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Incongruence between molecular phylogeny and morphological classification in amphipod crustaceans: A case study of Antarctic lysianassoids

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ABSTRACT

In Antarctic waters, the superfamily Lysianassoidea is one of the most important amphipod groups both in terms of species number and abundance. Dominant members of this superfamily are species of the orchomenid complex, found throughout the Southern Ocean. This study presents the first molecular phylogenetic analysis based on a representative subset of the Antarctic species belonging to different orchomenid genera and hence provides a framework for a systematic revision of these taxa. The current classification of the orchomenid genera is mainly based on mouthpart morphology. The validity of these morphological characters was assessed by resolving phylogenetic relationships using nuclear 28S rRNA and mitochondrial cytochrome oxidase subunit I sequences. The molecular data rejected most of the previously proposed taxonomic subdivisions within this complex. The genera *Abyssorchomene* and *Orchomenella* as well as the subgenus *Orchomenopsis* appeared to be non-monophyletic. This implies that the supposed diagnostic characters are likely a result of convergent evolution. Further, our results indicated the necessity of a revision of the family-level systematics.

1. Introduction

For a long time, the concept of a global-scale increase in species richness from the poles to the equator (Clarke and Johnston, 2003) let assume that the Southern Ocean was depressed in species richness. Recently, the number of studies on Antarctic biodiversity and biogeography increased and challenged this view for several higher taxa. These studies suggested, in contrast, that the species richness in certain animal groups in the Southern Ocean might be comparable to this from temperate and tropical continental slopes in the Southern Hemisphere (Brandt et al., 2007), with species endemism rates of around 50% (Griffiths et al., 2009).

With more than 1500 strictly Antarctic species, the Southern Ocean is nowadays considered as a hotspot of biodiversity and that of endemisms for several orders of peracarid crustaceans (Malacostraca) like isopods and amphipods. Moreover, peracarids have undergone spectacular adaptive radiations in the Southern Ocean (Watling and Thurston, 1989; Brandt, 1999; Lörz and Brandt, 2004; Lörz and Held, 2004; Brandt, 2005). Among them, amphipods are the most diverse with more than 815 gammaridean and corophiidean species in the Southern Ocean *sensu lato* and more than 500 species from the Antarctic region only (De Broyer et al., 1999, 2003a, 2007).

The superfamily Lysianassoidea is one of the dominant gammaridean amphipod groups in Antarctic waters, both in number of species and abundance (Arnaud et al., 1986; De Broyer et al., 2001). Members of the group are common in deep oceanic basins as well as in shallow waters in high latitudes. Many species are scavengers and play a key role in deep-sea benthic communities by consuming and dispersing food falls of all sizes (Slattery and Oliver, 1986; De Broyer et al., 2004). In the Southern Ocean, dominant members of this superfamily are species of the orchomenid genus complex comprising the genera *Abyssorchomene* De Broyer, 1984, *Falklandia* De Broyer, 1985, *Orchomenella* G.O. Sars, 1895 (including the subgenera *Orchomenella* and *Orchomenopsis*), *Orchomenyx* De Broyer, 1984 and *Pseudorchomene* Schellenberg, 1926. The genera *Falklandia*, *Orchomenyx* and *Pseudorchomene* are endemic to the Southern Ocean *sensu lato*. Although the other two genera, *Orchomenella* and *Abyssorchomene*, may be considered as cosmopolitan (Barnard and Karaman, 1991), they also harbour some species endemic to the Southern Ocean.

Amphipods have a history of taxonomic instability concerning higher ranks: there has been much contention concerning their classification and phylogenetic relationships (Bousfield and Shih, 1994). In fact, higher-level relationships within Amphipoda are still so uncertain that several taxonomic treatments simply list families alphabetically (Barnard and Karaman, 1975; Barnard and

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Barnard, 1983; Barnard and Ingram, 1990; Martin and Davis, 2001). The masking effects of convergent or homoplastic morphology was reasserted as a major issue in amphipod taxonomy (Englisch et al., 2003; Macdonald et al., 2005; Hou et al., 2007; Fišer et al., 2008; Ito et al., 2008).

Despite several studies intending to clarify the systematics of the orchomenid genus complex (Shulenberger and Barnard, 1976; De Broyer, 1983, 1984, 1985a; Barnard and Karaman, 1991), the relationships among these taxa remain obscure (Table 1). The taxonomic history of this orchomenid genus complex dates back to Barnard (1964) who put the genera *Orchomenella*, *Orchomenopsis* and *Allogaussia* Schellenberg, 1926, in synonymy with *Orchomene*. In his revision of this group, De Broyer (1983, 1984, 1985a,b) deemed that the morphology of mouthparts was of prime importance in the systematics of the Lysianassoidea. Taking this new set of morphological characters into account, he was able to identify a combination of characters that supported the revalidation of the genus *Orchomenella*, to combine *Orchomenopsis* to *Orchomenella* as a subgenus, together with *Orchomenyx* as a new subgenus, and to identify *Abyssorchomene* and *Falklandia* as new genera. Barnard and Karaman (1991) found these new generic characters very difficult to evaluate and considered, as a conservative measure, all these taxa but *Pseudorchomene* as a monophyletic assemblage within a supergenus *Orchomene* in the family Lysianassidae. Lowry and Stoddart (1997) raised *Orchomenyx* to the generic level and moved it together with *Orchomenella* and *Pseudorchomene* to the Tryphosinae. This subfamily was established within Lysianassidae, with the notable exception of *Abyssorchomene* and *Falklandia* which were omitted from that revision. The most recent systematic classification (De Broyer et al., 2007) followed Lowry and Stoddart (1997) and corrected those omissions in placing *Falklandia* in the Lysianassidae (Tryphosinae), and *Abyssorchomene* within the Uristidae.

Given this framework, the present study aims at resolving the phylogenetic relationships of the orchomenid complex of genera of the Southern Ocean and testing the validity of the morphological characters used for their taxonomy. This study is the first molecular phylogenetic analysis of a representative subset of this species assemblage, using DNA sequences of the mitochondrial cytochrome oxidase subunit I (COI) and the nuclear 28S rRNA genes. It could serve as a basis for further systematic studies of this dominant group in the Southern Ocean.

