

Census of Antarctic Marine Life  
SCAR-Marine Biodiversity Information Network

# BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

## ► CHAPTER 5.19. TANAIDACEA.

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# THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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## 5.19. Tanaidacea

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### 1. Introduction

Tanaidaceans are small Peracarida, which are commonly found in almost all marine benthic habitats around the world. With few exceptions tanaidaceans are truly marine crustaceans, well-represented in a wide range of depths from tidal zones to marine trenches. Their usually elongated bodies rarely exceed a few millimetres in length, although in the abyssal depths some gigantic representatives can reach over 30 mm (Kudinova-Pasternak 1978).

Tanaidaceans are almost exclusively free-living. *Exspina typica*, a species that has been found burrowing in the body wall of the holothurian *Protelpidia murrayi* (Theel, 1879) is the only documented tanaidacean parasite (Alvaro *et al.* 2011). Members of the family Mirandotanaidae are thought to be commensal in the buccal cavity of some terebellid polychaetes (Suarez-Morales *et al.* 2011), while other species are known to inhabit the ostia of tropical sponges (Bamber & Bird 1997), scleractinian corals (Sieg & Zibrowius 1988) or bryozoans colonies (unpublished data). Symbionts of tanaidaceans include nicothoid copepods (Bamber & Boxshall 2006), tantulocarids (Boxshall & Lincoln 1987), acanthocephalan larva (Escobar-Briones *et al.* 1999), and bivalve mollusks (Sieg 1993). The members of the order can be divided into five trophic groups: detritophages (the majority), sestonophages, phytophages, euryphages and predators (Kudinova-Pasternak 1991, Błażewicz-Paszkowycz & Ligowski 2002). As a part of the marine food web, they serve as prey for, in particular, other crustaceans and marine fishes (Larsen 2005, and references therein).

With a few exceptions of tanaids occurring on algal turfs or the aforementioned commensals and parasites, most species are usually burrowing in soft sediments (Apseudomorpha, Neotanaidomorpha) or building tubes (Tanaidomorpha) using sometimes precisely selected particles that are glued together by secretion of tegumental, spinning glands (Johnson & Attramadal 1982, Hassak & Holdich 1987). Whilst some tanaids (*Leptochelia*) are good swimmers, using their pleopods for paddling, most are slow-moving. Mature tanaidomorphs only leave their tubes when they are forced to by adverse environmental conditions and are considered to have restricted dispersal ability.

Currently over 1100 nominal species of tanaidaceans are known (Anderson 2013, Błażewicz-Paszkowycz *et al.* 2012), possibly representing only a fraction of the potential diversity of this group. Indeed, data gathered by the Census of Marine Life (CoML) suggest that our present state of knowledge only covers ca. 2-5% of all tanaidaceans inhabiting the oceanic realm, implying that the real number of tanaidacean species might reach 40,000 (Appeltans *et al.* 2012).

The long history of systematic research of the Antarctic Tanaidacea was initiated at the end of the 19th century with species descriptions based on the material collected during the expeditions of SMS *Gazelle* and HMS *Challenger* (Studer 1884, Beddard 1886a, b). During the next decades, Antarctic tanaidaceans received only moderate attention, until two publications by Shino (1970, 1979) and two monographs by Sieg (1986a, b) doubled the number of tanaidaceans recorded on the Antarctic shelf, i.e. above 1000 m (Clarke & Harris 2003) (Table 1). Tanaidaceans below the shelf-edge were less systematically collected and only recorded in remote locations along the routes of scientific expeditions such as those of RV *Akademik Kurchatov*, RV



Photo 1 *Nototanais antarcticus* (Hodgson, 1902): male in dorsal view, female in lateral view. Image: M. Błażewicz-Paszkowycz © University of Łódź.

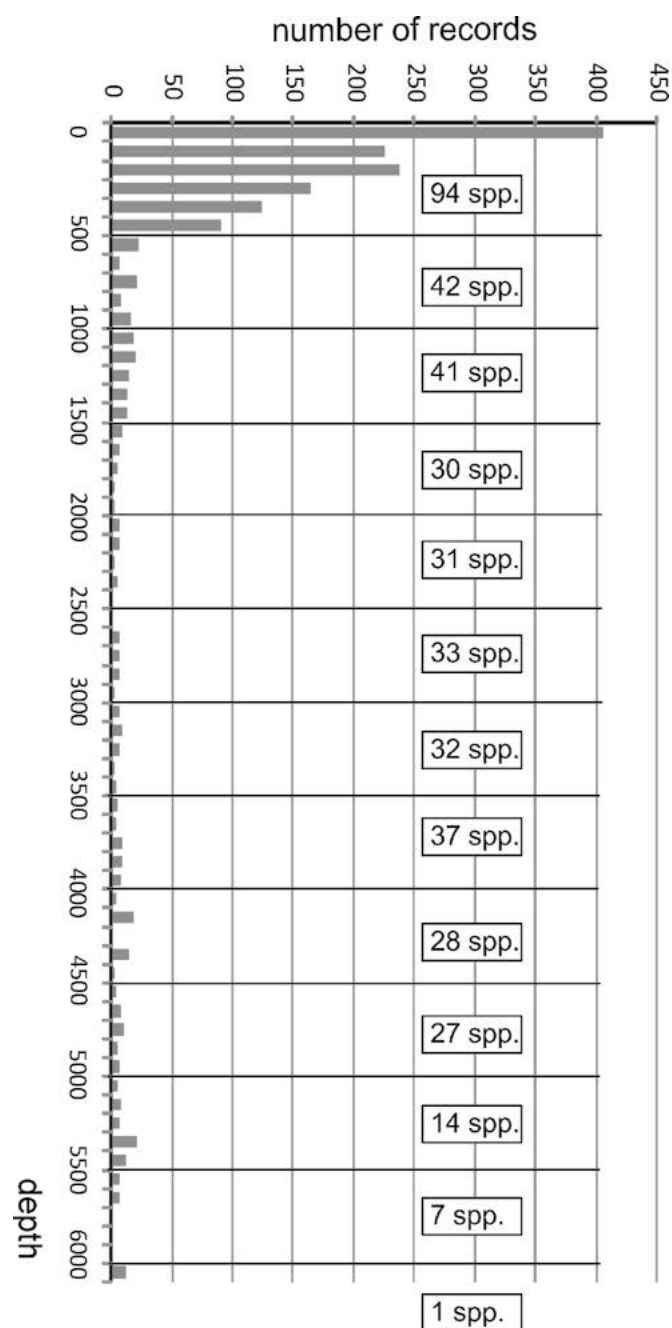


Figure 1 Number of records of Tanaidacea versus depth below 55°S.

Ob, RV *Eltanin* and RV *Polarstern*. Hence, these deep-sea stations are rare, sparsely scattered throughout the vast area of the Southern Ocean (Fig. 1). Since most of the deep-sea species are only known from their type locality, current records are insufficient to serve as a basis for reliable zoogeographical analyses (Kudinova-Pasternak 1975, 1990, 1993, Kudinova-Pasternak & Pasternak 1981, Błażewicz-Paszkowycz 2005a, b, 2007, Błażewicz-Paszkowycz & Larsen 2004, 2005, *inter alia*).

### 2. Methods

The taxonomic classification presented here is according to the Register of Antarctic Marine Species (RAMS) operated by the World Register of Marine Species (WoRMS) and supplied by the Peracarida Home Page (Anderson 2013).

The numbers of the species recorded in various regions of the Southern Ocean (below 55°S) were collated from the literature (Table 3) into a database including over 1500 records; a further 150 records, mainly from the Ross Sea, represent unpublished data.

Bathymetric classification of the genera was assessed by analysing the type depths. To assess whether a genus shows either deep or shallow water preference, the type localities of all species in that genus other than Antarctic species were analyzed. This decision is based on the fact that the boundary between the shelf and the deep ocean in the Antarctic is situated deeper than anywhere else (Clarke & Harris 2003), facilitating the phenomenon of polar emergence (Brey *et al.* 1996). Those genera for which all records outside the Antarctic were below 200 m have been classified as 'deep-water' taxa (D), while those with records located above 200 m are classified as 'shallow water' taxa (S); any genus in which type localities were located both on the shelf and deeper were classified as a 'shallow/deep water taxon' (S/D) (Table 2). Together with the Antarctic species, five apparently polyphyletic genera, *Apseudes*, *Leptognathia*, *Protanaissus*, *Pseudotanaids*, and *Typhlotanaids*, have been excluded from the analysis. Although some other tanaidacean genera in the analysis might also be polyphyletic, they are presumed to constitute groups of closely related taxa, and for the purpose of this study they are treated as monophyletic.

Table 1 Review of surveys on Tanaidacea on the shelf of the Southern Ocean.

