea	23	F. Sinniger	AB247348	AY995926	EU591538
<i>Epizoanthus arenaceus</i> “Spain”	NW Mediterranean Sea	5	P. Chevaldonné	EF672672	EF687812	–
<i>Epizoanthus arenaceus</i> “Italy”	NW Mediterranean Sea	111	H. Zibrowius	EF672673	AY995927	–
Parazoanthid “EBISCO”	New Caledonia	~860	B. Richer-de-Forges	EU591617	EU591601	EU591560, EU591561
Parazoanthid “NC2”	New Caledonia	~860	B. Richer-de-Forges	EU591615	EU591600	EU591562, EU591563
Parazoanthid “NC3”	New Caledonia	~860	B. Richer-de-Forges	EU591616	EU591602	EU591558
Parazoanthid “CORSARO72”	S Mediterranean Sea	690	H. Zibrowius	EF672665	EF687824	EU591559
Parazoanthid “Principe”	Principe	45	P. Wirtz	EU591618	AY995932	EU591553
Parazoanthid “M2”	N Madagascar	10	F. Sinniger	EU591619	EU591599	EU591554
Parazoanthid “Cape Verde”	E Atlantic	17	P. Wirtz	AB247357	AY995931	EU591556, EU591557
<i>Mesozoanthus fossii</i>	Chile	20	G. Försterra	EF672653	EF687822	EU591545, EU591542
<i>Mesozoanthus fossii</i>	Chile	29	V. Häussermann	EF672654	EF687821	EU591543, EU591544
<i>Mesozoanthus fossii</i>	Chile	18	V. Häussermann	EF672655	EF687823	–
<i>Parazoanthus puertoricense</i>	W Caribbean Sea	17	F. Sinniger	AB247351	AY995933	EU591585, EU591584
<i>Parazoanthus</i> sp. “Senegal”	E Atlantic	39	P. Petitdevoize	EF672656	EF687820	EU591582
<i>Parazoanthus</i> sp.5 “Sulawesi”	Sulawesi, Indonesia	16	M. Boyer	EU591627	AY995934	EU591583
<i>Parazoanthus</i> sp. “New Zealand”	Tasmania, Australia	17	K.L. Gowlett-Holmes	EU591620	EU591610	–
<i>Parazoanthus</i> sp. New Caledonia “Deep”	New Caledonia	32	F. Sinniger	EU591623	EU591605	EU591578
<i>Parazoanthus</i> sp. New Caledonia “Deep”	New Caledonia	50	F. Sinniger	EU591624	EU591609	EU591579, EU591580
<i>Parazoanthus</i> sp. New Caledonia “Shallow”	New Caledonia	5	F. Sinniger	EU591626	EU591607	EU591568
<i>Parazoanthus</i> sp. New Caledonia “Shallow”	New Caledonia	3	F. Sinniger	EU591625	EU591606	EU591569
<i>Parazoanthus</i> sp. Japan	Japan	3	J.D. Reimer	EU591630	EU591608	EU591566
<i>Parazoanthus</i> sp.3 “Sulawesi”	Sulawesi, Indonesia	31	M. Boyer	AB247354	AY995937	EU591575
<i>Parazoanthus parasiticus</i>	W Caribbean Sea	15	F. Sinniger	EF672663	AY995938	EU591577, EU591581
<i>Parazoanthus</i> sp. “Mada3”	N Madagascar	9	F. Sinniger	EF672664	EF687825	EU591576
<i>Parazoanthus swiftii</i>	W Caribbean Sea	30	F. Sinniger	AB247350	AY995936	EU591573, EU591572
<i>Parazoanthus axinellae</i> “Mediterranea”	NW Mediterranean Sea	7	F. Sinniger	AB247355	AY995935	EU591570
<i>Parazoanthus axinellae</i> “Ireland”	NE Atlantic	27	P. Chevaldonné	EF672659	EF687826	EU591571
<i>Parazoanthus anguicomus</i>	NE Atlantic	42	P. Chevaldonné	EF672660	EF687827	EU591574
<i>Parazoanthus elongatus</i> . “NZ”	New Zealand	5	N. Shears	EF672662	EF687828	EU591564
<i>Parazoanthus elongatus</i> “Chile”	Chile	20	V. Häussermann	EF672661	EF687829	EU591565
<i>Parazoanthus elongatus</i> “Chile2”	Chile	25	D. Thompson	EU591621	EU591603	–
<i>Parazoanthus elongatus</i> “Chile3”	Chile	15	G. Försterra	EU591622	EU591604	–
<i>Savalia</i> aff. <i>savaglia</i>	E Atlantic	17	P. Wirtz	EF672657	AY995930	EU591546, EU591547
<i>Savalia savaglia</i>	NW Mediterranean Sea	41	F. Sinniger	AB247356	AY995925	EU591548, EU591549
<i>Savalia lucifica</i>	NE Pacific	?	E. Sala	EF672658	EF687819	EU591550, EU591551



Table 1. (continued)