2. Material and methods

2.1. Sampling

Specimens were collected with the research vessel *Polarstern* during several Antarctic expeditions: EASIZ II (ANTARKTIS XV-3, De Broyer et al., 1999), LAMPOS (ANTARKTIS XIX-5, De Broyer et al., 2003b), ANDEEP I, II, III (De Broyer et al., 2003b, 2006), ANTARKTIS XXIII-8 (d'Udekem d'Acoz and Robert, 2008). These campaigns provided shelf and deep-sea samples from the Scotia Sea, the Scotia Arc, the eastern shelf of the Antarctic Peninsula, the Weddell Abyssal Plain, the eastern Weddell Sea and Bouvet Island. Additional samples from the Ross Sea and from King George Island (South Shetland Islands) were provided by the National Institute of Water and Atmospheric Research (New Zealand) and the Polish Antarctic IPY Expedition 2007, respectively. The following collecting gears were used: Agassiz and bottom trawls, dredges, epibenthic sledges, grabs and multi-box corers as well as baited traps. Specimens for DNA analysis were fixed in 96% or absolute ethanol, pre-chilled at −20 °C.

Forty-one ingroup specimens representing 17 orchomenid species were used for the genetic analyses (Table 2). This sampling included 13 known Antarctic species (Table 1), and an undescribed species closely related to *Abyssorchomene scotianensis*, an undescribed species belonging to *Pseudorchomene* and a species closely related to *Orchomenella pinguides* (*Orchomenella* aff. *pinguides*). Moreover, specimens of *Abyssorchomene chevreuxi*, so far only recorded in Atlantic deep-sea, were found in the Southern Ocean and were included in this study.

Further, we added five specimens assigned to other lysianassoid genera (*Tryphosella*, *Kerguelenia*, *Eurythenes*, *Ambasiopsis*) as outgroup taxa, of which only the most closely related taxon (*Ambasiopsis* sp.) was eventually used in phylogenetic analyses. Detailed collection data and GenBank accession numbers are listed in Table 2.

2.2. Laboratory techniques

Total genomic DNA was extracted from the sixth pereiopod using the QIAamp DNA Mini Kit (Qiagen). Amplification of the COI marker was carried out in polymerase chain reactions using the universal primers LCOI1490 and HCOI2198 (Folmer et al., 1994). For 28S rRNA, the primers 28F and 28R (Hou et al., 2007) were used. The reaction mix contained 2.5 µl dNTPs (2 mM), 2.5 µl 10× PCR buffer including $MgCl_2$ (Sigma), 2.5 µl of each primer (2 µM), 0.25 µl of Taq DNA polymerase (5 units/µl), DNA template (around 40–80 ng) and water (depending on initial DNA concentration) in an end volume of 25 µl. PCR settings for amplifying COI sequences consisted of an initial denaturation of 180 s at 94 °C, followed by 10 cycles of 40 s at 94 °C, 40 s at 45 °C, 60 s at 72 °C, then 30 cycles of 40 s at 94 °C, 40 s at 50 °C and 60 s at 72 °C and a final elongation for 10 min at 72 °C. PCR settings for 28S sequences consisted of an initial denaturation of 180 s at 94 °C, followed by 40 cycles of 40 s at 94 °C, 40 s at 50 °C and 90 s at 72 °C and a final elongation for 10 min at 72 °C. Purified PCR products were sequenced bidirectionally using an ABI 3130xl DNA sequencer.

2.3. Phylogenetic analyses

Alignments were made manually and by MAFFT 6 web server (using the G-INS-i option) (Katoh et al., 2002; Katoh and Toh, 2008) for COI and 28S, respectively. In order to prevent the inclusion of pseudogenes in the analyses, COI sequences were translated into amino acids and checked for stop codons.

Phylogenetic analyses were conducted both on the separate and combined (COI + 28S) data sets. Parsimony analyses were carried out using Paup* 4.0b10 (Swofford, 2002). All characters were equally weighted and unordered. Alignment gaps were treated as a new state ("fifth character") or as missing data. Heuristic searches were carried out with random sequence addition (10 replicates) and using tree-bisection-reconnection (TBR) branch swapping. Branch support was evaluated using non-parametric bootstrapping (number of replicates was 2000).

Furthermore, Bayesian analyses were performed on the combined data set (COI + 28S) with four data partitions (three partitions for each codon position of COI and one partition for 28S). The best-fit model was selected using jModeltest 0.1.1 (Posada, 2008) by estimating and comparing maximum likelihood scores for different nucleotide substitution models. This has been carried out for each of the four data partitions. Different selection criteria (Akaike Information Criterion and Bayesian Information Criterion) identified the same best-fit substitution model for each data partition: the general time-reversible substitution model with a discrete γ correction for among site variation (GTR + G model). Hence, this model was used for each partition to conduct the Bayesian analyses using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Two parallel runs with four chains each were run for 2 mil-

Table 1
Known classifications of the Antarctic orchomenid species. Species names are according to De Broyer et al. (2007). Genetically investigated species are marked in bold.