Region	number of species	references	densities
Kerguelen Is.	22	Studer (1884) <sup>1</sup> ; Beddard (1886a, b) <sup>2</sup> ; Vanhöffen (1914) <sup>5</sup> ; Stephensen (1947) <sup>10</sup> ; Kussakin, (1967) <sup>14</sup> ; Shiino (1979) <sup>13</sup> ; Tzareva (1982) <sup>14</sup>	56,000–146,000 ind/m <sup>2</sup> (Delille <i>et al.</i> 1985)
Heard I.	5	Shiino (1979) <sup>13</sup>	
Crozet Is.	4	Tzareva (1982) <sup>14</sup>	
Bouvet I.	1	Stephensen (1947)	
Macquarie I.	4	Hale (1937) <sup>9</sup>	
Falklands Is.	2	Stebbing (1914); Lang (1953)	
S. Shetland Is.	10	Stephensen (1947) <sup>10</sup>	
Admiralty Bay	14	Błażewicz & Jażdżewski (1996); Błażewicz-Paszkowycz & Jażdżewski (2000); Błażewicz-Paszkowycz & Sekulska Nalewajko (2004)	4030 ind/m <sup>2</sup> (Jażdżewski <i>et al.</i> 1986); 395/m <sup>2</sup> (Sicinski <i>et al.</i> 1996); 16,024 ind/m <sup>2</sup> (Błażewicz-Paszkowycz & Jażdżewski, 2000)
Danco Coast	5	Richardson (1906) <sup>4</sup> ; Sieg (1986a) <sup>15</sup>	
Biscoe I.	7	Sieg (1986a) <sup>15</sup>	
Bransfield Strait	18	Kudinova-Pasternak (1993); Sieg (1986a) <sup>15</sup> ; Sieg (1986b) <sup>16</sup>	
Greenwich I.	7	Shiino (1970) <sup>12</sup> ; Gallardo <i>et al.</i> (1977)	
Palmer Archipelago	4	Sieg (1986a) <sup>15</sup>	
Anvers I.	22	Richardson (1906) <sup>4</sup> ; Lowry (1975); Sieg (1986a); Richardson & Hedgpeth (1977)	3617 ind/m <sup>2</sup> (Richardson & Hedgpeth, 1977)
S. Georgia	1	Lang (1953); Sieg (1977)	
Brabant I.	5	Sieg (1986a) <sup>15</sup>	
Weddell Sea (East)	21	Sieg (1986b) <sup>16</sup> ; Kudinova-Pasternak (1993)	994 ind/m <sup>2</sup> (Gerdes <i>et al.</i> 1992)
Gauss Station	11	Vanhöffen (1914) <sup>5</sup>	
Ross Sea	37	Sieg (1983); Gambi <i>et al.</i> (1994, 2000)	
McMurdo Sound	1	Oliver & Slattery (1985); Dayton & Oliver (1977)	53,512 ind/m <sup>2</sup> (Dayton & Oliver 1977); 17,360 ind/m <sup>2</sup> (Oliver & Slattery 1985)
Cape Adare	1	Hodgson (1902) <sup>3</sup>	
Adélie Land	2	Hale (1937) <sup>9</sup> ; Amar and Roman (1974)	
Mac Robertson Land	1	Larsen 2000	
Davis Sea	5	Kussakin (1967) <sup>14</sup> ; Tzareva (1982) <sup>14</sup> ; Tucker (1988)	
Cosmonauts Sea	4	Tzareva (1982) <sup>14</sup>	
Tierra del Fuego	23	Shiino (1970) <sup>12</sup> ; Sieg (1986a) <sup>14</sup> ; Monod (1926) <sup>7</sup> ; Schmidt & Brandt (2001)	
Isla de los Estados	15	Sieg (1986a) <sup>15</sup>	

1. S.M.S *Gazelle* (1874–76); 2. *Challenger* Expedition (1872–76); 3. *Southern Cross* (1902); 4. *Français* (1903–1895); 5. Deuxième Expédition Antarctique Française (1908–1910); 6. Deutsche Südpolar-Expedition (1901–1903); 7. *Belgica* 1897–99; 8. *Terra Nova* Expedition; 9. Australasian Antarctic Expedition (1911–1914); 10. Norwegian Antarctic Expedition (1927–28); 11. and 12. XXII Chilean Antarctic Expedition; 13. *Marion Dufresne*; 14. Russian Antarctic Expedition (1965–1971); 15. *Hero* (1961–1983); 16. Deutschen Antarktis Expedition (1983).

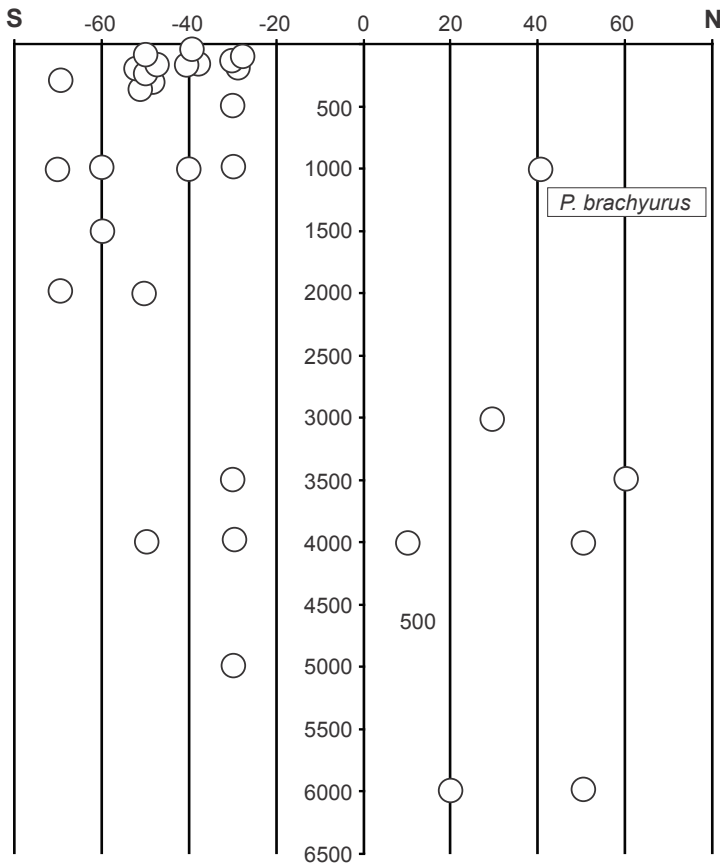


Figure 2 Bathymetrical and latitudinal distribution of species of *Peraeospinosus*.

Faunistic similarity between various well-recognised localities of the Southern Ocean shelf was assessed based on the presence/absence of species and calculated using a hierarchical clustering method based on the Bray-Curtis similarity index and group-average linking (Statistica 6 package). The similarity matrix was then subjected to ordination using non-metric multidimensional scaling (nMDS). Regions of the Southern Ocean where there are only a few tanaidacean records, as well as regions at abyssal or bathyal depths, characterised by single tanaidacean records only, have been excluded from the analysis.

The classification of the bioregions in the Antarctic was based on the work by Hedgpeth (1970) and latter confirmed in studies by Knox and Lowry (1977), De Broyer & Jażdżewski (1993) and De Broyer *et al.* (2007). This classification divides the Southern Ocean (s.l.) into two Regions: the Antarctic and sub-Antarctic. In the first region, two provinces are distinguished, the West and East Antarctic, while most sub-Antarctic Islands and the Magellan Region are included in the sub-Antarctic. The arrangement of the regions included in the biogeographical analysis of the Tanaidacea is given in Table 2.

3. Biodiversity

Tanaidacea are represented in the Southern Ocean (SO) by 160 species: 12% belong to the Apseudomorpha, 6% to the Neotanaidomorpha and 82% to the Tanaidomorpha (see Table 3 and the citations therein).

4. Diversity versus bathymetric distribution

Apseudomorpha, with 19 recorded species, are represented by four shallow-water (S) and four deep-water (D) genera (Table 2) with one or two species in each. The exception is *Leviapseudes* with eight species. *Apseudes* has not been assessed into depth groups since it is considered a polyphyletic taxon.

The Tanaidomorpha of the SO are classified into two superfamilies, the Tanaoidea (8 species) and the Paratanaoidea (119 species). The Tanaoidea are represented in the SO by one family — the Tanaidae. Two genera, *Allotanais* and *Langitanais*, with four species, are Antarctic endemics. With the exception of three records, one of *L. magnus* at 3025 m depth and two records of *L. willemoesi* at 1218 m and 2925 m depth (Shiino 1979), all records of Tanaidae below 55°S are situated at shelf depths.

The Paratanaoidea are represented by 15 families. The Typhlotanaidae (36 spp.) is the most speciose, followed by the Colletteidae (15 spp.), Tanaellidae (9 spp.), Pseudotanaidae (7 spp.), Leptognathiidae (7 spp.), Akanthophoreidae (6 spp.), Agathotanaidae (5 spp.) and Tanaissuidae (5 spp.). Much more poorly represented are the Leptocheliidae (4 spp.), Anarthruridae (3 spp.), Cryptocopidae (3 spp.), Tanaopsidae (3 spp.), Nototanaidae (2 spp.), Mirandotanaidae (1 sp.) and Paratanaidae (1 sp.) Intriguingly, most of the genera have representatives outside the SO, occurring in the deep sea (39% of the genera) or being characterised by a wide bathymetric range (26%) (Table 3). Only four genera (8%), namely *Pseudoleptochelia*, *Pseudonototanais*, *Pseudoparatanais* and *Tanaissus*, are typical shallow-water taxa with their representatives found outside the SO above 200 m.

Eleven genera (22%) of the Paratanaoidea are Antarctic endemics. Six of them, *Allodaposia*, *Andrognathia*, *Dimorphognathia*, *Mimicarhaphura*,

**Table 2** List of tanaidacean families and genera recorded below 55°S based on type-localities and type-depths. (1) number of records of all species per genus excluding the Antarctic records (see WoRMS); (2) number records in the Antarctic (in bracket unpublished records); (3) bathymetric distribution in the Antarctic; (4) number of species recorded on the shelf (<200 m) outside the Antarctic; (5) number of species recorded below the shelf (>200 m) outside the Antarctic; (6) classification to shallow water (S), or deep water (D); endemic (E).

