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## Antarctic reptant decapods: more than a myth?

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**Abstract** The impoverished Antarctic decapod fauna is one of the most conspicuous biodiversity phenomena in polar science. Although physiological and ecological approaches have tried to explain the reason for the low decapod biodiversity pattern in the Southern Ocean, the complexity of this problem is still not completely understood. The scant records of crabs south of the Polar Front were always considered as exceptional, and have mostly been ignored by marine biologists world-wide, creating one of the most dogmatic paradigms in polar science. We herein review the record of both adults and larvae of reptants from the Southern Ocean. At present, several species of only lithodid crabs maintain considerable adult populations in circum-Antarctic waters, although they remain absent from the high-Antarctic shelves.

### Introduction

“Everybody who has worked in Antarctic waters has been struck by the peculiar absence of crabs, lobsters, shrimps.....in shallow waters” (H. Broch 1961).

The impoverished Antarctic decapod fauna, compared with the high diversity of decapod crustaceans recorded in the Subantarctic (Gorny 1999), constitutes one of the most enigmatic phenomena in present-day marine biodiversity research. Although Broch (1961) described the decapod diversity pattern in the Southern Ocean particularly in shallow waters, his statement was not strictly correct, since the first Antarctic caridean shrimp species (*Chorismus antarcticus*, *Notocrangon antarcticus*) had already been discovered by the Expe-

dition of the German Polar Commission to South Georgia in 1882–1883 (Pfeffer 1887).

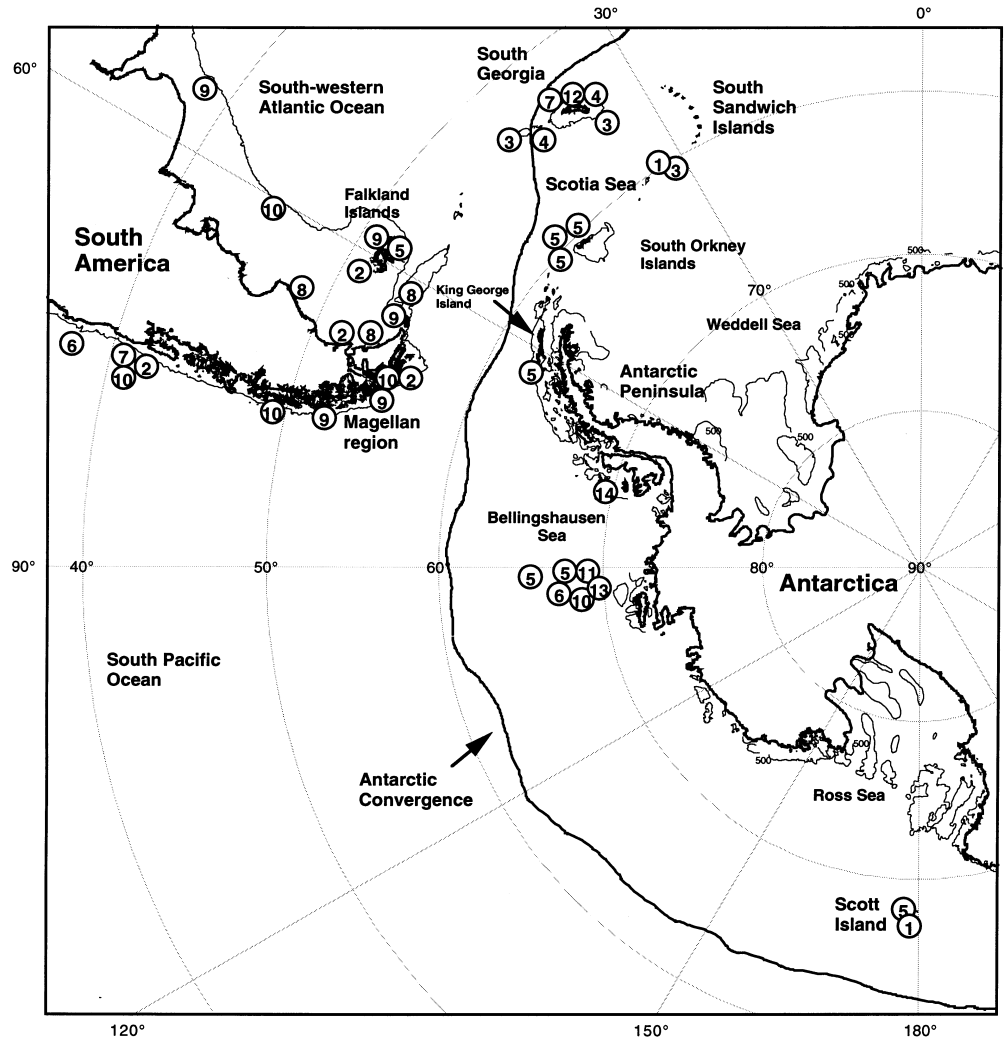
Since then, a few new species and records of decapods have been reported from the Southern Ocean (Yaldwyn 1965; Kirkwood 1984; Tiefenbacher 1990; Thatje 2003). However, known Antarctic decapod diversity remains poor, represented by approximately only a dozen benthic natant (caridean shrimp) species. Some of those species are known to occur in high abundances on the high-Antarctic Weddell Sea shelf (Arntz and Gorny 1991; Arntz et al. 1992; Gorny 1999).