Species	Described as	Barnard (1964)	De Broyer (1983, 1984, 1985)	Barnard and Karaman (1991)	Lowry and Stoddart (1997)	De Broyer et al. (2007)
Abyssorchomene charcoti (Chevreux, 1912)	*Orchomenopsis*	*Orchomene*	*Abyssorchomene*	Supergenus *Orchomene* (Lysianassidae)		*Abyssorchomene* (Uristidae)
Abyssorchomene nodimanus (Walker, 1903)	*Orchomenopsis*					
Abyssorchomene plebs (Hurley, 1965)	*Orchomenella*					
Abyssorchomene rossi (Walker, 1903)	*Orchomenopsis*					
Abyssorchomene scotianensis (Andres, 1983)	*Orchomenopsis*					
Falklandia reducta (Schellenberg, 1931)	*Orchomenopsis*		*Falklandia*			*Falklandia* (Lysianassidae, Tryphosinae)
Orchomenella (*Orchomenella*) *chelipes* (Walker, 1906)	*Orchomenella*		*O.* (*Orchomenella*)		*Orchomenella* (Lysianassidae, Tryphosinae)	*O.* (*Orchomenella*) (Lysianassidae, Tryphosinae)
Orchomenella (Orchomenella) franklini (Walker, 1903)	*Orchomenella*					
Orchomenella (*Orchomenella*) *guillei* De Broyer, 1985	*O.* (*Orchomenella*)					
Orchomenella (*Orchomenella*) *hureaui* (De Broyer, 1973)	*Orchomene*					
Orchomenella (*Orchomenella*) *kryptopinguides* (Andres, 1983)	*Orchomene*					
Orchomenella (Orchomenella) pinguides (Walker, 1903)	*Orchomenella*					
Orchomenella (*Orchomenella*) *ultima* (Bellan-Santini, 1972)	*Orchomene*					
Orchomenella (*Orchomenopsis*) *aahu* (Lowry & Stoddart, 1983)	*Orchomene*		*O.* (*Orchomenopsis*)			*O.* (*Orchomenopsis*) (Lysianassidae, Tryphosinae)
Orchomenella (Orchomenopsis) acanthurus (Schellenberg, 1931)	*Orchomenopsis*					
Orchomenella (Orchomenopsis) cavimanus (Stebbing, 1888)	*Orchomene*					
Orchomenella (*Orchomenopsis*) *cavimana rostrata* (Schellenberg, 1931)	*Orchomenella*					
Orchomenella (*Orchomenopsis*) *chilensis* (Heller, 1868)	*Anonyx*					
Orchomenella (*Orchomenopsis*) *denticulata* Rauschert, 1995	*O.* (*Orchomenopsis*)					
Orchomenella (*Orchomenopsis*) *goniops* (Walker, 1906)	*Orchomene*					
Orchomenella (*Orchomenopsis*) *hiata* (Andres, 1983)	*Orchomene*					
Orchomenella (*Orchomenopsis*) *macrophthalma* (Birstein & Vinogradov, 1962)	*Allogausia*					
Orchomenella (*Orchomenopsis*) *rotundifrons* K.H. Barnard, 1932	*Orchomenella*					
Orchomenella (*Orchomenopsis*) *zschaui* (Pfeffer, 1888)	*Anonyx*					
Orchomenyx macronyx (Chevreux, 1905)	*Orchomenella*		*O.* (*Orchomenyx*)		*Orchomenyx* (Lysianassidae, Tryphosinae)	*Orchomenyx* (Lysianassidae, Tryphosinae)
Orchomenyx schellenbergi (Thurston, 1972)	*Orchomene*					
Orchomenyx tabarini (Thurston, 1972)	*Orchomene*					
Pseudorchomene coatsi (Chilton, 1912)	*Orchomenopsis*		*Pseudorchomene*	*Pseudorchomene*	*Pseudorchomene* (Lysianassidae, Tryphosinae)	*Pseudorchomene* (Lysianassidae, Tryphosinae)

lion generations, every 100th generation was sampled (resulting in 20,000 sample trees). The level of convergence was monitored, and we set the "burn-in" value accordingly. The first 25% of the trees were discarded and the last 15,000 trees were used to reconstruct a consensus tree and estimate Bayesian posterior probabilities.

3. Results

In total, COI and 28S sequences of 46 specimens were obtained (see Table 2). The aligned COI sequences consisted of 658 positions. No stop codons were observed and DNA sequences showed higher

Table 2
Data on specimens used for this study (n.a. = not analyzed).