			n species		bathymetric distribution	n records outside A			
			World (incl. ANT)	ANT only	(m)	>200 m	<200 m		
suborder	family/subfamily	genus	1	2	3	4	5	6	
Apseudomorpha: 8 genera, 19 species	Apseudinae	<i>Apseudes</i> *	46	4	?	polyphyletic			
		<i>Langapseudes</i>	2	1	3804-3808	—	1	D	
		<i>Paradoxapseudes</i>	12	1	13-903	11	—	S	
	Pugiodactylinae	<i>Pugiodactylus</i>	5	1	3-232	4	—	S	
	Leviapseudinae	<i>Leviapseudes</i>	28	8	326-4802	x	20	D	
		<i>Fageapseudes</i>	4	1	3804	x	3	D	
	Kalliapseudidae	<i>Acutihumerus</i>	2	1	20-50	1	—	S	
	Metapseudidae	<i>Synapseudes</i>	23	2	intertidal-903(?)	21	—	S	
Neotanaidomorpha	Neotanaidae	<i>Neotanaïs</i>	40	9	223-7934	—	35	D	
		<i>Carololangia</i>	1	1	5054	—	1	D	
Tanaidomorpha: 16 families, 57 genera, 131 species	Tanaoidea	Tanaidae	<i>Allotanaïs</i>	1	1	0-285	n/a	n/a	E
			<i>Langitanaïs</i>	3	3	40-3025	n/a	n/a	E
			<i>Pancoloides</i>	2	1	litoral-160	1	—	S
			<i>Zeuxo</i>	27	1	0-50	21	—	S
			<i>Zeuxoides</i>	10	2	0-140	6	—	S
	Paratanaoidea	Agathotanaidae	<i>Paragathotanaïs</i>	12	1	1019-4696	—	11	D
			<i>Paranarthrura</i>	18	4	289-3808	—	15	D
		Akanthophoreidae	<i>Akanthophoreus</i>	13	3	0-7218	4	5	DS
			<i>Chauliopleona</i>	9	2	135(?)–2061	3	5	DS
			<i>Paraleptognathia</i>	8	1	330-410	—	8	D
		Anarthruridae	<i>Anarthrura</i>	2	(1)	1410	1	1	DS
			<i>Siphonolabrum</i>	5	1	49-253	1	3	DS
			<i>Anarthruridae</i> sp.	—	1	410	—	—	—
		Colletteidae	<i>Collettea</i>	18	10	90-7100	—	11	D
			<i>Filitanaïs</i>	5	2	757-4535	—	3	D
			<i>Leptognathiella</i>	7	1(+1)	1410	—	6	D
			<i>Leptognathioides</i>	4	1	4535	—	3	D
		Leptocheliidae	<i>Heterotanoides</i>	4	1	25-36	1	1	DS
			<i>Pseudoleptochelia</i>	14	1	0-358	12	—	S
			<i>Pseudonototanaïs</i>	3	2	1.5-235	1	—	S
		Leptognathiidae	<i>Leptognathia</i> *	36	5 (+2)	?	polyphyletic		
		Mirandotanaidae	<i>Mirandotanaïs</i>	1	1	84-1279	n/a	n/a	E
		Nototanaidae	<i>Nototanaïs</i>	2	2	2-1367 (5120?)	n/a	n/a	E
		Paratanaidae	<i>Paratanaïs</i>	25	1	0-903?	21	3	DS
		Cryptocopidae	<i>Cryptocopoides</i>	5	2	67-5630	1	2	DS
			<i>Paraiungentitanaïs</i>	1	1	1600	n/a	n/a	E
		Pseudotanaidae	<i>Pseudotanaïs</i> *	41	6(+1)	?			
		Tanaellidae	<i>Araphura</i>	15	3	39-6145	4	8	DS
			<i>Arhaphuroides</i>	5	1	113-6145	2	2	DS
			<i>Arthrura</i>	5	1	124-1279	—	4	D
			<i>Tanaella</i> *	16	5	40-6150	4	8	DS
		Tanaopsidae	<i>Tanaopsis</i>	11	3	0-730	6	2	DS
		Tanaissuidae	<i>Protanaissus</i> *	4	2(+1)	?	polyphyletic		
			<i>Bathytanaissus</i>	2	(1)	410	—	1	D
			<i>Tanaissus</i>	4	1	1105-1660	4	—	S
		Typhlotanaidae	<i>Larsenotanaïs</i>	2	1	2893-3683	—	1	D
			<i>Meromonakantha</i>	6	3	100-4392	—	4	D
			<i>Obesutanaïs</i>	2	(1)	84-458		1	D
			<i>Paratyphlotanaïs</i>	9	2	84-3102	2	5	DS
			<i>Peraeospinosus</i>	12	8	17-5523	1	6	DS?
			<i>Pulcherella</i>	4	2	443-3963	—	1	D
			<i>Torquella</i>	10	3	2147-5631	—	8	D
			<i>Typhlamia</i>	3	1	4304-4392	—	2	D
			<i>Typhlotanaïs</i> *	48	10(+3)	?	polyphyletic		
			<i>Typhlotanaoides</i>	1 (2?)	1	20-316	n/a	n/a	E
			<i>Hamatipeda</i>	2	2	720-3861	n/a	n/a	E
		incertae sedis	<i>Exspina</i>	1?	1	669-1837	—	1?	D
			<i>Allodaposia</i>	1	1	198-1669	n/a	n/a	E
			<i>Andrognathia</i>	1	1	67	n/a	n/a	E
			<i>Dimorphognathia</i>	1	1	0-903	n/a	n/a	E
			<i>Mimicarhaphura</i>	1	1	410-423	n/a	n/a	E
			<i>Monstrotanaïs</i>	2	1	3543	—	1	D
			<i>Parafilitanaïs</i>	3	(1)	410	—	3	D
			<i>Pseudoparatanaïs</i>	3	2	67-410	1	—	S
		<i>Robustochelia</i>	6	2	2600-3910	—	5	D	
		<i>Singula</i>	1	1(+1)	410-4304	n/a	n/a	E	
		<i>Pseudoleptognathia</i>	1	1	70-515	n/a	n/a	E	



*Singula* and *Pseudoleptognathia*, are currently not classified into a family. The monotypic *Exspina*, the aforementioned parasite of several species of holothurians (Alvaro *et al.* 2011), is probably the most widespread tanaidacean taxon (Brandt *et al.* 2012).

Most species of the tanaids (81%) in the SO might be considered endemic, while the rest (19%) have their type locality elsewhere. Ninety-seven species (61%) of Tanaidacea in the Southern Ocean were recorded on the shelf and 70 (43%) have never been found below a depth of 1000 m. Twenty-seven species have been found both on the shelf and below its edge, and some of these have a surprisingly wide depth range extending a few thousands of metres, such as *Akanthophoreus australis*, *Araphura parabrevimanus*, *Arhaphuroides parabreviremis*, *Collettea antarctica*, *C. arnaudi*, *Cryptocopoides antarctica* and *Pseudotanaeis nordenskioldi*, amongst others (Table 3). *Pugiodactylus*, *Paranarthrura*, *Pseudoleptognathia*, *Tanaella*, *Pulcherella* and *Peraeospinosus* are typical deep-sea genera, which means that they usually do not occur on the shelf. An exception to this pattern occurs in the SO where the representatives of these genera are recorded on the shelf and are considered an example of polar emergence phenomenon. Bathymetric distribution plotted against latitude for the genus *Peraeospinosus* (Fig. 2) shows that the shallowest records of this genus are recorded in the Antarctic and SE Australia.

The remaining 63 species of Tanaidacea (39%) are deep-water taxa. Two thirds of these are known from only one locality and often from only one specimen, 17 others are known from two localities and only four extra species have been recorded three or more times. Such scant data are insufficient for biogeographical studies and were thus omitted in the zoogeographical analysis.

## 5. Biogeography

The zoogeographic analysis of the tanaidaceans recorded in 19 shelf localities of the Southern Ocean revealed three poorly associated groups (Fig. 3A). The first group includes the South Orkney Is. and Elephant I. with a similarity of less than 40%, while the two others, the sub-Antarctic (B) and Antarctic (C) regions, have an equally low similarity. In the sub-Antarctic region, two sub-groups are distinguished, the Magellan Region (B1) and a group of three remote sub-Antarctic islands, i.e. the Kerguelen Is., Crozet Is. and Heard I. (B2). The third group (C) contains five regions, i.e. the West Antarctic (C1), three large seas of the East Antarctic (C2) and a weakly-supported group of the Scotia Sea, the Falkland Is. and the South Sandwich Is. (C3). In this analysis, the Cosmonaut Sea was distinctly dissimilar to all the other analysed localities.

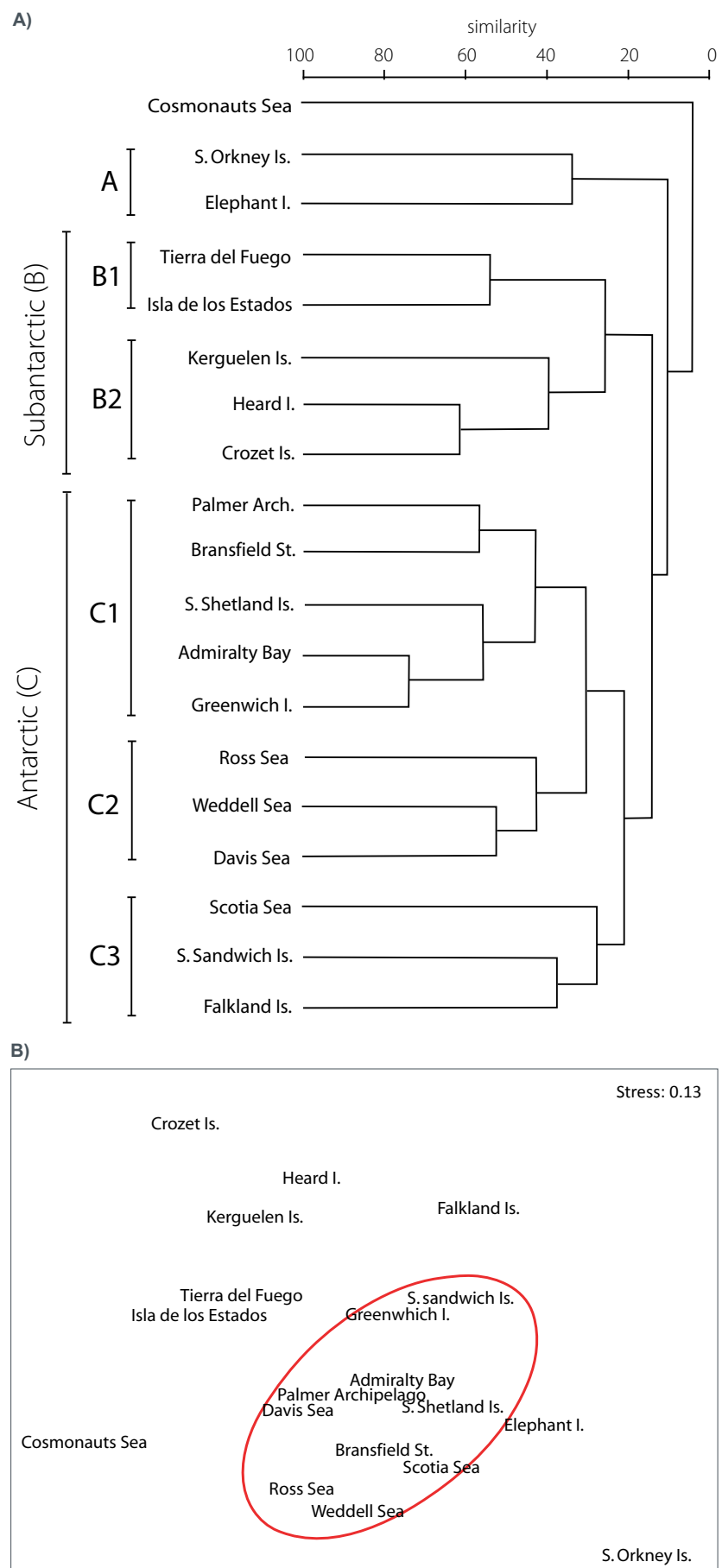
The MDS analysis is presented in Figure 3B with a stress value of 0.13; this shows that all the Antarctic Regions made a feasible group that involves all regions from groups B and C with the Falklands as the only exception. Sub-Antarctic regions made a more ill-defined group in the MDS, but the Cosmonaut Sea and South Orkney Is. represented again the most distinct regions.