Sample name	Locality	Depth (m)	Collector/donor	COI	mt 16S rRNA	ITS-rDNA
Zoanthid "302"	N Madagascar	39	F. Sinniger	EF672666	EF687831	EU591594
"Yellow Polyps"	aquarium trade	?	F. Sinniger	AB247358	AY995939	EU591595, EU591596
" <i>Parazoanthus</i> " aff. <i>tunicans</i> "white"	W Caribbean Sea	15	F. Sinniger	EF672667	AY995941	EU591586, EU591588
" <i>Parazoanthus</i> " <i>gracilis</i> "Japan"	Japan	17	J.D. Reimer	AB214178	AB219194	AB214161
" <i>Parazoanthus</i> " <i>gracilis</i> "New Caledonia"	New Caledonia	33	J.L. Menou	EU591629	EU591612	EU591592, EU591593
" <i>Parazoanthus</i> " <i>gracilis</i> "New Caledonia"	New Caledonia	25	J.L. Menou	EU591628	EU591611	EU591591
" <i>Parazoanthus</i> " <i>gracilis</i> "Sulawesi"	Sulawesi, Indonesia	28	M. Boyer	EF672668	AY995942	EU591590
" <i>Parazoanthus</i> " aff. <i>tunicans</i> "black"	W Caribbean Sea	15	F. Sinniger	AB247353	AY995940	EU591587, EU591589
Zoanthid "Mada 1"	N Madagascar	10	F. Sinniger	EF672669	EF687830	–
<i>Palythoa heliodiscus</i> "M1"	N Madagascar	?	C. Solterer	AB219216	–	–
<i>Palythoa heliodiscus</i> "EK1"	Japan	19	J.D. Reimer	–	AB219224	DQ997882
<i>Palythoa heliodiscus</i> "LL1"	Saipan, N Mariana Islds.	3	J.D. Reimer	AB219214	AB219223	DQ997883
<i>Palythoa psammophila</i>	N Madagascar	22	F. Sinniger	AB247360	EF687832	–
<i>Palythoa mutuki</i> "YS1"	Japan	0	J.D. Reimer	AB219213	AB219222	DQ997890
<i>Palythoa mutuki</i> "M11"	Japan	0	J.D. Reimer	AB219217	AB219225	DQ997889
<i>Palythoa tuberculosa</i> "M111"	Japan	2	J.D. Reimer	AB219199	AB219218	–
<i>Palythoa tuberculosa</i> "YoS1"	Japan	1	J.D. Reimer	AB219204	AB219219	DQ997921
<i>Palythoa tuberculosa</i> "Mada"	N Madagascar	10	F. Sinniger	AB247359	EF988096	DQ997901

**Morphology.** Tentacles 20–34 (fewer on smaller, immature polyps); length two times oral disc diameter; transparent whitish grey to brownish, with circular knob at tip. Pharynx oval, whitish. Oral disc and distal column transparent whitish-grey, with 12–20 whitish capitular ridges. Column dark brown due to heavy incrustations of sand grains. Incrustations more abundant in ectoderm, extend into mesoglea. Polyps arise from flat, thin stolons nearly as wide as bases of polyps, tightly attached to rocky substratum. Polyps arise 0.5–2 cm along stolon; tentacles of neighbouring polyps can touch (Fig. 4a,b).

**Cnidae.** Spirocysts, basitrichs, microbasic b-mastigophores, microbasic p-mastigophores, holotrichs (Table 2, Fig. 3).

### Diagnosis

This species can be clearly distinguished morphologically and ecologically from other *Epizoanthus* reported from Chile: *E. patagonichus* has rust-red tentacles and is smaller (Carlgren 1899); *E. balanorum* is associated with cirripeds of the genus *Balanus*, smaller and possesses more tentacles (38–40). European *E. arenaceus* is clearly different morphologically, and has not been found at any intermediate locations between the Mediterranean Sea/North East Atlantic and the region studied here.

### Habitat and distribution

This species is typical of the inner fjords in the Northern and Central Patagonian Zones. It is usually found on rocky substrata between Comau Fjord (42°09.722'S, 072°35.915'W) and Estero Farquhar (48°29.187'S, 74°12.257'W), at 15–34 m depth, usually not abundantly. It also occurs on rocky walls with small amounts of fine sediment, which regularly covers the stolons.

### Biology and associated species

Usually the colonies are small. *Epizoanthus fiordicus* sp. n. regularly associates with the stony coral *Tethocyathus endesa* that can withstand moderate sedimentation, and with the primnoid gorgonian *Primnoella chilensis* on moderately steep walls in areas less influenced by sediment.

### Family Parazoanthidae Delage & Hérouard, 1901

#### Diagnosis

This family traditionally groups macrocnemic zoanthids possessing an endodermal sphincter. Member species are frequently associated with other organisms, which are used as substrata.

**Table 2.** Types (in the nomenclature of England 1991), relative abundances and sizes of cnidae in the three zoanthid species common in shallow waters of Chilean fjords.