	Individual codes	Locality	Longitude/latitude	Depth	Accession nos.	
					COI	28S
Uristidae						
Abyssorchomene charcoti (Chevreux, 1912)	AC-SS205	Scotia Sea	62°43′S 55°30′W	205	GU109230	GU109189
Abyssorchomene chevreuxi (Stebbing, 1906)	AC-WS4700	Weddell Sea	65°00′S 43°02′W	4700	GU109248	GU109219
Abyssorchomene chevreuxi (Stebbing, 1906)	AC-P3076	Peninsula	65°17′S 51°35′W	3076	GU109229	GU109197
Abyssorchomene sp.	An-SS3406	Scotia Sea	62°11′S 49°29′W	3406	GU109239	GU109218
Abyssorchomene sp.	An-WS3088	Weddell Sea	70°39′S 14°43′W	3088	GU109236	GU109186
Abyssorchomene nodimanus (Walker, 1903)	AN-WS393	Weddell Sea	70°48′S 10°39′W	393	GU109241	GU109183
Abyssorchomene nodimanus (Walker, 1903)	AN-WS387	Weddell Sea	70°49′S 10°39′W	387	GU109260	GU109205
Abyssorchomene plebs (Hurley, 1965)	AP-SS1943	Scotia Sea	61°48′S 47°27′W	1943	GU109255	GU109209
Abyssorchomene plebs (Hurley, 1965)	AP-SS270	Scotia Sea	57°41′S 26°24′W	270	GU109258	GU109195
Abyssorchomene plebs (Hurley, 1965)	AP-LB383	Larsen B	65°59′S 60°24′W	383	GU109233	GU109204
Abyssorchomene scotianensis (Andres, 1983)	AS-SS3408	Scotia Sea	62°11′S 49°29′W	3408	GU109242	GU109217
Abyssorchomene scotianensis (Andres, 1983)	AS-P3076	Peninsula	65°17′S 51°35′W	3076	GU109240	GU109184
Lysianassidae						
Tryphosinae						
Falklandia reducta (Schellenberg 1931)	FR-SS285	Scotia Sea	61°23′S 55°26′ W	285	GU109256	GU109193
Orchomenella (*Orchomenella*) *franklini* (Walker, 1903)	OF-SS259-1	Scotia Sea	60°52′S 55°27′W	259	GU109226	GU109203
Orchomenella (*Orchomenella*) *franklini* (Walker, 1903)	OF-SS259-3	Scotia Sea	60°52′S 55°27′W	259	GU109235	GU109221
Orchomenella (*Orchomenella*) *pinguides* (Walker, 1903)	OP-WS387	Weddell Sea	70°49′S 10°39′W	387	GU109247	GU109215
Orchomenella (*Orchomenella*) *pinguides* (Walker, 1903)	OP-WS395	Weddell Sea	70°48′S 10°39′W	395	GU109259	GU109207
Orchomenella (*Orchomenella*) aff. *pinguides*	OP-WS175	Weddell Sea	71°06′S 11°32′W	175	GU109237	GU109199
Orchomenella (*Orchomenopsis*) *acanthurus* (Schellenberg, 1931)	OA-RS252	Ross Sea	71°38′S 170°13′E	252	GU109263	GU109190
Orchomenella (*Orchomenopsis*) *acanthurus* (Schellenberg, 1931)	OA-WS284	Weddell Sea	70°56′S 10°31′W	284	GU109225	GU109223
Orchomenella (*Orchomenopsis*) *acanthurus* (Schellenberg, 1931)	OA-P137	Peninsula	61°20′S 55°31′W	137	GU109266	GU109222
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-WS1017-4	Weddell Sea	71°18′S 13°56′W	1017	GU109249	GU109220
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS349	Scotia Sea	61°07′S 56°08′W	349	GU109250	GU109224
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-WS847	Weddell Sea	72°47′S 19°29′W	847	GU109261	GU109206
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-WS1017-5	Weddell Sea	71°18′S 13°56′W	1017	GU109243	GU109216
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-WS387	Weddell Sea	70°49′S 10°39′W	387	GU109244	GU109188
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS349-1	Scotia Sea	61°07′S 56°08′W	349	GU109251	GU109210
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS349-4	Scotia Sea	61°07′S 56°08′W	349	GU109252	GU109211
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-WS515	Weddell Sea	72°49′S 19°30′W	515	GU109257	GU109196
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS413	Scotia Sea	54°32′S 55°55′W	413	GU109262	GU109194
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS1943	Scotia Sea	61°48′S 47°27′W	1943	GU109254	GU109191
Orchomenella (*Orchomenopsis*) *cavimanus* (Stebbing, 1888)	OC-SS293	Scotia Sea	53°25′S 42°40′W	293	GU109264	GU109192
Orchomenyx macronyx (Chevreux, 1905)	OM-JI151	Joinville Island	61°20′S 55°29′W	151	GU109231	GU109200
Orchomenyx macronyx (Chevreux, 1905)	OM-JI161	Joinville Island	62°33′S 55°41′W	161	GU109228	GU109202
Orchomenyx schellenbergi (Thurston, 1972)	OS-KGI210	King George Island	58°27′S 62°09′W	210	GU109265	GU109198
Orchomenyx tabarini (Thurston, 1972)	OT-P211	Peninsula	62°27′S 55°25′W	211	GU109227	GU109201
Pseudorchomene coatsi (Chilton, 1912)	PC-SS349	Scotia Sea	31°07′S 56°08′W	349	GU109245	GU109185
Pseudorchomene coatsi (Chilton, 1912)	PC-SS2889-4	Scotia Sea	61°44′S 60°45′W	2889	GU109232	GU109213
Pseudorchomene coatsi (Chilton, 1912)	PC-SS2889-5	Scotia Sea	61°44′S 60°45′W	2889	GU109234	GU109212
Pseudorchomene sp.	Pn-WS847	Weddell Sea	72°47′S 19°29′W	847	GU109238	GU109187
Pseudorchomene sp.	Pn-SS1943	Scotia Sea	61°48′S 47°27′W	1943	GU109253	GU109208
Tryphosella murrayi (Walker, 1903)	TM-RS456	Ross Sea	71°58′S 171°58′E	456	GU109268	n.a.
Tryphosella sp.	Ts-WS401	Weddell Sea	70°57′S 10°48′W	401	GU109267	n.a.
Adeliellid group						
Ambasiopsis sp.	As-BI260	Bouvetøya Island	54°31′S 03°14′E	260	GU109246	GU109214
Eurytheneidae						
Eurythenes gryllus Lichtenstein, 1822	EG-P3049	Peninsula	65°19′S 51°31′W	3049	GU109270	n.a.
Kergueleniid group						
Kerguelenia sp.	Ks-WS274	Weddell Sea	70°56′S 10°31′W	274	GU109269	n.a.

mutation rates in third codon positions which is typical for protein-coding genes. The matrix of aligned 28S sequences contained 1334 positions. The combined dataset was 1992 base pairs in length, 534 positions were parsimony informative (140 bp of COI and 394 of 28S).

According to our preliminary molecular results, an unknown species of the genus *Ambasiopsis* was the most closely related lysianassoid taxon to the orchomenid group and was therefore used as outgroup. Interestingly, the genus *Tryphosella* belonging to the same subfamily (Tryphosinae) as the genera *Orchomenella*, *Pseudorchomene* and *Orchomenyx* was found clearly outside of the ingroup. Together with other distantly related taxa (*Eurythenes* and *Kerguelenia*) they were removed from subsequent analyses.

Similar topologies were obtained for the separate data sets of 28S and COI, and conflicting nodes received low support. In most cases, the separate analysis of COI sequences (tree not shown) showed generally strong support at the terminal nodes. Separate 28S analyses (tree not shown) assisted to resolve more basal phylogenetic relationships. Topologies of both parsimony analyses (with gaps treated as missing or fifth characters, respectively) based on the combined data set did not differ but bootstrap values were generally higher when the gaps were treated as fifth characters (Fig. 1). Both Bayesian and parsimony analyses revealed similar topologies without conflicting nodes. In the combined analyses, most clades were supported by high bootstrap values and Bayesian posterior probabilities.

The monophyly of all species represented by multiple specimens was confirmed.

Parsimony analyses and Bayesian inference gave clear evidence for the non-monophyletic nature of the genera *Abyssorchomene*