More than half (57%) of tanaidacean species are known from only one of the four regions distinguished by De Broyer *et al.* (2007) and only three (*Akanthophoreus australis*, *Nototanaeis dimorphus* and *Typhlotanaeis greenwichensis*) were found in all four regions. Twelve species might be considered strictly Antarctic taxa, being recorded both in its West and East Province, and ten others have their distribution extended to the Magellan Province, although they were not recorded in any other part of the sub-Antarctic. Only four species (*Allotanaeis hirsutus*, *Apseudes spectabilis*, *Pseudotanaeis guilleri* and *Zeuxoides pseudolitoralis*) are typical sub-Antarctic taxa recorded in the Magellan and sub-Antarctic Island Provinces whilst eight are characterised by a distribution encompassing the Magellan Province and the West Antarctic. Two species, *Leptognathia glandiceps* and *Tanaopsis kerguelensis*, occur on Sub-Antarctic Islands, but were also found in the East Antarctic.

## 6. Discussion

The Bray-Curtis biogeographical classification (Fig. 3A) supports the division of the Southern Ocean into two Regions (Antarctic and sub-Antarctic) and it demonstrates the relatively close similarity between the East and West Antarctic. The Falklands region, which usually fits into the Magellan Province (Linse *et al.* 2006, De Broyer *et al.* 2007), constituted a group with the South Sandwich Is. and the Scotia Sea, which were distinct from the South Orkney Is. and Elephant I. (A). This result is not supported by non-metric multidimensional scaling (nMDS), which associated all localities of the Antarctic into a well-established group. In both the dendrogram and the MDS plot (Figs. 3A, B) the Cosmonaut Sea appeared to be the most isolated region. This result may be rationalized by the low sampling effort characterizing this region, although Elephant I., with five species only, associated quite closely with the Antarctic Region.

The phylogenetic relationships within the order Tanaidacea are not fully understood. Since the oldest fossil, dating back to the Carboniferous, appears to be most similar to apseudomorphans. This suborder is assumed to represent the most plesiomorphic forms (Larsen & Wilson 2002). Due to the lack of fossils being conserved in the abyssal plain, it is unlikely to retain information about the ancestors of neotanaidomorphs; however, it is known that the oldest known tanaidomorph dates back to the Jurassic (Vonk & Schram 2007). The first phylogenetic study by Kakui *et al.* (2011), based on nuclear 18S rDNA sequence data, confirmed the general viewpoint that tanaidomorphs might be a phylogenetically young suborder and closely related to the Neotanaidomorpha rather than to the Apseudomorpha. This study included mainly shallow-water

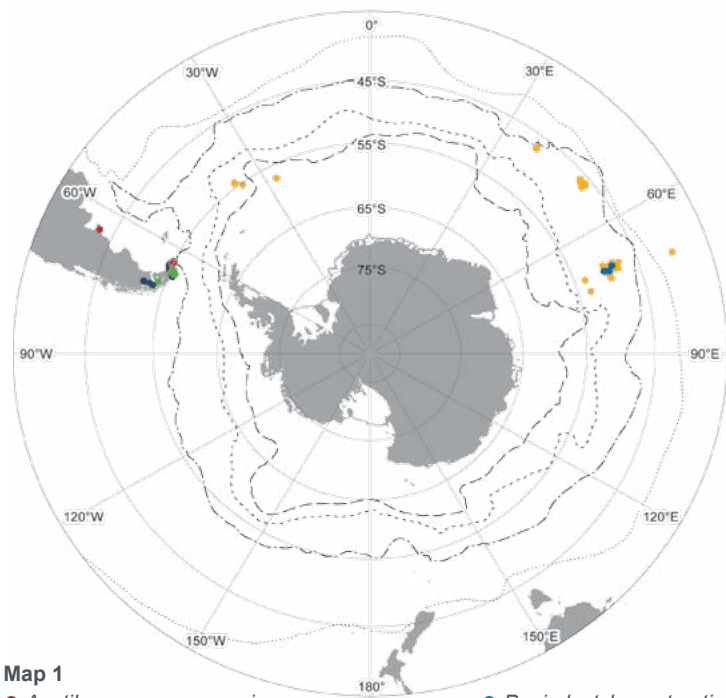


**Figure 3** Similarity of tanaidacean fauna between the 19 localities in the Southern Ocean based on the published and unpublished data using: A. Bray-Curtis similarity, group-average clustering method); B. non-metric multidimensional scaling (nMDS).

tanaidomorphs, with the exception of species of the genus *Chauliopleona* sampled at bathyal depths. The preliminary results from mitochondrial COI sequence data, isolated from tanaidaceans sampled from 200 to almost 3000 m depth during the IceAGE Program (Icelandic Animal Genetic and Ecology) showed that deep-sea tanaidomorphs might be more apomorphic than their shallow-water relatives, e.g. members of the Tanaidae, Leptognathiidae and Paratanaididae (unpublished data).

Over four-fifths of Antarctic tanaidaceans are represented by the Tanaidomorpha, the presumed phylogenetically young suborder. With the exception of 15 species, belonging to the presumed plesiomorphic Tanaidomorpha, i.e. Tanaidae, Leptocheliidae, Paratanaidae, and Nototanaidae, the majority (over 97%) of Antarctic tanaidomorphs are blind. Since the loss of vision is interpreted as a consequence of living in the darkness (Raupach *et al.* 2009) it reinforces the assumption that the origin of Antarctic tanaids lies in the abyss (Sieg 1992).

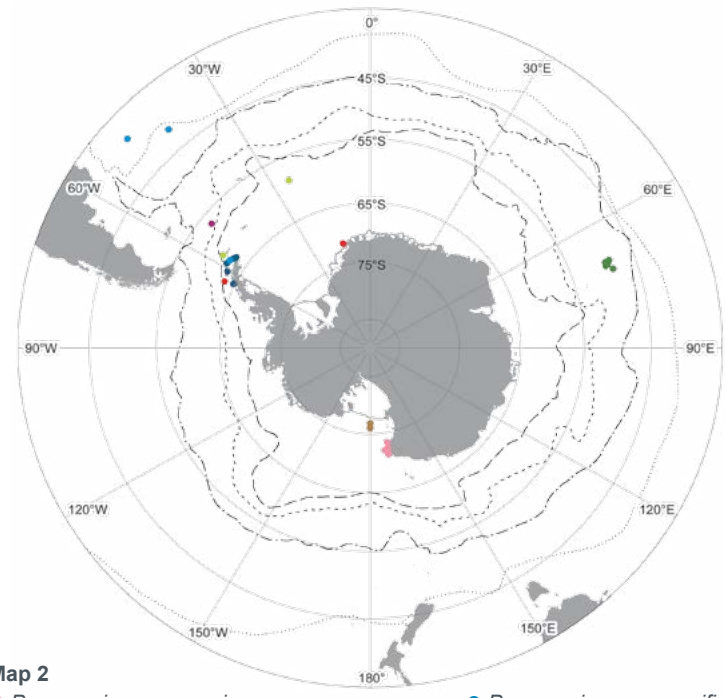
The Neotanaidomorpha is an exclusively deep-sea taxon. Their most shallow records on the deep Antarctic shelf also represent the most shallow records globally. Deep-sea Apseudomorpha (*Glabroapseudes*, *Leviapseudes*)



Map 1

● *Acutihumerus cavooreni*  
● *Apseudes spectabilis*  
● *Paradoxapseudes heroae*

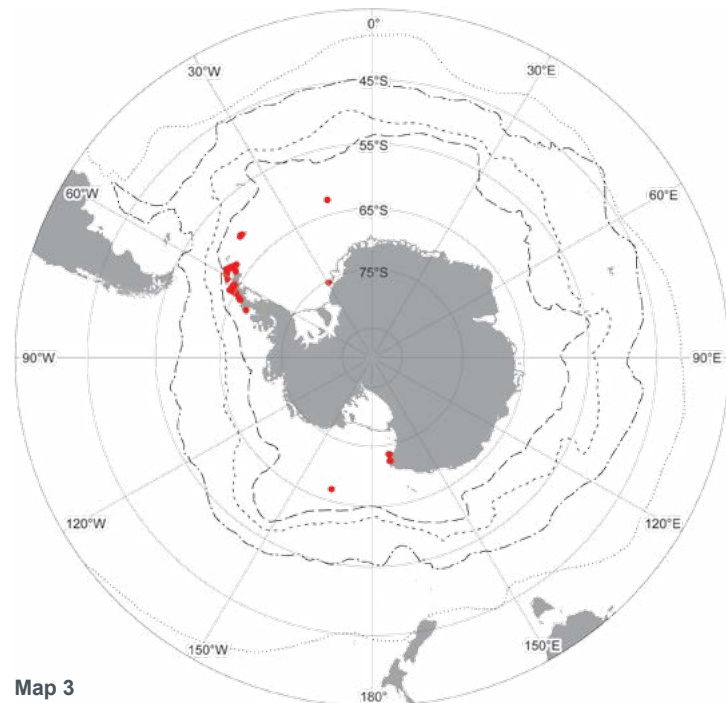
● *Pugiodactylus antarcticus*  
● *Synapseudes aflagellatus*  
● *Synapseudes idios*