Tissue	Cnidae type	<i>Epizoanthus fiordicus</i> sp. n.	<i>Parazoanthus elongatus</i>	<i>Mesozoanthus fossii</i> gen. n., sp. n.
Tentacles	Spirocysts	v; 24–30 × 3–5 (A)	v; 30–33 × 4–5 (A)	v; 20–30 × 3–5 (A)
	b-mastigophores	f; 13–22 × 3–5 (B)	1: v; 24–33 × 3–4 (B) 2: r; 39–40 × 4–5 (C)	c; (15)19–26(30) × 4–6 (8) (B)
	Holotrichs	c; 32–34 × 12–13 (C)		r; 26–33 × 16–19 (C)
	Basitrichs	f; 15–20 × 3–5 (D)	c; 20–26 × 3 (D)	s; 16–21 × 3–4 (D)
Column	Holotrichs 1	s; 34–37 × 14–17 (E)	c; 32–41 × 14–19 (E)	c; 28–35 × 13–17 (E)
	Holotrichs 2	c; 15–25 × 7–11 (F)	c; 19–21 × 13–14 (F)	c; 15–24 × 8–10 (F)
	Spirocysts		f; 12–30 × 3–4	
	p-mastigophores		s; 19 × 8	
Pharynx	Basitrichs	v; 25 × 4–5 (G)	c; 7–10 × 1.5–2 (G)	v; 18–23 × 3–5 (G)
	Spirocysts	c; 20–23 × 4 (H)	c; 20–32 × 3–4 (H)	
	p-mastigophores	c; 21–22 × 6–8 (I)	f; 24–26 × 5–6 (I)	
	b-mastigophores	s; 21–26 × 4 (J)	s; 22–26 × 3–5 (J)	f; 11–23 × 4–5 (H)
	Holotrichs 1	v; 17–19 × 7–11 (K)	c; 12–14 × 3–4 (K)	c; 16–20 × 9–11 (I)
	Holotrichs 2	f; 30–36 × 12–14 (L)	r; 22–28 × 8–10 (L)	r; 32–33 × 14–18 (J)
	Holotrichs 3	s; 8–9 × 2–3 (M)		v; 6–9 × 3–4 (K)
Mesenterial filaments	p-mastigophores	v; 20–22 × 5–6 (N)	c; 18–24 × 5–6 (M)	v; 17–21 × 6–7 (L)
	b-mastigophores	f; 30–35 × 5 (O)	s; 30 × 6 (N)	1: s; (16)20–22(27) × 4–6 (M) 2: s; 39–40 × 6–8 (N)
	Holotrichs 1	v; 15–17 × 7 (P)	<sup>a</sup>	v; 15–20 × 9–11 (O)
	Holotrichs 2	f; 32–38 × 14–15 (Q)		f; 30–32 × 14–18 (P)
	Holotrichs 3	s; 9 × 6 (R)		v; 7–11 × 4–6 (Q)
	Basitrichs		s; 32 × 4	f; 18–24 × 4–5 (R)
	Spirocysts	r; 27–28 × 5	<sup>a</sup>	c; 19–25 × 5–6

Capital letters between brackets refer to cnidae illustrations in Fig. 3.

Minor-case letters followed by a semicolon indicate relative abundance of the respective cnidae type in the respective species, as follows (in decreasing order): v = very common, c = common, f = few, r = rare, s = sporadic.

Number ranges indicate cnidae dimensions (length × width) in  $\mu\text{m}$ .

<sup>a</sup>One destroyed holotrich and one spirocyst were observed in filaments of *Parazoanthus elongatus*.

## *Parazoanthus* Haddon & Shackleton, 1891

### Type species

*Parazoanthus axinellae* Schmidt, 1862.

### Diagnosis

Colonial zoanthids characterised by a mesogleal lacuna and by canals forming a ‘ring sinus’ in distal part of polyp. Fine mineral particles incorporated in polyps.

## *Parazoanthus elongatus* McMurrich, 1904

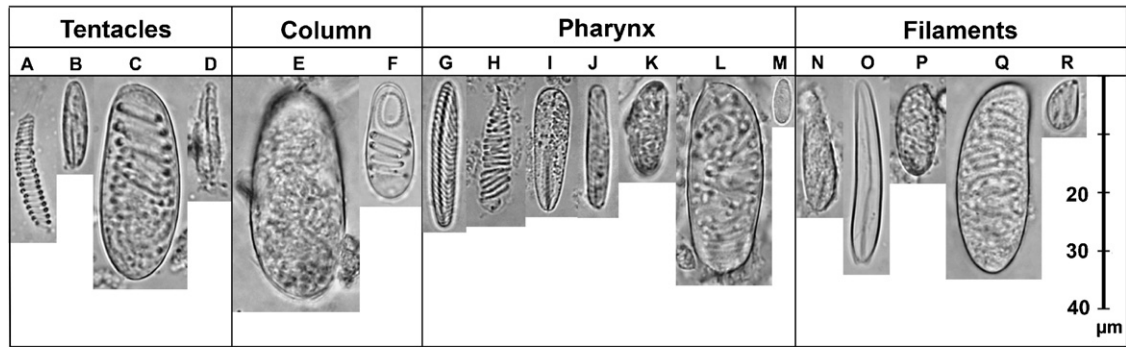
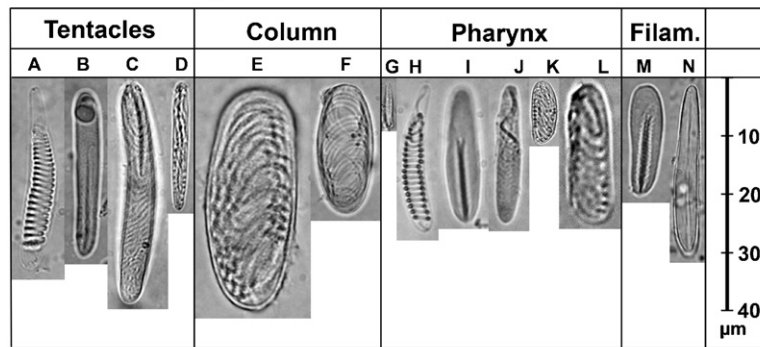
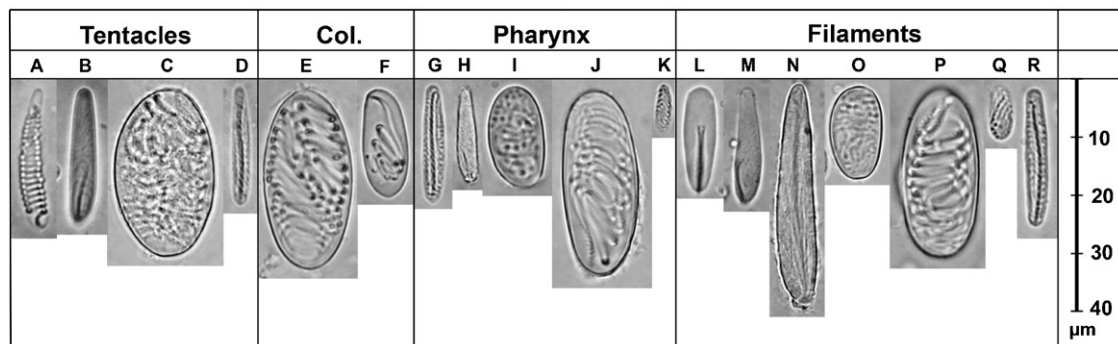
### Material examined