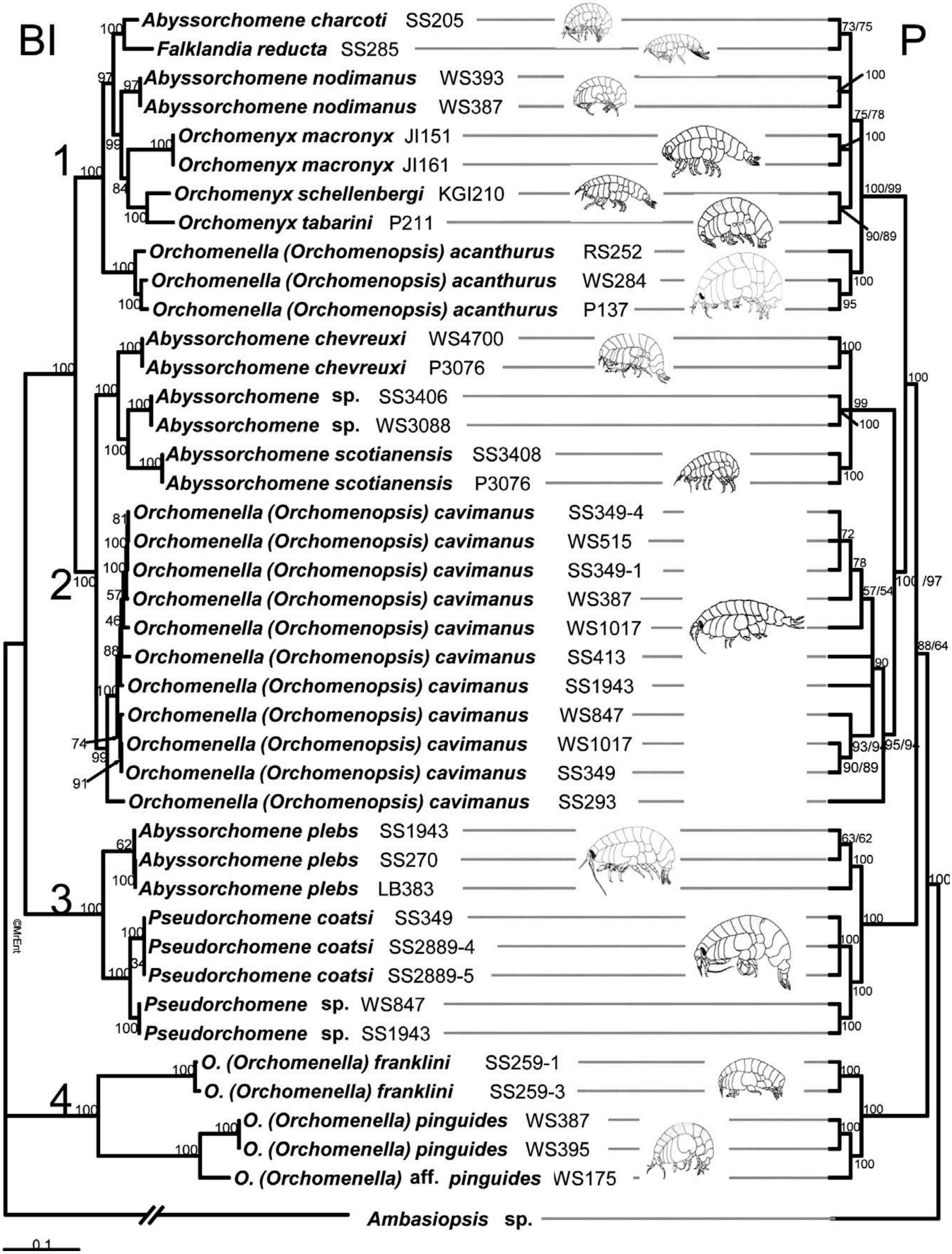

Fig. 1. Phylogenetic trees based on the combined data set (28S rRNA and COI). The Bayesian tree with posterior probabilities is shown on the left (BI), the parsimony tree with bootstrap values is shown on the right (P). When two values are shown on the parsimony tree, the bootstraps differ when gaps were treated as fifth characters versus missing data. Drawings were used/modified after Stebbing (1888), Chevreux (1913), Bellan-Santini (1972a, b), Thurston (1972), De Broyer (1983, 1985b).

and *Orchomenella* as well as the subgenus *Orchomenopsis* (Fig. 1). Only the genus *Pseudorchomene* and the subgenus *Orchomenella* were retrieved as monophyletic. The clade comprising *A. scotianensis*, *A. chevreuxi* and *Abyssorchomene* sp. formed a monophyletic assemblage, sister to *O. cavimanus*. Furthermore, the different analyses yielded incongruent relationships between *Orchomenyx macronyx*, *Orchomenyx schellenbergi* and *Orchomenyx tabarini* but *O. tabarini* and *O. schellenbergi* formed a well-resolved clade. Thus, the monophyly of the genus *Orchomenyx* remained unresolved. Finally, *Falklandia reducta* appeared to be the sister taxon of *A. charcoti*.

In all phylogenetic analyses, four main clusters consistently received high bootstrap values and Bayesian posterior probabilities of 1.00 (Fig. 1). Strikingly, none of them but the subgenus *Orchomenella* corresponded to a monophyletic assemblage according to the current systematics of the genus complex:

(1) *Abyssorchomene charcoti* + *F. reducta*, *Abyssorchomene nodimanus*, three *Orchomenyx* species and *Orchomenella* (*Orchomenopsis*) *acanthurus*;
(2) *Orchomenella* (*Orchomenopsis*) *cavimanus* and the clade of *A. chevreuxi*, *Abyssorchomene* sp. and *A. scotianensis*;
(3) *Abyssorchomene plebs*, *Pseudorchomene coatsi* and *Pseudorchomene* sp.;
(4) *Orchomenella* (*Orchomenella*) *pinguides*, *Orchomenella* (*Orchomenella*) aff. *pinguides* and *Orchomenella* (*Orchomenella*) *franklini*.

Although phylogenetic relationships between these four main groups received high bootstrap support, only the sister relationship between the first two groups are well supported by the Bayesian analyses (posterior probabilities >99%).

4. Discussion

4.1. Polyphyly of some orchomenid genera

Phylogenetic patterns revealed by our molecular study consistently differ from the traditional, morphology-based taxonomy in many respects, and casts doubt on the monophyly of some of the genera currently used in the lysianassoid systematics. Two orchomenid genera are clearly polyphyletic. The most striking example is *Abyssorchomene*. This genus is found in three clades and it may be paraphyletic or monophyletic in each of them. The genus *Orchomenella* is polyphyletic, as its subgenus *Orchomenopsis*. In contrast, sampled species of the subgenus *Orchomenella* are grouped in a monophyletic assemblage. Finally, the monophyly of the genus *Orchomenyx* could not be confirmed due to the ambiguous and less supported position of *O. macronyx* in relation to some *Abyssorchomene* species.