Map 2

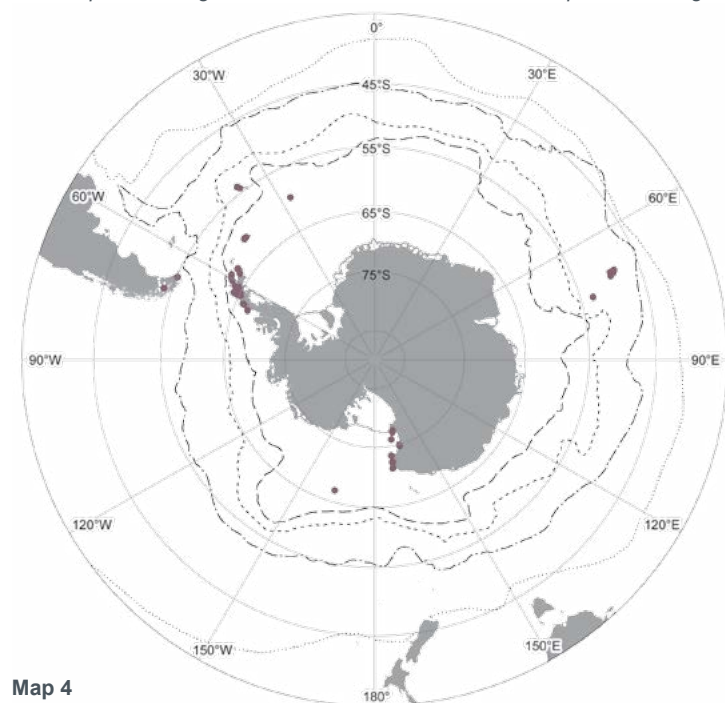
● *Peraeospinosus acruxi*  
● *Peraeospinosus emergensis*  
● *Peraeospinosus exiliremis*  
● *Peraeospinosus kerguelensis*

● *Peraeospinosus magnificus*  
● *Peraeospinosus pushkini*  
● *Peraeospinosus rectus*  
● *Peraeospinosus subtileatus*



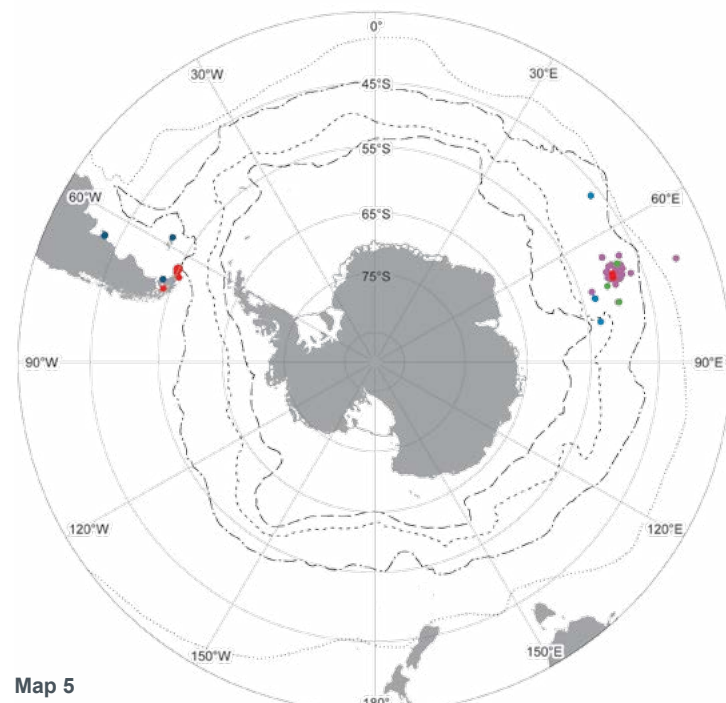
Map 3

● *Nototanaeis antarcticus*



Map 4

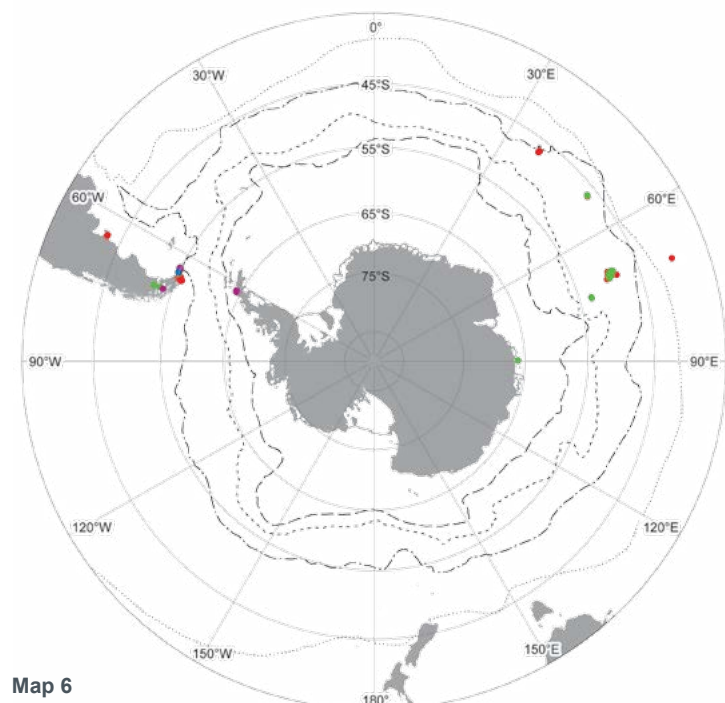
● *Nototanaeis dimorphus*



Map 5

● *Langitanaeis bifidirostris*  
● *Langitanaeis magnus*  
● *Langitanaeis willemoesi*

● *Paratanaeis oculatus*  
● *Pseudoleptochelia antarctica*



Map 6

● *Allotanaeis hirsutus*  
● *Pancoloides littoralis*

● *Zeuxo phytalensis*  
● *Zeuxoides ohlini*

**Tanaidacea Maps 1–6** Map 1. *Acutihumerus cavooreni* (Băcescu & Absalão, 1985), *Apseudes spectabilis* Studer, 1884, *Paradoxapseudes heroae* (Sieg, 1986), *Pugiodactylus antarcticus* (Beddard, 1886), *Synapseudes aflagellatus* Sieg, 1986, *S. idios* Gardiner, 1973. Map 2. *Peraeospinosus acruxi* Błażewicz-Paszkowycz, 2007, *P. emergensis* Błażewicz-Paszkowycz, 2005, *P. exiliremis* Błażewicz-Paszkowycz, 2005, *P. kerguelensis* (Beddard, 1886), *P. magnificus* (Kudinova-Pasternak, 1970), *P. pushkini* (Tzareva, 1982), *P. rectus* (Kudinova-Pasternak, 1966), *P. subtileatus* Błażewicz-Paszkowycz, 2005. Map 3. *Nototanaeis antarcticus* (Hodgson, 1902). Map 4. *Nototanaeis dimorphus* (Beddard, 1886). Map 5. *Langitanaeis bifidirostris* Shiino, 1978, *L. magnus*, Shiino, 1978, *Langitanaeis willemoesi* (Studer, 1883), *Paratanaeis oculatus* (Vanhöffen, 1914), *Heterotanaeis antarcticus* (Lang, 1953). Map 6. *Allotanaeis hirsutus* (Beddard, 1886), *Pancoloides littoralis* (Vanhöffen, 1914), *Zeuxo phytalensis* Sieg, 1980, *Zeuxoides ohlini* (Stebbing, 1914).



were collected within the Antarctic Circle, although never at shelf depths (<1000 m). In contrast, their shallow-water relatives (*Apseudes*, *Paradoxapseudes*, *Pugiodactylus*, *Acutihumerus*, *Synapseudes*; see Map 1) were recorded only as far as 55°S, i.e. at the Southern Antarctic Circumpolar Front (Murphy *et al.* 2007). Most genera of Tanaidomorpha recorded on the Antarctic shelf have either a wide bathymetrical distribution outside the Southern Ocean or represent truly deep-sea taxa, e.g. *Peraeospinosus*, *Paranarthrura*, *Collettea*, *Arthrura* (Table 2, Appendix 2 at the end of volume). The presence of deep-sea fauna on the shelf at high latitudes is recognised as a consequence of the polar emergence (e.g. Thatje *et al.* 2005, Brandt *et al.* 2012). Indeed, the colonization of the Southern Ocean shelf by abyssal fauna is thought to be driven by isothermal conditions along the continental slope, but undoubtedly other environmental conditions such as periodic darkness and a decrease in primary production equally contribute to this phenomenon. Berkman *et al.* (2004) noted that increases in late Pliocene sea-ice coverage in the Antarctic coastal areas could have diminished wave action and enhanced the accumulation of fine sediments. The latter consequence might have been of great importance to the tanaidaceans, which burrow or build tubes in the sediments (Błażewicz-Paszkowycz & Jażdżewski 2000) and are quite resistant to high rates of sedimentation (Błażewicz-Paszkowycz & Sekulska Nalewajko 2004).

The ratio between deep-sea and shallow-water taxa as well as the lack of taxa bearing eyes on the shelf certainly are in favour of Sieg's (1992) hypothesis, assuming that most Antarctic tanaidaceans have a deep-sea origin and that the colonisation of the Antarctic shelf took place after the glaciation of Antarctica. However, recent studies of the Tanaidacea of SE Australia (Błażewicz-Paszkowycz & Bamber, 2012) appear to question the age of this event. The bathymetric and latitudinal distribution of *Peraeospinosus* might highlight this, since the only record of the genus on the shelf, except on the SO shelf, is situated in the Bass Strait (38–41°S, SE Australia) (Figure 2, Map 2). The origin of the distribution of *Peraeospinosus* dates back to the Paleocene or even to the Cretaceous, when Antarctica and South Australia were situated within the Antarctic Circle. The colonisation of both shelves may have taken place during this period, where the deep-sea tanaids had inhabited the Antarctic shelf before its full isolation and the glaciations in the Miocene. This scenario would mean that the deep-sea invaders had to survive glaciations events followed by an allopatric speciation and radiation event, simultaneously in Australia and in the Antarctic. Brandt (1999) argued that some Antarctic Peracarida could have survived the glacial periods on the Antarctic shelf, referring to the observation of flourishing benthic communities under the ice shelf (Lipps *et al.* 1979). Also Thatje *et al.* (2005) have postulated that the Antarctic fauna could have survived Cenozoic glaciations in isolated glacial shelters present both during interglacials as well as during maximum cooling events in the SO. In the case of tanaidaceans, assumed to have a deep-sea origin and being pre-adapted to cold water and high pressure equally well, both of these scenarios could be correct.