Chile, Comau Fjord, Pta Llonco (42°20.634'S, 72°27.429'W), 20 m, 12.02.2004, leg. VH and GF; MNHG INVE54347 (96% ethanol), MNHG INVE54348 (10% formalin). Chile, Comau Fjord, Pta Huinay

(42°22.483'S, 72°25.693'W), 25 m, 25.12.2004, leg. VH and GF; RMNH Coel. 38800 (70% ethanol). Chile, Reñihué Fjord, 25 m, 16.10.2006, leg. D. Thompson; ZSM 20080024 (10% formalin), ZSM 20080025 (96% ethanol). Chile, Reñihué Fjord, 25 m, 16.10.2006, leg. D. Thompson; MNHG INVE54349 (96% ethanol and 10% formalin). Chile, Reñihué Fjord, 15 m, 19.07.2006, leg. VH and GF; ZSM 20080026 (96% ethanol). Chile, Reñihué Fjord, 25 m, 19.07.2006, leg. VH and GF; ZSM 20080027 (10% formalin). New Zealand, Mokohinan Islands, 5 m, 04.04.2005, leg. Nick Shears; MNHG INVE54350 (96% ethanol).

### Description

*Size.* Living polyps with oral disc diameter up to 10 mm; column diameter up to 6 mm; height up to 70 mm; proximal and distal parts of polyp slightly broader than column. Contracted polyp with oral disc

***Epizoanthus fiordicus******Parazoanthus elongatus******Mesozoanthus fossii***

**Fig. 3.** Cnidae in the tentacles, column, pharynx and filaments of *Epizoanthus fiordicus* sp. n., *Parazoanthus elongatus* and *Mesozoanthus fossii* gen. n., sp. n. respectively; letters A to R correspond to cnidae listed in Table 2.

length and diameter up to 8 mm. Preserved polyps with column diameter up to 6 mm, up to 20 mm high.

**Morphology.** Tentacles 40–48 (smaller, immature polyps can have fewer); length two times oral disc diameter; transparent whitish-yellow to orange, pointed. Oral disc and column yellow to orange; the 20–22 capitular ridges and pharynx lighter; around mouth a yellow to orange ring; 20–24 pairs of mesenteries visible as white lines from pharynx to margin. Column clearly visible; encrusted particles of small size and relatively low abundance. Incrustations can reach outer mesoglea. Polyps densely arise from a basal coenenchyme; in some colonies patches connected by creeping stolons (Fig. 4d, f).

**Cnidae.** Spirocysts, basitrichs, microbasic b-mastigophores, microbasic p-mastigophores, holotrichs (Table 2, Fig. 3).