In our molecular analysis, the clade of *Abyssorchomene* comprising *A. chevreuxi*, the type species of this genus, *A.* sp. and *A. scotianensis* forms a well-supported monophyletic unit. This clade harbours species recorded at abyssal depths, which can be morphologically distinguished from other *Abyssorchomene* species by the presence of non-ommatidian eyes. This character probably represents an adaptation to the low light environment of the deep-sea. Within clade 3, *P. coatsi* is clustered with *A. plebs*. According to morphology, the genus *Pseudorchomene* is closely related to other orchomenid species, but radically differs in the strong elongation of the first pair of gnathopods which was the reason for establishing a new genus for this species (Schellenberg, 1926).

The apparent non-monophyly of most of these genera and subgenera has important consequences since it implies (1) that the synapomorphies currently identified to delineate them (De Broyer, 1984) are not valid anymore, (2) that new sets of characters should be considered in attempt to identify new synapomorphies.

4.2. Parallel evolution of trophic adaptations

The main taxonomical decisions that led to the current classification and diagnoses of these genera were mostly justified by characters representing trophic adaptations, such as the morphology of mouthpart (e.g. *Abyssorchomene*, *Falklandia*; De Broyer, 1983, 1984, 1985b), or that of gnathopods (e.g. *Pseudorchomene*). The seven species assigned to the genus *Abyssorchomene* are considered to be the most adapted to necrophagy within the orchomenid species group, due to the peculiar shape of the molar process of the mandible (very elongated, with a reduced triturative surface), the enlarged convex cutting edge of the incisor, as well as the stomodeum extended to the seventh pereionite segment instead of the fourth one (De Broyer, 1983). An elongated stomodeum is interpreted as an adaptation to a strictly necrophagous feeding strategy allowing enhanced food storage capacity in oligotrophic deep-sea habitats where the occurrence of food sources (e.g. benthic carcasses) is unpredictable (De Broyer, 1983). These characters are also present in exclusively necrophagous genera such as *Eurythenes* (Lysianassoidea, Eurytheneidae) and *Hirondellea* (Lysianassoidea, Hirondelleid group) (Dahl, 1979; Thurston, 1979; Lowry and Stoddart, 1994; De Broyer et al., 2004). This fact indicates that a scavenger mode of nutrition has arisen several times independently during the evolution of the Lysianassoidea (Dahl, 1979; De Broyer et al., 2004) probably as an evolutionary response to an ecological opportunity. Our molecular analysis refutes the monophyly of *Abyssorchomene*, implying that a similar trophic morphology evolved several times independently, even within closely related lineages.

Recent molecular studies have shown that characters linked to the mode of nutrition are easily lost and independently acquired many times. Cichlid fishes (Rüber et al., 1999) or leeches (Apakupakul et al., 1999) yielded examples to illustrate the parallel evolution of trophic adaptations. Thus, character states related to feeding, such as morphological traits of mouthparts, are plastic and may be independently lost or acquired in the course of evolution. The possible occurrence of homoplasies represents a major problem in the phyletic classification of amphipod crustaceans, which is often based on the mouthpart morphology, not only in gammarideans but also in caprellideans, hyperiids and others (see Bousfield and Shih (1994)). Bousfield (1983) also suggested to consider not only the gnathopods or mouthparts of amphipods and that taxonomic analyses should include broader sets of characters.

Therefore, a re-examination of the orchomenid genera of the Southern Ocean is highly desirable using other morphological characters. *Falklandia* gives a good illustration of the issue at hand. This monotypic genus was originally erected to accommodate *Orchomenopsis reducta* Schellenberg, 1931 (De Broyer, 1985b). The exclusion of this species from *Orchomenopsis* was exclusively justified by differences in the mouthparts. Our phylogenetic analysis does not give any support to this decision since *F. reducta* appears to be the sister species of *A. charcoti*. However, a recent reassessment of phylogenetic relationships among amphipods of Lake Baikal has illustrated that morphological and molecular evolution might be uncoupled during their radiation (Macdonald et al., 2005). It gives an example of close genetic relatives with extreme morphological and ecological divergence. Thus, caution must be taken when taxonomic decisions are based on characters supposedly having evolutionary plasticity.

The observation that a classification based on characters related to feeding is unreliable in the Lysianassoidea could have deep consequences and reach the subfamily-level systematics and beyond. Our molecular analyses show that the polyphyletic *Abyssorchomene*, currently assigned to the Uristidae, is related to representatives of the Lysianassidae. They also indicate that specimens of the genera *Tryphosella* (Lysianassidae, Tryphosinae, not shown in the tree, see reasons above) are much more distantly related to the ingroup than *Ambasiopsis*, a genus outside the Lysianassidae (De Broyer et al., 2007). Therefore, polyphyly may also impact the family-level systematics. It is worth noting that all taxonomic decisions that led to the recognition of the Uristidae were justified by an assessment of characters linked to trophic adaptations. Hurley (1963) established the subfamily Uristinae for lysianassid amphipods and included a number of genera but never indicated the full extent of this group. Lowry and Stoddart (1992) elevated the subfamily to family rank and further defined this family by the presence of a 7/4-crown setal tooth arrangement on first maxilla.

4.3. Conclusions and taxonomic recommendations

Our results show that the molecular phylogeny and morphological taxonomy of lysianassoid amphipods are largely incongruent. In our study, molecular analyses rejected some of the previously proposed classifications within the orchomenid complex and indicated the presence of homoplasic trophic characters. This study shows that a revision of the orchomenid genus complex based on other morphological characters is badly needed. Unfortunately, the original descriptions of most genera and subgenera of this genus complex are so brief and undiscriminating that such work will require a scrutiny of all relevant types, which is clearly out of the scope of this paper. However, some taxonomic changes could be suggested. The genus *Abyssorchomene* could be restricted to the monophyletic abyssal clade, comprising the type species *A. chevreuxi*, as well as *Abyssorchomene* sp. and *A. scotianensis* and possibly other abyssal species. Alternative options would be to adopt the proposal of Barnard (1964) who considered all these genera but *Pseudorchomene* as a single genus called *Orchomene*, or that of Barnard and Karaman (1991) who assembled all these genera but *Pseudorchomene* as a monophyletic unit within the supergenus *Orchomene*. However, the embedded position of *Pseudorchomene* within this assemblage suggests its inclusion in the genus or supergenus *Orchomene*. Finally, a revision of the family-level systematics is needed due to the apparent polyphyly of Lysianassidae (Tryphosinae).