An opposite distributional pattern, compared with that of *Peraeospinosus*, is shown by *Nototanaïs*, which is currently known from two species commonly occurring on the Antarctic shelf. *N. antarcticus* (Map 3) has not been recorded north of 60°S; all records are located close to the Antarctic continent and its adjacent islands, and south to the Weddell Front (Sieg 1986a, Murphy *et al.* 2007). *N. dimorphus* (Map 4) extends further north, and is present at sub-Antarctic islands such as Kerguelen and Macquarie Is. In the West Antarctic, the northern border of the species *N. dimorphus* is more restricted. It was frequently recorded on South Orkney Is. (Błażewicz-Paszkowycz, unpublished), but was absent on South Sandwich Is., South Georgia, Elephant I. or the Falkland Is., although it is known from a single record in the Beagle Channel (Schmidt & Brandt 2001), two records in Tierra del Fuego (Sieg 1986a; Sieg's records are only shown on his map (66: figure 36) and are absent from his listings on pages 2 to 10) and even in Chilean fjords (50°S, 74°W) (Esquete *et al.* 2012).

Recently, a third member of the genus *Nototanaïs* was discovered on the slope of SE Australia (unpublished). Although it was found below the photic zone, the species has retained eyes. Assuming that *Nototanaïs* prefers cold water, it can be hypothesised that this genus was characterised by an Australian-Antarctic distribution in the Cretaceous (similar to that mentioned before for *Peraeospinosus*) and subsequently became extinct on the Australian SE coast due to climate warming.

*Nototanaïs antarcticus* and *N. dimorphus* are the most common tanaidaceans in the SO. Despite their explicit sympatric speciation in the Antarctic, they clearly occupy different niches. *N. antarcticus* prefers soft sediments, and tolerates noticeable sedimentation rates. This tolerance allows the species to occur frequently in shallow, innermost bays (Błażewicz-Paszkowycz & Sekulska-Nalewajko 2004, Siciński *et al.* 2011, 2012). *N. dimorphus* is much more often recorded in regions influenced by oceanic waters and in habitats with sand and algae (Gambi *et al.* 1994, 2000, Błażewicz-Paszkowycz & Sekulska-Nalewajko 2004). Although this species has not been recorded in association with fronds or holdfasts so far (Pabis & Siciński 2010), dispersal by rafting might explain its wide distribution, assuming that the species is able to survive such transport. Edgar (1986) has calculated that 260 days are required to raft from Kerguelen Is. to Macquarie Is., or 580 days from South America to the same destination. Tanaidaceans, characterised by relatively fast turnover rates of generations, probably do not live longer than two seasons (Błażewicz-Paszkowycz 2001). In theory, this duration might be enough for *N. dimorphus* to survive on a floating raft,

transported by the Antarctic Circumpolar Current (ACC) from South Orkney Is. to Macquarie Is. with a stop at the Kerguelen Is.

Different patterns for the colonization of the Antarctic shelf can be proposed for *Paratanaïs oculatus* and *Pancoloides litoralis*, two other species bearing eyes. Both genera, which are characterized by pan-tropical and pan-temperate distributions, contain exclusively shallow-water taxa. *P. oculatus* and *P. litoralis* are frequently recorded at South Georgia and South Sandwich Is. (unpublished), as well as at the coast of Tierra del Fuego and Isla de los Estados (Map 5). Hence, these species could have invaded the Antarctic by means of island-hopping through the Scotia Arc (Sieg 1992, Brandt 1999) or by means of rafting. Indeed, species of the genus *Pancoloides* are known to be associated with algal turf (Monod 1926, R. Bamber pers. comm.) and thus could disperse by drifting on algal mats towards Kerguelen Is. or even Macquarie Is.

## 7. Conclusions

The biogeographical classification of tanaidacean species supports the division of the Southern Ocean into an Antarctic Region and a Sub-Antarctic Region, as well as supporting a high similarity in tanaidaceans between the East and West Antarctic.

The shallow-water Apseudomorpha with pan-tropical and pan-temperate distributions are poorly represented in the Southern Ocean and have not been found south of the Southern Antarctic Circumpolar Front (SACCF). Most of the apseudomorphs appear to have radiated in the Indo-West Pacific, characterised by a physiology adapted to tropical environments, which might pose a barrier to the colonisation of polar regions. The same could be true for the plesiomorphic Tanaidomorpha belonging to the family Tanaidae. The deep-sea Neotanaidomorpha and Apseudomorpha are relatively well represented in the Southern Ocean; the only deep-sea apseudomorphs absent from the Antarctic are members of the family Sphyrapodidae.

The present state of knowledge supports Sieg's hypothesis (1992) concerning the extinction of tropical or temperate representatives of the Tanaidacea during glaciations, and of the vacant habitats on the Antarctic shelf being colonised by deep-sea taxa. One exception to this hypothesis is *Paratanaïs oculatus*, which may have migrated by island-hopping along the Scotia Arc, using the different islands as "stepping stones", while *Nototanaïs* may have survived glaciations in shallow-water refugia on the Antarctic shelf. It cannot be excluded that Tanaidacea might have colonised remote areas by means of rafting. However, this hypothesis needs to be confirmed by genetic population research.

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► Appendix 2 at the end of volume



Appendix 2: Tanaidacea (Chap. 5.19)

Table 3. List of records and depth ranges of Southern Ocean Tanaidacea. Classification of Regions and Provinces according to De Broyer et al. (2007). Data sources: (1) Alvaro et al. (2011), (2) Beddard (1886b), (3) Błażewicz-Paszkowycz (2004), (4) Błażewicz-Paszkowycz (2005a), (5) Błażewicz-Paszkowycz (2005b), (6) Błażewicz-Paszkowycz (2007), (7) Larsen & Błażewicz-Paszkowycz (2003), (8) Błażewicz-Paszkowycz & Larsen (2004), (9) Błażewicz-Paszkowycz & Larsen (2005), (10) Błażewicz-Paszkowycz & Jażdżewski (1996), (11) Błażewicz-Paszkowycz & Sekulska-Nalewajko (2004), (12) Delille et al. (1985), (13) Gallardo & Castillo (1977), (14) Gambi et al. (1994), (15) Gambi et al. (2000), (16) Guerrero-Kommritz & Błażewicz-Paszkowycz (2004a), (17) Guerrero-Kommritz & Błażewicz-Paszkowycz. (2004b), (18) Guerrero-Kommritz (2004), (19) Guerrero-Kommritz (2005), (20) Hale (1937), (21) Hodgson (1902), (22) Józwiak & Błażewicz-Paszkowycz (2007a), (23) Józwiak & Błażewicz-Paszkowycz (2007b), (24) Józwiak & Błażewicz-Paszkowycz (2011), (25) Kudinova-Pasternak (1975), (26) Kudinova-Pasternak & Pasternak (1981), (27) Kudinova-Pasternak (1990), (28) Kudinova-Pasternak (1993), (29) Kusakin (1967), (30) Lang (1953), (31) Lang (1973), (32) Larsen (2000), (33) Lowry (1975), (34) Olivier & Slattery (1985), (35) Richardson (1906), (36) Richardson (1911), (37) Richardson (1913), (38) Richardson & Hedgpeth (1977), (39) Shiino (1970), (40) Shiino (1979), (41) Schmidt & Brandt (2001), (42) Sieg (1984), (43) Sieg (1986a), (44) Sieg (1986b), (45) Sieg (1977), (46) Sieg & Dojiri (1989), (47) Stebbing (1914), (48) Stephensen (1947), (49) Studer (1884), (50) Tucker (1988), (51) Tzareva (1982), (52) Vanhöffen (1914), ud – unpublished data.

	Sub-Antarctic									Antarctic																							
	Sub-Antarctic Is.						Magellan			West Antarctic								East Antarctic															
	Kerguelen Is.	Heard I.	Crozet Is.	Bouvet I.	Macquarie I.	Marion/Edward Is.	Falkland Is.	Tierra del Fuego	Isla de los Estados	Palmer Arch.	S. Shetland Is.	Admiralty Bay	Greenwich I.	Elephant I.	Bransfield St.	S. Orkney Is.	S. Sandwich Is.	S. Georgia	Scotia Sea	Weddell Sea	Queen Maud Ld	Mawson Sea	Cosmonauts Sea	Davis Sea	Mc Robertson Ld	Adélie/Prince V Coast	Ross Sea	Balleny Is.	Amundsen Sea	Argentina/S. Atlantic	S. Pacific	NZ	Depth range (m)
<i>Acutihumerus cavooreni</i> (Băcescu & Absalão, 1985)																													1			20-50	43
<i>Akanthophoreus antarcticus</i> (Vanhöffen, 1914)									1	1					1				1	1				1								0-1376	18, 28, 42, 43, 44, 52, ud
<i>Akanthophoreus australis</i> (Beddard, 1886)	1	1					1	1	1	1	1	1	1	1		1		1								1						15-7218	2, 10, 11, 18, 25, 28, 38, 39, 40, 41, 43, 44, 51
<i>Akanthophoreus weddellensis</i> Sieg, 1986										1			1	1	1					1												139-1376	28, 44, 18
<i>Allodaposia abbreviata</i> (Vanhöffen, 1914)							1									1				1				1								198-1669	52, 25, 44,
<i>Allotanaïs hirsutus</i> (Beddard, 1886)	1		1			1		1	1																				1			0-285	2, 19, 40, 41, 43
<i>Anarthura simplex</i> G.O. Sars, 1882*																			1													1410	28
<i>Anarthuridae</i> sp.**																											1					410	ud
<i>Andrognathia plumosa</i> Sieg, 1983																											1					67	42
<i>Apseudes spectabilis</i> Studer, 1884	1	1	1	1		1		1																								4-952	26, 39, 40, 48, 49, 51
<i>Apseudes abyssalis</i> Błażewicz-Paszkowycz & Larsen, 2004																	1			1						1						2663-4931	8, 23
<i>Apseudes paragracilis</i> Kudinova-Pasternak, 1975							1				1								1													1105-3808	23, 25
<i>Apseudes spinosus</i> (M. Sars, 1858)*																			1													3660-3100	28
<i>Araphura elongata</i> (Shiino, 1970)							1	1		1	1	1					1															73-757	10, 11, 38, 39, 25, 43
<i>Araphura joubinensis</i> Sieg & Dojiri, 1989										1																						39	46
<i>Araphura parabrevimanus</i> (Lang, 1968)*							1												1													100-6145	28
<i>Arhaphuroides parabreviremis</i> Sieg, 1986										1					1				1													113-6145	25, 43
<i>Arthrura monacantha</i> (Vanhöffen, 1914)							1	1									1	1		1				1								124-1279	24, 25, 41, 44, 52
<i>Bathytanaissus</i> sp. A**																										1						410	ud
<i>Carololangia plumata</i> (Kudinova-Pasternak, 1975)*																					1											5054	26
<i>Chauliopleona armata</i> (Hansen, 1913)*																			1													2531-8006 (6052-6150)	
<i>Chauliopleona hastata</i> (Hansen, 1913)*								1																								135-580	19
<i>Chauliopleona nickeli</i> Guerrero-Kommritz, 2005																				1												1583-2061	19, 27, 41, 51?
<i>Collettea</i> sp. A																	1															7100	9
<i>Collettea alicjae</i> Błażewicz-Paszkowycz & Larsen, 2005																				1						1		1				3049-4304	9
<i>Collettea antarctica</i> (Vanhöffen, 1914)																	1		1				1			1						353-5120	52, 25, 28, ud
<i>Collettea arnaudi</i> (Shiino, 1978)		1																														90	40
<i>Collettea</i> sp. B																				1												6030	9