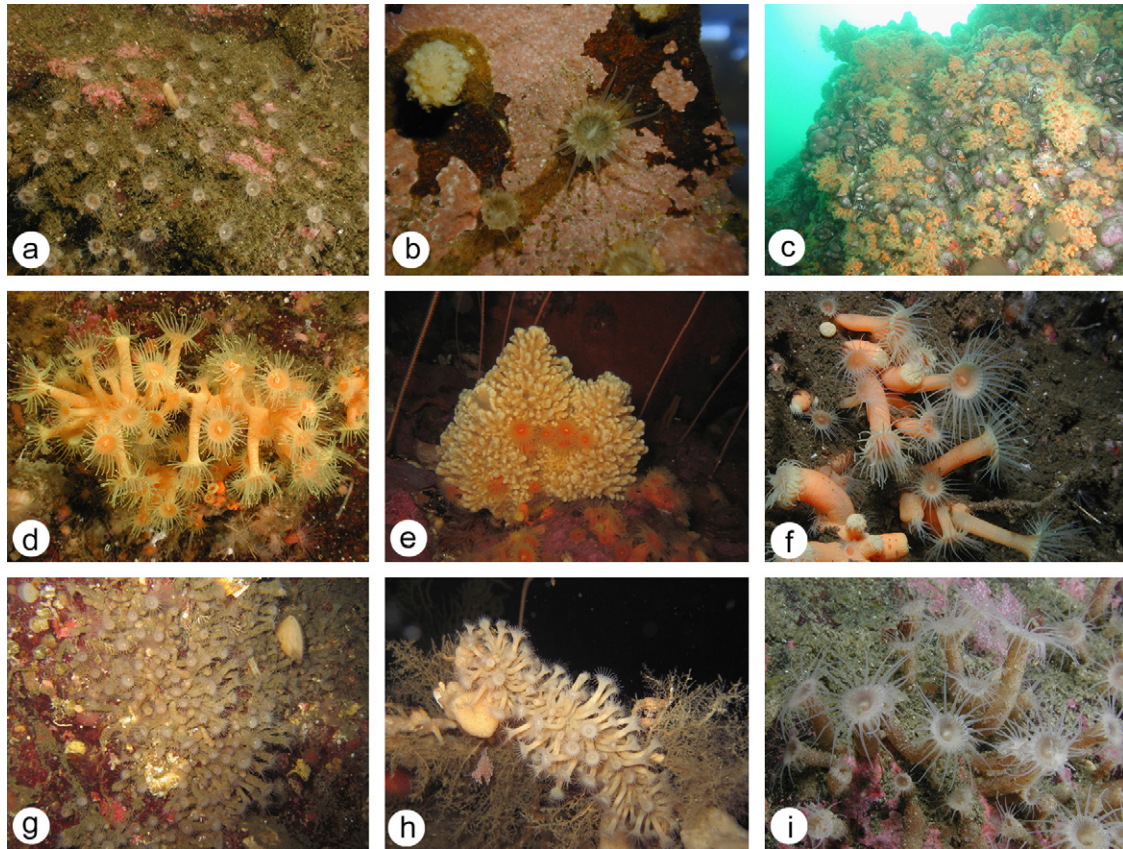
**Diagnosis**

The only yellow zoanthid known from the Chilean and surrounding waters. Morphologically, this species could be confused with *P. axinellae*, but the latter is found in the Mediterranean Sea and North East Atlantic only.

**Habitat and distribution**

Previously, *P. elongatus* was reported from Calbuco (approx. 41°45'S, 73°06'W; S1 in Fig. 1), thus only from





**Fig. 4.** In situ photographs. (a) *Epizoanthus fiordicus* colony. (b) *E. fiordicus* close up. (c) Overview of a rocky area colonised by *Parazoanthus elongatus*. (d) *P. elongatus* on a dead gorgonian. (e) *P. elongatus* on a sponge. (f) *P. elongatus* close up. (g) *Mesozoanthus fossii* colony on a rock. (h) *M. fossii* on a dead gorgonian. (i) *M. fossii* close up.

the tenth region of the Northern Patagonian Zone. In the present study it was found in the inner fjords and channels between Lenca (41°38.303'S, 72°40.116'W) and Reñihué Fjord (42°33'S, 72°36'W), at depths between 10 and 35 m. Locally very abundant, it grows on rocky and biogenic substrata including dead gorgonians, the mytilid *Aulacomya atra*, the gastropod *Crepidula dilatata*, the balanid *Austromegabalanus psittacus*, and the sponges *Iophon proximum* and *Axinella crinita*.

#### Biology and associated species

*Parazoanthus elongatus* colonies comprising thousands of polyps can cover several square meters. Colonies often fragment into subcolonies consisting of a few to several dozens of polyps (Fig. 4c). Occurring more abundantly towards the fjord entrances, where sedimentation is lower; *P. elongatus* seems to tolerate less sediment than *E. fiordicus* sp. n. The coenenchyme, however, can be covered by sediment. Asexual reproduction by budding is an important propagation mode in this zoanthid, as fragments of colonies can detach themselves from the mother colony and fix elsewhere. *Parazoanthus elongatus*, like *Parazoanthus* species

belonging to the 'axinellae, anguicomus, elongatus, swiftii' group, is able to colonise sponges but does not depend on such association to survive (Fig. 4e). *Parazoanthus elongatus* often lives in close association with the sponges *Iophon proximum*, *Axinella crinita*, *Cliona chilensis* or *Clathria (Cornulotrocha) rosetafiordica*. In steep-wall habitats, this species co-occurs with the brachiopod *Magellania venosa* and the scleractinian coral *Desmophyllum dianthus*, whereas at moderately steep sites it is found near the polychaete *Chaetopterus* sp., the primnoid gorgonian *Primnoella chilensis*, or the sea anemones *Anthothoe chilensis* and *Corynactis* sp. Between colonies of *P. elongatus*, individuals of the gastropod *Berthella platei* have been observed feeding on cnidarians. Cases of symbiosis with *Symbiodinium* zooxanthellae are not known. The occurrence of *P. elongatus* in New Zealand suggests widespread distribution in similar environments across the South Pacific.

#### *Mesozoanthus* gen. n.

##### Type species

*Mesozoanthus fossii* sp. n.

### Diagnosis

Macrocnemic with *Parazoanthus*-like growth-form. Well-developed polyps with long and pointed tentacles; polyps form clusters linked by a basal coenenchyme. DNA sequences significantly differ from those in other genera (Fig. 2, Table 3). In contrast to *Parazoanthus*, members of *Mesozoanthus* usually occur in small patches and are not known to colonise demossponges. No symbioses with *Symbiodinium* zooxanthellae.

### *Mesozoanthus fossii* sp. n.

#### Etymology

This species is dedicated to Günter (“Fossi”) Försterra, who discovered this zoanthid.