The phylogeny and classification of these taxa involves many challenges for future work requiring more thorough taxon and gene sampling. Moreover, an understanding of lysianassoid systematics is essential for answering questions on the origin of the Southern Ocean deep-sea fauna, its relationships with the fauna of the continental slope, the origin of Antarctic benthic community structures and the evolution of trophic traits (Brandt, 1999, 2000; Thatje et al., 2005; Raupach et al., 2009).

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References

Apakupakul, K., Siddall, M.E., Burreson, E.M., 1999. Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. Mol. Phylogenet. Evol. 12, 350–359.

Arnaud, P.M., Jażdżewski, K., Presler, P., Siciński, J., 1986. Preliminary survey of benthic invertebrates collected by Polish Antarctic Expeditions in the Admiralty Bay (King George Island, South Shetlands, Antarctica). Pol. Polar Res. 7, 7–24.

Barnard, J.L., 1964. Marine Amphipoda of Bahia de San Quintin, Baja California. Pacific Naturalist 4, 56–139.

Barnard, J.L., Barnard, C.M., 1983. Freshwater Amphipoda of the World I & II. Hayfield Associates, Mt. Vernon, VA. p. 471.

Barnard, J.L., Ingram, C., 1990. Lysianassoid Amphipoda (Crustacea) from deep-sea hydrothermal vents. Smithson. Contrib. Zool. 499, 1–80.

Barnard, J.L., Karaman, G.S., 1975. The higher classification in amphipods. Crustaceana 28, 304–310.

Barnard, J.L., Karaman, G., 1991. The families and genera of marine Gammaridean Amphipoda (except marine Gammaroids). Part 1. Rec. Aust. Mus. 13, 1–866.

Bellan-Santini, D., 1972a. Amphipodes provenant des contenus stomacaux de trois espèces de poissons Nototheniidae récoltés en Terre Adélie (Antarctique). Tethys 4, 683–702.

Bellan-Santini, D., 1972b. Invertébrés marins des XIIème et XVème expéditions antarctiques françaises en Terre Adélie. 10. Amphipodes gammariens. Tethys Suppl. 4, 157–238.

Bousfield, E.L., 1983. An updated phyletic classification and palaeohistory of the Amphipoda. In: Schram, F.R. (Ed.), Crustacean Phylogeny, Crustacean Issues 1. A.A. Balkema, Rotterdam, pp. 257–277.

Bousfield, E.L., Shih, C., 1994. The phyletic classification of amphipod crustaceans: problems in resolution. Amphipacifica 1, 76–134.

Brandt, A., 1999. On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). Sci. Mar. 63, 261–274.

Brandt, A., 2000. Hypotheses on Southern Ocean peracarid evolution and radiation (Crustacea, Malacostraca). Antarct. Sci. 12, 269–275.

Brandt, A., 2005. Evolution of Antarctic biodiversity in the context of the past: the importance of the Southern Ocean deep sea. Antarct. Sci. 17, 509–521.

Brandt, A., Gooday, A.J., Brandão, S.N., Brix, S., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Mesel, I., Diaz, R.J., Gillan, D.C., Ebbe, B., Howe, J.A., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Pawlowski, J., Raupach, M., Vanreusel, A., 2007. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. Nature 447, 307–311.

Chevreux, E., 1913. Amphipodes. In: Joubin, L. (Ed.), Deuxième Expédition Antarctique Française (1908–1910) Commandée par le Dr. Jean Charcot. Sciences Naturelles: Documents Scientifiques. Masson et Cie, Paris, p. 93.

Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanogr. Mar. Biol. Annu. Rev. 41, 47–114.

Dahl, E., 1979. Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. Oikos 33, 167–175.

De Broyer, C., 1983. Recherches sur la systématique et l'évolution des crustacés amphipodes gammarides antarctiques et subantarctiques. Université Catholique de Louvain, Louvain-la-Neuve, Belgium, Unpublished PhD thesis.

De Broyer, C., 1984. Evolution du complexe *Orchomene* Boeck (Amphipoda, Lysianassidae). Ann. Soc. R. Zool. Belg. 114, 197–198.

De Broyer, C., 1985a. Amphipodes lysianassoïdes nécrophages des îles Kerguelen (Crustacea): 1. *Orchomenella guillei* n. sp. Bull. Mus. Natl. Hist. Nat. Sect. A 7, 205–217.

De Broyer, C., 1985b. Description de *Falklandia* gen. n. de l'Océan Austral et définition des Lysianassoidea uristidiens (Crustacea, Amphipoda). Zool. Scr. 14, 303–312.

De Broyer, C., Rauschert, M., Scailteur, Y., 1999. Structural and ecofunctional biodiversity of the benthic amphipod taxocenoses. In: Arntz, W., Gutt, J. (Eds.), The expedition ANTARKTIS XV/3 (EASIZ II) of Polarstern in 1998. Ber. Polarforsch. vol. 301, pp. 163–174.

De Broyer, C., Scailteur, Y., Chapelle, G., Rauschert, M., 2001. Diversity of epibenthic habitats of gammaridean amphipods in the eastern Weddell Sea. Polar Biol. 24, 744–753.

De Broyer, C., Dauby, P., Nyssen, F., Martin, P., 2003a. Biodiversity, molecular phylogeny and trophodynamics of amphipod crustaceans in the Antarctic deep sea. In: Fütterer, D.K., Brandt, A., Poore, G.C.B. (Eds.), The expeditions ANTARKTIS XIX/3-4 of the Research Vessel POLARSTERN in 2002. Ber. Polar. Meeresforsch. vol. 470, pp. 81–86.

De Broyer, C., Nyssen, F., Rauschert, M., Lörz, A.-N., Cariceo, Y., Ríos, C., 2003b. Biodiversity, biogeography, phylogeny and trophodynamics of amphipod and isopod crustaceans. In: Arntz, W.E., Brey, T. (Eds.), Report of the R/V Polarstern Cruise ANT XIX/3 LAMPOS in 2002. Ber. Polar. Meeresforsch. vol. 462, pp. 34–44.

De Broyer, C., Nyssen, F., Dauby, P., 2004. The crustacean scavenger guild in Antarctic shelf, bathyal and abyssal communities. Deep Sea Res. II: Top. Stud. Oceanogr. 51, 1733–1752.