	Sub-Antarctic						Antarctic																											
	Sub-Antarctic Is.						Magellan		West Antarctic								East Antarctic																	
	Kerguelen Is.	Heard I.	Crozet Is.	Bouvet I.	Macquarie I.	Marion/Edward Is.	Falkland Is.	Tierra del Fuego	Isla de los Estados	Palmer Arch.	S. Shetland Is.	Admiralty Bay	Greenwich I.	Elephant I.	Bransfield St.	S. Orkney Is.	S. Sandwich Is.	S. Georgia	Scotia Sea	Weddell Sea	Queen Maud Ld	Mawson Sea	Cosmonauts Sea	Davis Sea	Mc Robertson Ld	Adélie/Prince V Coast	Ross Sea	Balleny Is.	Amundsen Sea	Argentina/S. Atlantic	S. Pacific	NZ	Depth range (m)	References
<i>Cryptocopoides pruinosus</i> (Guerrero-Kommritz & Błażewicz-Paszkowycz, 2004)							1													1													938-2077	17
<i>Dimorphognathia heroae</i> Sieg, 1986								1	1																								0-903	43
<i>Exspina typica</i> Lang, 1968*																1			1							1							669-1837	1, 25, 44
<i>Fageapseudes suprema</i> (Józwiak & Błażewicz-Paszkowycz, 2007)										1										1							1						3804	23
<i>Filitanais curticaudus</i> Kudinova-Pasternak, 1993																			1														4535	28
<i>Filitanais rebaini</i> Kudinova-Pasternak, 1975															1		1																757-1837	25, 28
<i>Hamatipeda trapezoida</i> Błażewicz-Paszkowycz, 2007																			1														2375-3861	6
<i>Hamatipeda longa</i> (Kudinova-Pasternak, 1975)							1																										720	25
<i>Heterotanais antarcticus</i> (Lang, 1953)							1	1	1																				1				0-358	30, 43
<i>Heterotanoides meridionalis</i> Sieg, 1986								1	1																								25-63	43
<i>Langapseudes</i> sp.										1																							3804-3808	23
<i>Langitanais bifidirostris</i> Shiino, 1978		1	1																														70-130	40
<i>Langitanais magnus</i> Shiino, 1978	1																																365-3025	40
<i>Langitanais willemoesi</i> (Studer, 1884)	1																																44-2925	2, 25, 40, 51
<i>Larsenotanais amabilis</i> Błażewicz-Paszkowycz, 2007																			1														2893-3680	6
<i>Leptognathia breviremoides</i> Sieg, 1986								1												1	1			1		1							316-2705	28, 44, 52, ud
<i>Leptognathia glandiceps</i> Shiino, 1978	1																										1						37-410	39, 40, ud
<i>Leptognathia lineata</i> Shiino, 1978	1																																3-95	40, 51
<i>Leptognathia luykeni</i> Vanhöffen, 1914	1																																littoral	52
<i>Leptognathia vanhoeffeni</i> Gutu, 1972																							1										385	52
<i>Leptognathia</i> aff. <i>microcephala</i> Kudinova-Pasternak, 1978**																										1							474	ud
<i>Leptognathia</i> sp. A**																										1							410-515	ud
<i>Leptognathiella</i> sp. A**																										1							410	ud
<i>Leptognathiella subaequalis</i> (Hansen, 1913)*																			1														1410	27
<i>Leptognathioides rectus</i> Kudinova-Pasternak, 1993																				1													4535	28
<i>Leviapseudes aberrans</i> (Lang, 1968)*																															1		4410	26
<i>Leviapseudes angelikae</i> Józwiak & Błażewicz-Paszkowycz, 2007*																				1													326-4802	23, 25
<i>Leviapseudes conspicuus</i> (Lang, 1968)*																															1		4790	26
<i>Leviapseudes galathea</i> (Wolff, 1956)*																															1		2320	26
<i>Leviapseudes gracillimus</i> (Hansen, 1913)*																	1				1												3700-3920	25,26
<i>Leviapseudes pleonudus</i> Błażewicz-Paszkowycz & Larsen, 2004										1																1					1		3756-4728	8, 23
<i>Leviapseudes shiinoi</i> (Lang, 1968)*																															1		2320	26



	Sub-Antarctic									Antarctic																									
	Sub-Antarctic Is.						Magellan			West Antarctic								East Antarctic																	
	Kerguelen Is.	Heard I.	Crozet Is.	Bouvet I.	Macquarie I.	Marion/Edward Is.	Falkland Is.	Tierra del Fuego	Isla de los Estados	Palmer Arch.	S. Shetland Is.	Admiralty Bay	Greenwich I.	Elephant I.	Bransfield St.	S. Orkney Is.	S. Sandwich Is.	S. Georgia	Scotia Sea	Weddell Sea	Queen Maud Ld	Mawson Sea	Cosmonauts Sea	Davis Sea	Mc Robertson Ld	Adélie/Prince V Coast	Ross Sea	Balleny Is.	Amundsen Sea	Argentina/S. Atlantic	S. Pacific	NZ	Depth range (m)	References	
<i>Monstrothanais ingens</i> Józwiak & Błażewicz-Paszkowycz, 2007																									1								3543	22	
<i>Neotanais affinis</i> Wolff, 1956*																													1				5180-5225	28	
<i>Neotanais americanus</i> Beddard, 1886*																		1					1										3060-3100	28	
<i>Neotanais antarcticus</i> Kussakin, 1967							1	1										1		1	1							1					223-4450	25, 26	
<i>Neotanais hadalis</i> Wolff, 1956*																				1													2920	26	
<i>Neotanais hessleri</i> Gardiner, 1975*																									1									3105	26
<i>Neotanais krappschickelae</i> Larsen & Błażewicz-Paszkowycz, 2003							1																											500-570	7
<i>Neotanais kurchatovi</i> Kudinova-Pasternak, 1975																	1																	7218-7934	25
<i>Neotanais magnificus</i> Kudinova-Pasternak, 1972																		1					1											2986-3782	26, 28
<i>Neotanais tricarinatus</i> Gardiner, 1975*																								1		1								2750-4789	26
<i>Nototanais antarcticus</i> (Hodgson, 1902)										1	1	1	1	1	1					1				1			1							2-1376 5110-5120?	2, 10, 11, 14, 15, 21, 28, 33, 35, 38, 39, 43, 44, 48, 50, 51, ud
<i>Nototanais dimorphus</i> (Beddard, 1886)	1	1						1		1	1	1	1		1									1			1							10-515	2, 10, 11, 14, 20, 26, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 50, 51, 52, ud
<i>Obesutanais</i> sp. A**																											1							84-458	ud
<i>Pancoloides litoralis</i> (Vanhöffen, 1914)	1	1	1					1	1															1										0-160	40, 43, 52
<i>Paradoxapseudes heroae</i> (Sieg, 1986)								1	1																									13-903	41, 43
<i>Parafilitanais</i> sp. A**																										1								410	ud
<i>Paragathotanais ipy</i> Józwiak & Błażewicz-Paszkowycz, 2011																	1			1	1													1019-4696	24
<i>Paraungentitanais longidigitatus</i> (Kudinova-Pasternak, 1975)							1																											1660	28
<i>Paraleptognathia multiserratooides</i> Guerrero-Kommritz, 2004										1	1			1					1	1							1							330-410	18, ud
<i>Paranarthrura arctowskii</i> Józwiak & Błażewicz-Paszkowycz, 2011											1						1	1		1						1?			1?	1				489-3808	24
<i>Paranarthrura fortispina</i> Sieg, 1986																				1							1		1					410-474	24, 44
<i>Paranarthrura insignis</i> Hansen, 1913*							1										1		1															720-1729	25, 27
<i>Paranarthrura meridionalis</i> Sieg, 1986																				1														289-423	44
<i>Paratanais oculatus</i> (Vanhöffen, 1914)	1							1	1														1											0-903	20, 31, 40, 43, 51, 52
<i>Paratyphlotanais armatus</i> (Vanhöffen, 1914)										1		1			1	1	1	1	1					1			1							84-1425	10, 11, 28, 43, 51, 52, ud
<i>Paratyphlotanais alveolus</i> Błażewicz-Paszkowycz, 2007															1					1														1030-3102	6
<i>Peraeospinosus acruxi</i> Błażewicz-Paszkowycz, 2007											1									1														1030-2118	6
<i>Peraeospinosus emergensis</i> Błażewicz-Paszkowycz, 2005																											1							347-399	5
<i>Peraeospinosus exiliremis</i> Błażewicz-Paszkowycz, 2005																	1		1															2293-5523	5
<i>Peraeospinosus kerguelenensis</i> (Beddard, 1886)	1																																	17-1390	2, 40