#### Material examined

*Holotype*. Chile, Comau Fjord, Punta Huinay (42°22.483'S, 72°25.693'W), 20 m, 03.05.2005, leg. GF; MNHG INVE54343 (96% ethanol).

*Paratypes*. Chile, Bernardo Area, Fjord Bernardo S. (48°29'37.4"S, 74°05'02.0"W), 29 m, 27.03.2005, leg. VH and GF; MNHG INVE54344 (96% ethanol). Chile, Isla Lavinia (49°00'48.1"S, 74°58'37.5"W), 18 m, 13.03.2006, leg. VH and GF; MNHG INVE54345 (96% ethanol and 10% formalin) and RMNH Coel. 38801 (96% ethanol), RMNH Coel. 38802 (4% formalin). Chile, Seno Waldemar (48°23'48.5"S, 74°43'48.8"W), 25 m, 15.03.2006, leg. VH and GF; ZSM 20080028 (96% ethanol), ZSM 20080029 (4% formalin). Chile, Canal Fallos (48°27'44.6"S, 75°03'53.7"W), 27 m, 14.03.2006, leg. VH and GF; ZSM 20080030 (4% formalin). Chile, Boca West, Canal Cochrane (48°49'33.5"S, 75°03'06.5"W), 25 m, 14.03.2006, leg. VH and GF; MNHG INVE54346 (10% formalin). Chile, Fiordo Comau, Pta Llonco (42°20.634'S, 72°27.429'W), 25 m, 14.04.2006, leg. VH and GF; MNHG INVE54347 (10% formalin).

*Sequences*. For GenBank accession numbers of sequences obtained from type specimens, see Table 1.

#### Description

*Size*. Living polyps with oral disc diameter up to 10 mm; column diameter up to 6 mm; height up to 35 mm. Oral disc wider than column, diameter up to 8 mm. Preserved polyps with column diameter up to 6 mm; height up to 15 mm.

*Morphology*. Tentacles 36–46 (fewer in smaller, immature polyps); length up to 1.5 times oral disc diameter; transparent whitish-grey. Pharynx oval, whitish. Oral disc greyish to beige; mesentery insertions visible at outer regions of oral disc. Coenenchyme and column uniformly whitish-grey to beige; 20–23 whitish capitular ridges; column brownish-grey due to coarse sand-grain incrustations. This species appears to encrust particles of a size and abundance intermediate between those in *Epizoanthus* and *Parazoanthus*. Whether the size of incorporated sediment particles depends on taxon-specific preferences or on environmental factors remains to be studied. Incrustations restricted to ectoderm. Polyps arise from flat stolons; variable concentration of polyps depending on substrate availability (Fig. 4g, i).

*Cnidae*. Spirocysts, basitrichs, microbasic b-mastigophores, microbasic p-mastigophores, holotrichs (Table 2, Fig. 3).

#### Diagnosis

Greyish-brown colouration distinguishes this parazoanthid from the yellow- to orange-coloured *Parazoanthus elongatus*. Additionally, *Mesozoanthus fossii* ranges much farther to the south than *P. elongatus*.

#### Habitat and distribution

*Mesozoanthus fossii* occurs in the Northern and Central Patagonian Zones. We found it sporadically between Comau Fjord (42°22.483'S, 72°25.693'W) and

**Table 3.** Genetic distances among members of Parazoanthidae; values above table diagonal result from mitochondrial 16S rDNA sequences, values below diagonal from COI; bottom right quadrant of table shows distance values within *Parazoanthus*.

	<i>Savalia savaglia</i>	Parazoanthidae clade 1	<i>Mesozoanthus fossii</i> <sup>a</sup>	Parazoanthidae clade 2	<i>Parazoanthus</i>				
					<i>parasiticus</i>	<i>swiftii</i>	<i>axinellae</i>	<i>anguicomus</i>	<i>elongatus</i> <sup>a</sup>
<i>Savalia savaglia</i>		0.0286	0.0289	0.0269	0.0209	0.0171	0.0152	0.0152	0.0171
Parazoanthidae clade 1	0.0312		0.0719	0.0483	0.0445	0.0446	0.0446	0.0446	0.0447
<i>Mesozoanthus fossii</i> <sup>a</sup>	0.0256	0.0387		0.0586	0.0603	0.0621	0.0602	0.0602	0.0621
Parazoanthidae clade 2	0.0219	0.0350	0.0369		0.0290	0.0255	0.0221	0.0221	0.0238
<i>Parazoanthus parasiticus</i>	0.0127	0.0256	0.0200	0.0200		0.0116	0.0116	0.0116	0.0100
<i>Parazoanthus swiftii</i>	0.0145	0.0274	0.0219	0.0218	0.0018		0.0032	0.0032	0.0050
<i>Parazoanthus axinellae</i>	0.0163	0.0293	0.0237	0.0237	0.0036	0.0054		0.0000	0.0017
<i>Parazoanthus anguicomus</i>	0.0145	0.0274	0.0219	0.0218	0.0018	0.0036	0.0018		0.0017
<i>Parazoanthus elongatus</i> <sup>a</sup>	0.0163	0.0293	0.0237	0.0237	0.0036	0.0054	0.0072	0.0054	

<sup>a</sup>Chilean species.

Isla Lavinia (49°00'48.1"S, 74°58'37.5"W). The species inhabits moderate to steep rocky walls at depths between 15 and 35 m in the inner fjords and channels.