De Broyer, C., Danis, B., Heterier, V., 2006. Biodiversity, phylogeny and trophodynamics of amphipod crustaceans in the Antarctic deep sea. In: Fahrbach, E. (Ed.), The expedition ANTARKTIS XXII-3 of the Research Vessel Polarstern in 2005. Ber. Polar. Meeresforsch. vol. 533, pp. 135–141.

De Broyer, C., Lowry, J.K., Jażdżewski, K., Robert, H., 2007. Catalogue of the Gammaridean and Corophiidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. In: De Broyer C. (Ed.), Census of Antarctic Marine Life: Synopsis of the Amphipoda of the Southern Ocean. Bull. Inst. R. Sci. Nat. Belgique Biol. vol. 77, pp. 1–325.

Englisch, U., Coleman, C.O., Wägele, J.W., 2003. First observations on the phylogeny of the families Gammaridae, Crangonyctidae, Melitidae, Niphargidae, Megaluropidae and Oedicerotidae (Amphipoda, Crustacea), using small subunit rDNA gene sequences. J. Nat. Hist. 37, 2461–2486.

Fišer, C., Sket, B., Trontelj, P., 2008. A phylogenetic perspective on 160 years of troubled taxonomy of *Niphargus* (Crustacea: Amphipoda). Zool. Scr. 37, 665–680.

Folmer, O., Black, M., Hoeh, R., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Griffiths, H.J., Barnes, D.K.A., Linse, K., 2009. Towards a generalized biogeography of the Southern Ocean benthos. J. Biogeogr. 36, 162–177.

Hou, Z., Fu, J., Li, S., 2007. A molecular phylogeny of the genus *Gammarus* (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. Mol. Phylogenet. Evol. 45, 596–611.

Hurley, D.E., 1963. Amphipoda of the family Lysianassidae from the West Coast of North and Central America. Allan Hancock Foundation, Occasional Paper, vol. 25. University of Southern California Press, Los Angeles, pp. 1–165.

Ito, A., Wada, H., Aoki, M.N., 2008. Phylogenetic analysis of caprellid and corophioid amphipods (Crustacea) based on the 18S rRNA gene, with special emphasis on the phylogenetic position of Phtisicidae. Biol. Bull. 214, 176–183.

Katoh, K., Misawa, K., Kuma, K., Miyata, T., 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res. 30, 3059–3066.

Katoh, K., Toh, H., 2008. Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT-based framework. BMC Bioinformatics 9, 212.

Lörz, A.-N., Brandt, A., 2004. Phylogeny of Antarctic *Epimeria* (Epimeriidae: Amphipoda). J. Mar. Biol. Assoc. UK 84, 179–190.

Lörz, A.-N., Held, C., 2004. A preliminary molecular and morphological phylogeny of the Antarctic Epimeriidae and Iphimediidae (Crustacea, Amphipoda). Mol. Phylogenet. Evol. 31, 4–15.

Lowry, J.K., Stoddart, H.E., 1992. A revision of the genus *Ichnopus* (Crustacea: Amphipoda: Lysianassoidea: Uristidae). Rec. Aust. Mus. 44, 185–245.

Lowry, J.K., Stoddart, H.E., 1994. Crustacea Amphipoda: lysianassoids from the tropical western South Pacific Ocean. In: Crosnier, A. (Ed.), Résultats des campagnes MUSORSTOM 12. Mem. Mus. Natl. Hist. Nat. (France), vol. 161, pp. 127–233.

Lowry, J.K., Stoddart, H.E., 1997. Amphipoda Crustacea IV. Mem. Hourglass Cruises 10, 1–130.

Macdonald, K.S.I.I.I., Yampolsky, L., Duffy, J.E., 2005. Molecular and morphological evolution of the amphipod radiation in Lake Baikal. Mol. Phylogenet. Evol. 35, 323–343.

Martin, J.W., Davis, G.E., 2001. An updated classification of the Recent Crustacea. Natural History Museum of Los Angeles County Science Series 39, Los Angeles.

Posada, D., 2008. JModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25, 1253–1256.

Raupach, M.J., Mayer, C., Malyutina, M., Wägele, J.-W., 2009. Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. Proc. R. Soc. Lond. B.: Biol. Sci. 276, 799–808.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian Phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Rüber, L., Verheyen, E., Meyer, A., 1999. Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. Proc. Natl. Acad. Sci. USA 96, 10230–10235.

Schellenberg, A., 1926. Die Gammariden der Deutschen Südpolar-Expedition 1901–1903. Deutsch Südpolar-Exped. (Zool.) 18, 235–414.

Shulenberger, E., Barnard, J.L., 1976. Amphipods from an abyssal trap set in the North Pacific Gyre. Crustaceana 31, 241–258.

Slattery, P.N., Oliver, J.S., 1986. Scavenging and other feeding habits of lysianassid amphipods (*Orchomene* ssp.) from McMurdo Sound, Antarctica. Polar Biol. 6, 171–177.

Stebbing, T.R.R., 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76. Zoology 29, 1–1737 (pls. 1–210).

Swofford, D.L., 2002. PAUP*. Phylogenetic Analysis using Parsimony (*and other methods). Version 4.0b10. Sinuaer, Sunderland, Massachusetts.

Thatje, S., Hillenbrand, C.-D., Larter, R., 2005. On the origin of the Antarctic marine benthic community structure. Trends Ecol. Evol. 20.

Thurston, M.H., 1972. Two new species of *Orchomene* Boeck (Crustacea: Amphipoda) from the Falkland Islands, South Georgia and Graham Land. Br. Antarct. Surv. Bull. 30, 51–63.

Thurston, M.H., 1979. Scavenging abyssal amphipods from the North-East Atlantic Ocean. Mar. Biol. 51, 55–68.

d'Udekem d'Acoz, C., Robert, H., 2008. Systematic and ecological diversity of amphipods. In: Gutt, J. (Ed.), The expedition ANTARKTIS-XXIII/8 of the Research Vessel "Polarstern" in 2006/2007. Ber. Polar. Meeresforsch. vol. 569, pp. 48–56.

Watling, L.E., Thurston, M.H., 1989. Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the amphipod family Iphimediidae. In: Crame, J.A. (Ed.), Origins and Evolution of the Antarctic Biota. The Geological Society, London, pp. 297–313.