	Sub-Antarctic									Antarctic																								
	Sub-Antarctic Is.						Magellan			West Antarctic								East Antarctic																
	Kerguelen Is.	Heard I.	Crozet Is.	Bouvet I.	Macquarie I.	Marion/Edward Is.	Falkalnd Is.	Tierra del Fuego	Isla de los Estados	Palmer Arch.	S. Shetland Is.	Admiralty Bay	Greenwich I.	Elephant I.	Bransfield St.	S. Orkney Is.	S. Sandwich Is.	S. Georgia	Scotia Sea	Weddell Sea	Queen Maud Ld	Mawson Sea	Cosmonauts Sea	Davis Sea	Mc Robertson Ld	Adélie/Prince V Coast	Ross Sea	Balleny Is.	Amundsen Sea	Argentina/S. Atlantic	S. Pacific	NZ	Depth range (m)	References
<i>Protanaissus longidactylus</i> (Shiino, 1970)									1	1	1	1																					45-500	10, 11, 43, 39, 51
<i>Protanaissus makrotrichos</i> Sieg, 1986																										1				1			20-50	43, ud
<i>Protanaissus</i> sp. A**																										1							169	ud
<i>Pseudoleptognathia setosa</i> Sieg, 1986									1					1												1							70-515	43, 44, ud
<i>Pseudonototanaïs bransfieldensis</i> Sieg, 1986														1												1							176-235	43, 44
<i>Pseudonototanaïs werthi</i> (Vanhöffen, 1914)	1		1				1																1										1.5-217	40, 41
<i>Pseudoparatanaïs antarcticus</i> Sieg, 1983																										1							67-75	42
<i>Pseudoparatanaïs brachycephalus</i> Sieg, 1986														1						1						1							196-410	44, ud
<i>Pseudoparatanaïs dubius</i> (Tzareva, 1982)																			1				1										45	51
<i>Pseudotanaïs abyssii</i> Hansen, 1913									1					1						1			1										264-1376	28, 44, 52
<i>Pseudotanaïs affinis</i> Hansen, 1887																		1															1410	27
<i>Pseudotanaïs gaussi</i> Vanhöffen, 1914																1	1						1										385-4910	25, 52
<i>Pseudotanaïs guillei</i> Shiino, 1978	1						1																										10-32	40, 45
<i>Pseudotanaïs longisetosus</i> Sieg, 1977																	1																?	45
<i>Pseudotanaïs</i> sp. A**																										1							84-474	ud
<i>Pseudotanaïs nordenskiöldi</i> Sieg, 1977							1		1					1		1	1																277-6150	25, 44
<i>Pugiodactylus antarcticus</i> (Beddard, 1886)	1																																3-232	2, 40, 51
<i>Pulcherella juraszi</i> Błażewicz-Paszkowycz, 2007														1						1													1584-2663	6
<i>Pulcherella filatovae</i> (Kudinova-Pasternak, 1975)							1			1					1	1	1	1															443-3963	6, 25
<i>Robustochelia robusta</i> (Kudinova-Pasternak, 1970)*																1																	2600-3910	25
<i>Robustochelia virilis</i> Józwiak & Błażewicz-Paszkowycz, 2007																	1																2714-2727	22
<i>Singula cuncta</i> Błażewicz-Paszkowycz, 2005																											1						3543-4304	4
<i>Singula</i> sp. A**																										1							410	ud
<i>Siphonolabrum fastigatum</i> Sieg, 1986							1		1																								49-253	44
<i>Synapseudes afflagellatus</i> Sieg, 1986								1																									tidal	43
<i>Synapseudes idios</i> Gardiner, 1973							1	1																									0-903	41, 43
<i>Tanaella eltaninae</i> Guerrero-Kommritz & Błażewicz-Paszkowycz, 2004																1															1		3978-4742	16
<i>Tanaella kimi</i> Guerrero-Kommritz & Błażewicz-Paszkowycz, 2004																			1														2077	16
<i>Tanaella paraforcifera</i> (Lang, 1968)*																1																	6052-6150	25
<i>Tanaella rotundicephala</i> Sieg, 1986									1																								119-124	43
<i>Tanaella unisetosa</i> Sieg, 1986							1	1	1	1										1						1							40-137	43
<i>Tanaissus lilljeborgi</i> (Stebbing, 1891)*							1																										1105-1660	25
<i>Tanaopsis antarctica</i> Lang, 1967							1		1					1																			0-730	43
<i>Tanaopsis gallardoi</i> (Shiino, 1970)											1	1																					70-500	10, 11, 39
<i>Tanaopsis kerguelensis</i> Shiino, 1978	1																								1								16-474	40



	Sub-Antarctic							Antarctic																											
	Sub-Antarctic Is.						Magellan			West Antarctic									East Antarctic																
	Kerguelen Is.	Heard I.	Crozet Is.	Bouvet I.	Macquarie I.	Marion/Edward Is.	Falkland Is.	Tierra del Fuego	Isla de los Estados	Palmer Arch.	S. Shetland Is.	Admiralty Bay	Greenwich I.	Elephant I.	Bransfield St.	S. Orkney Is.	S. Sandwich Is.	S. Georgia	Scotia Sea	Weddell Sea	Queen Maud Ld	Mawson Sea	Cosmonauts Sea	Davis Sea	Mc Robertson Ld	Adélie/Prince V Coast	Ross Sea	Balleny Is.	Amundsen Sea	Argentina/S. Atlantic	S. Pacific	NZ	Depth range (m)	References	
<i>Typhlotanais adipatus</i> Tzareva, 1982							1		1													1										31-496	41, 43, 51		
<i>Typhlotanais andeepae</i> Błażewicz-Paszkowycz, 2007														1						1												1030-4931	6		
<i>Typhlotanais</i> aff. <i>cornutus</i> Sars, 1879**																			1						1							196-458	ud		
<i>Typhlotanais grahami</i> Błażewicz-Paszkowycz, 2004											1																						2-120	3, 10, 11	
<i>Typhlotanais greenwichensis</i> Shiino, 1970	1							1	1		1	1		1		1		1		1				1			1						12-5152	6, 10, 11, 13, 25, 26, 28, 39, 40, 42, 43, 44, 51, ud	
<i>Typhlotanais gruzovi</i> Tzareva, 1982	1																																3-140	51	
<i>Typhlotanais mimosis</i> Błażewicz-Paszkowycz, 2007																				1	1												2659-4655	6	
<i>Typhlotanais</i> aff. <i>mixtus</i> Hansen, 1913**																										1								135-375	ud
<i>Typhlotanais parvus</i> Sieg, 1986								1																										tidal	43
<i>Typhlotanais plicatus</i> Kudinova-Pasternak, 1993																				1														4803-5120	6, 28
<i>Typhlotanais</i> sp. A**																				1														4390-4392	ud
<i>Typhlotanais squamiger</i> Błażewicz-Paszkowycz, 2007																				1														4929-4931	6
<i>Typhlotanaoides rostralis</i> (Tzareva, 1982)								1	1											1			1	1			1							20-316	10, 11, 42, 51, ud
<i>Zeuxo phytalensis</i> Sieg, 1980								1																										0-50	43
<i>Zeuxoides ohlini</i> (Stebbing, 1914)								1	1	1		1																						0-140	43
<i>Zeuxoides pseudolitoralis</i> Sieg, 1980	1	1	1		1		1																											littoral	20, 40, 47, 48, 51
TOTAL:	19	7	6	1	1	3	17	25	16	23	17	12	7	4	23	3	24	5	30	46	5	2	4	21	1	7	39	3	3	6	3	4			



# THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

## Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on [www.biodiversity.aq](http://www.biodiversity.aq).

## The Census of Antarctic Marine Life (CAML)

CAML ([www.caml.aq](http://www.caml.aq)) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

## The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN ([www.scarmarbin.be](http://www.scarmarbin.be), integrated into [www.biodiversity.aq](http://www.biodiversity.aq)) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, [www.iobis.org](http://www.iobis.org)), under the aegis of SCAR (Scientific Committee on Antarctic Research, [www.scar.org](http://www.scar.org)). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with [biodiversity.aq](http://biodiversity.aq) provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

## The Editorial Team



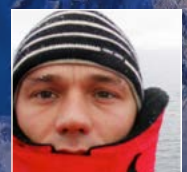
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**Ben RAYMOND** is a computational ecologist and exploratory data analyst, working across a variety of Southern Ocean, Antarctic, and wider research projects. His areas of interest include ecosystem modelling, regionalisation and marine protected area selection, risk assessment, animal tracking, seabird ecology, complex systems, and remote sensed data analyses.



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**Bruno DAVID** is CNRS director of research at the laboratory BIOGÉOSCIENCES, University of Burgundy. His works focus on evolution of living forms, with and more specifically on sea urchins. He authored a book and edited an extensive database on Antarctic echinoids. He is currently President of the scientific council of the Muséum National d'Histoire Naturelle (Paris), and Deputy Director at the CNRS Institute for Ecology and Environment.



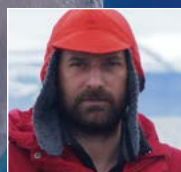
**Julian GUTT** is a marine ecologist at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, and professor at the Oldenburg University, Germany. He participated in 13 scientific expeditions to the Antarctic and was twice chief scientist on board *Polarstern*. He is member of the SCAR committees ACCE and AnT-ERA (as chief officer). Main foci of his work are: biodiversity, ecosystem functioning and services, response of marine systems to climate change, non-invasive technologies, and outreach.



**Graham HOSIE** is Principal Research Scientist in zooplankton ecology at the Australian Antarctic Division. He founded the SCAR Southern Ocean Continuous Plankton Recorder Survey and is the Chief Officer of the SCAR Life Sciences Standing Scientific Group. His research interests include the ecology and biogeography of plankton species and communities, notably their response to environmental changes. He has participated in 17 marine science voyages to Antarctica.



**Alexandra POST** is a marine geoscientist, with expertise in benthic habitat mapping, sedimentology and geomorphic characterisation of the seafloor. She has worked at Geoscience Australia since 2002, with a primary focus on understanding seafloor processes and habitats on the East Antarctic margin. Most recently she has led work to understand the biophysical environment beneath the Amery Ice Shelf, and to characterise the habitats on the George V Shelf and slope following the successful CAML voyages in that region.



**Yan ROPERT COUDERT** spent 10 years at the Japanese National Institute of Polar Research, where he graduated as a Doctor in Polar Sciences in 2001. Since 2007, he is a permanent researcher at the CNRS in France and the director of a polar research programme (since 2011) that examines the ecological response of Adélie penguins to environmental changes. He is also the secretary of the Expert Group on Birds and Marine Mammals and of the Life Science Group of the Scientific Committee on Antarctic Research.