### Biology and associated species

This species has been observed in the inner fjords, which suggests that it tolerates a certain degree of sedimentation. In high-sedimentation environments *M. fossii* inhabits biogenic substrata that protrude from the wall. In the Northern Patagonian Zone it was observed in association with the brachiopod *Magellania venosa*, close to the scleractinian coral *Desmophyllum dianthus* (which prefers overhanging portions of rocks), growing on dead gorgonians (*Primnoella chilensis*; Fig. 4h), or on polychaete tubes of the genus *Chaetopterus*. *Mesozoanthus fossii* was never found in association with sponges. As observed in most zoanthids, asexual reproduction seems to play an important role in colony growth.

### Molecular analyses

The three molecular markers were amplified successfully for *P. elongatus* and *M. fossii* gen. n., sp. n. whereas for *E. fiordicus* sp. n. only mt 16S rDNA and COI could be amplified and sequenced. Phylogenetic reconstructions based on the respective gene regions did not result in major differences. Fig. 2 shows the tree topology obtained from mt 16S rDNA. The COI tree distinguished the species as independent clades, but most phylogenetic relationships were unresolved. The nuclear ITS-rDNA offered phylogenetic resolution similar to the one obtained with 16S, and topology congruent with that from the latter, mitochondrial marker. However, the presence of paralogues in ITS-rDNA, even though these always clustered within a species, cautions against reliance on the ITS-rDNA results before more ITS-rDNA sequences become available. The three species discussed in the present study were always clearly separated from closely related species (based on morphology, ecology and DNA), and each formed a monophylum with high bootstrap support. At a higher taxonomic level, the basal position of *Mesozoanthus fossii* gen. n., sp. n. within Parazoanthidae appears

only in the mt 16S rDNA tree (weakly supported by 52% bootstrap), whereas in the ITS-rDNA and COI trees its position within the family Parazoanthidae was unresolved. Despite its precise position remaining uncertain, *Mesozoanthus* always formed a distinct, well supported clade in Parazoanthidae. The position of *P. elongatus* in the same monophyletic clade with the closely related species *P. axinellae*, *P. anquicomus* and *P. swiftii* was well supported in both the mt 16S rDNA and ITS-rDNA trees. *Epizoanthus fiordicus* sp. n. branched close to the ecologically similar Mediterranean species *E. arenaceus*.

## Discussion

### Distinguishing features of zoanthids

In addition to the information from the molecular markers, the number of tentacles, the polyp size, general appearance of the colony, ecological characteristics (e.g. substratum use), and the geographic distribution all aided in identifications at the species level. We also consider colour as a criterion useful for identification of macrocnemic zoanthids. In contrast to brachycnemic zoanthids, which show significant intra-specific variation in colour (Herberts 1972; Reimer et al. 2004), macrocnemic species are usually uniform in colouration. Slight colour variation can occur (such as the different shades of yellow in Mediterranean *P. axinellae*), but only to a limited extent. Table 4 shows the main morphological features of the different zoanthids recorded in Chile.

In zoanthids, characters of the sphincter muscle have proven to be of limited significance for species identification (Lwowsky 1913). Even though cnidome analyses (cnidae types and size ranges) are commonly used in other soft-bodied hexacorals (e.g. actiniarians; Fautin 1988; Williams 1996, 1998, 2000), these analyses have not been proven useful at species or population levels in the order Zoantharia, not even by high-quality research (Ryland et al. 2004). Cnidae size ranges differ strongly among areas of the same colony, are often correlated

**Table 4.** Comparison of some external characteristics among Chilean zoanthid species.

	Column colour	Tentacle colour	Column incrustations	Tentacle number	Column diameter (mm)
<i>Epizoanthus balanorum</i>	Brown-violet	?	Light	38–40	3
<i>Epizoanthus fiordicus</i>	Brown	Transparent	Heavy	20–34	Up to 5
<i>Epizoanthus patagonichus</i>	Sandy grey	Rust-red	Heavy	32	Up to 5
<i>Parazoanthus elongatus</i>	Yellow	Yellow	Light	40–48	Up to 6
<i>Parazoanthus fuegiensis</i>	?	?	Heavy	34	3.5
<i>Mesozoanthus fossii</i>	Grey to beige	Whitish grey	Intermediate	36–46	Up to 6

? = no data available.



with polyp size, and more than 50 capsules per tissue need to be measured to obtain statistically significant data (Ryland and Lancaster 2004). Recently, based solely on analyses of the cnidome and other morphological features, a new zoanthid species has been described (Ocana and Brito 2004). However, specimens analysed in the original description may include specimens from different genera (Ocana et al. 2007). Cnidaria may be useful to distinguish genera within any single geographic region; thus it is useful to document cnidaria types in combination with the corresponding approximate size ranges (see Fig. 3, Table 2).

## Molecular results

The relationships between genera or species groups of zoanthids are not resolved. This is the case particularly with the COI tree, in which parazoanthid interspecific relationships are almost completely unresolved. However, species are usually well distinguished from each other. Additionally, all species for which more than one sample was examined showed no intraspecific variation in COI and 16SrDNA, with the exception of the *P. gracilis/tunicans* species complex, which is under revision. We do not discuss the phylogeny of the family Parazoanthidae in detail here, as a general revision of the family is ongoing.

Tables 3 and 5 show genetic distances among various zoanthid taxa. Epizoanthidae and Parazoanthidae are represented independently, as Epizoanthidae seems to have a higher rate of evolution or a longer speciation history. The three Chilean zoanthids branch are placed within well defined clades. *Epizoanthus fiordicus* sp. n. branches out clearly within *Epizoanthus* species. The distances obtained (Table 5) show similar interspecific values for the different *Epizoanthus* species analysed (16S: 0.0031–0.0375; COI: 0.0182–0.0369). *Parazoanthus elongatus* falls within the *Parazoanthus axinellae/P. swiftii/P. anguicomus* group. *Mesozoanthus fossii* gen. n., sp. n. shows clear divergence from all other known parazoanthids (16S: 0.0289–0.719, COI: 0.02–0.0369) of a magnitude at least similar to that observed for the divergence between *Savalia* and other

parazoanthids (Table 3). Indeed, the distances among *Parazoanthus* species (as currently defined) and parazoanthid generic-level clades, respectively, amount to interspecific but intrageneric values ranging from 0 to 0.0116 for 16S and from 0.0018 to 0.0072 for COI, whereas intergeneric values range from 0.0152 to 0.0621 for 16S and from 0.0145 to 0.0524 for COI. These values are congruent with the slow rates of mitochondrial gene evolution observed in anthozoans (Shearer et al. 2002). The interspecific variation values also fit with the results obtained for some tropical zoanthids (Reimer et al. 2007b).

Bootstrap support was lowered by sequence conservation in many situations. This suggests that during the resampling process of the bootstrap, variable sites were not always sampled. Therefore, identical sequences did not always appear monophyletic, but in some cases they appeared within an unresolved group of closely related sequences. The best example of such an artefact are the COI sequences of *P. elongatus* specimens. The two samples showed identical sequences, yet the monophyly of these sequences was supported by only 86% bootstrap. With a more variable marker such as ITS-rDNA the monophyly of these identical sequences is supported by 100% bootstrap (data not shown).

## *Epizoanthus fiordicus* and other Chilean members of the family Epizoanthidae

*Epizoanthus balanorum* lives in association with a barnacle. Carlgren (1899) originally described it from a location off the Argentine coast (44°14'S, 61°23'W, i.e. east of S3 in Fig. 1; depth 60 fathoms); several specimens from Calbuco were later assigned to this species (McMurrich 1904), mainly due to their rust-red tentacles. Neither of these two species was found during the present study. *Epizoanthus fiordicus* sp. n. differs from the other Chilean species by the different colouration of its tentacles, as well as by habitat. The north-eastern Pacific *Epizoanthus scotinus* is similar to *E. fiordicus* in external morphology, but the molecular sequences clearly differ (J.D. Reimer, pers. comm. 2008).

## The family Parazoanthidae

Members of this family are considered as characterised by an endodermal sphincter. Even though the validity of this feature is still under debate, as its use has led to occasional misidentifications in the past, that does not cause problems in the identification of Chilean zoanthids. Indeed, all known Chilean zoanthids that do not belong to Epizoanthidae belong to the Parazoanthidae 'sensu stricto' clade (Fig. 2). A revision

**Table 5.** Genetic distances within *Epizoanthus*; values above table diagonal result from mitochondrial 16S rDNA sequences, values below diagonal from COI.

<i>Epizoanthus</i>	<i>fiordicus</i> <sup>a</sup>	<i>arenaceus</i>	<i>paguricola</i>	<i>illoricatus</i>
<i>fiordicus</i> <sup>a</sup>		0.0182	0.0223	0.0375
<i>arenaceus</i>	0.0031		0.0176	0.0375
<i>paguricola</i>	0.0176	0.0221		0.0278
<i>illoricatus</i>	0.0369	0.0346	0.0305	

<sup>a</sup>Chilean species.

of the currently paraphyletic Parazoanthidae and of the genus *Parazoanthus* will be published elsewhere.

### *Parazoanthus elongatus* McMurrich

Different morphotypes of yellow to orange *Parazoanthus* specimens have been found in the Chilean fjords. Because of the lack of suitable identification methods, we are presently unable to precisely determine whether these morphotypes belong to the same species or to closely or distantly related species. As the characters we analysed did not show significant divergence, and given the current state of knowledge in *Parazoanthus* taxonomy, we here consider all these morphotypes as belonging to *P. elongatus*. This species ecologically corresponds to the closely related but genetically distinct *P. axinellae* from European temperate waters. In previous studies, various morphotypes of uncertain specific status have been described also for *P. axinellae* (Pax and Müller 1962). Photographs exist of a *Parazoanthus* colony from 25 m depth off the central Chilean coast that differs in colour and tentacle length, but unfortunately we did not have access to these specimens for inclusion in the present study. Molecular data (supported by ecological data and external morphology) from New Zealand suggest that *P. elongatus* may be present throughout the southern Pacific Ocean, although further research is necessary to evaluate this hypothesis.

### The genus *Mesozoanthus* gen. n.

So far, no zoanths have been reported that are closely related to *Mesozoanthus fossii*. The molecular divergence between this taxon and the established parazoanthid genera justifies classification of the former in a separate genus. Moreover, unlike for *Parazoanthus* sensu stricto, *M. fossii* has never been observed in association with sponges at any of the nearly 100 localities examined in the Chilean fjord region (*M. fossii* is present at seven of these sites).

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