Low temperature is the main physiological impact on life in polar areas, and results in low metabolic rates in polar ectotherms (Clarke 1983; Peck 2001). Low temperatures in general have been hypothesised to reduce decapod activity, especially in combination with high  $[Mg^{2+}]$  levels in the haemolymph, as  $[Mg^{2+}]$  has a relaxant effect (Frederich 1999; Frederich et al. 2001). Since Reptantia regulate  $[Mg^{2+}]_{HL}$  only slightly below the  $[Mg^{2+}]$  of seawater, their activity should be hampered. In contrast, Natantia are known to regulate  $[Mg^{2+}]_{HL}$  to very low levels (Tentori and Lockwood 1990; Frederich et al. 2001). The combined effect of low temperatures and high  $[Mg^{2+}]_{HL}$  might explain the limits of cold tolerance in decapods and might be the principal reason for the absence of reptant decapods from the high polar regions (Frederich et al. 2001).

At present only lithodids may tolerate environmental and physiological constraints imposed by the low temperatures and short periods of food availability at high-Antarctic latitudes (Clarke 1983), a pattern that appears to be very similar in the Arctic ( $>70^{\circ}N$ , Woll and Burmeister 2002; Zaklan 2002). This may be due to their prolonged brooding, as well as food independent and completely endotrophic and abbreviated larval development. These life-history features, among others, may allow lithodids to sustain the mismatch of prolonged developmental times at low temperatures and in short periods of food availability (see Clarke 1983; for review, see Anger et al. 2003, 2004; Kattner et al. 2003; Thatje et al. 2003a; Thatje 2004).

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**Fig. 1** Lithodid records from the Southern Ocean (southernmost America and Antarctic Peninsula; Antarctic without indication of ice shelves; 500-m isobath has been marked). Information obtained from the literature: Arana and Retamal (1999); Báez et al. (1986); Birstein and Vinogradov (1972); Boschi et al. (1992); Collins et al. (1992); Garcia-Raso et al. (2004); Gorny (1999); Klages et al. (1995); López and Balguerías (1994); Macpherson (1988a); Retamal (1981, 1992); Takeda and Hatanaka (1984); Zaklan (2002)



<i>Paralomis spectabilis</i>	①	<i>Lithodes confundens</i>	⑧
<i>P. granulosa</i>	②	<i>L. santolla</i>	⑨
<i>P. formosa</i>	③	<i>L. murrayi</i>	⑩
<i>P. spinosissima</i>	④	<i>L. turkayi</i>	⑪
<i>P. birsteini</i>	⑤	<i>L. sp. undet. 1</i>	⑫
<i>P. tuberipes</i>	⑥	<i>L. sp. undet. 2</i>	⑬
<i>Neolithodes diomedea</i>	⑦	<i>P. sp. undet. 1</i>	⑭

**Systematics**

Boas (1880) and Borradaile (1907) introduced a systematic division of the Decapoda into the suborders Reptantia and Natantia. Recently, Kästner (1993) divided the taxon into the suborders Dendrobranchiata (infraorder Penaeidae) and Pleocyemata (infraorders Stenopodidea, Caridea, Astacidea, Thalassinidea, Palinura, Anomura and Brachyura), thus dissolving the suborders Reptantia and Natantia. Kästner's classification (1993) considers the Natantia to be paraphyletic (Abele 1991; Scholtz and Richter 1995), but does not consider the Reptantia as a true monophyletic group (Scholtz and Richter 1995). As the systematics of the Decapoda are still unresolved (Abele 1991; Kästner 1993; Scholtz and Richter 1995), the present work refers

to the division into Reptantia and Natantia (Boas 1880; Borradaile 1907) to facilitate discussion of low reptant decapod diversity in high-Antarctic latitudes.

This review includes Antarctic (south of the Antarctic Convergence) and southernmost South American records of larval and adult reptant crabs (Fig. 1, Table 1), including also the local South American literature. It also includes a brief outline of the relevant fossil record of those regions.

**The fossil record in an Antarctic context**

Antarctic marine biodiversity is strongly influenced by the geological and glaciological history of the Antarctic continent. The origin of distinct benthic marine inver-

Table 1 Records of reptant crabs (adults and larvae) from Antarctic waters

Suborder	Family	Species	Antarctic record	Bathymetric distribution	Life-history stage	Remarks	Reference
Brachyura	Pinnotheridae	<i>Pinnotheres</i> sp.	King George Island (62°14.33'S, 58°43.81'W)		Larvae (early and advanced zoeae)	Superficial plankton samples (10–0 m)	Thatje and Fuentes (2003)
Palinura	Polychelidae	<i>Stereomastis submi</i>	Drake Passage (57°08.5'S, 55°06.0'W)		Larvae (Eryoneitic stage)	Plankton samples from 400 to 800 m	Tiefenbacher (1994)
Anomura	Hippidae	<i>Emerita</i> sp.	King George Island (62°14.33'S, 58°43.81'W)		Larvae (early zoeae)	Superficial plankton samples (10–0 m)	Thatje and Fuentes (2003)
Anomura	Lithodidae	<i>Lithodes murrayi</i>	Peter I Island, Bellingshausen Sea (68°52.0'S, 90°51.2'W; 68°51.4'S, 90°52.6'W)	183–257 m	Adult specimens, carapace length from 36 to 100 mm	4 males trawled, 5 specimens video observed; water temperature +1.8°C salinity 34.7	Klages et al. (1995)
Anomura	Lithodidae	<i>Lithodes turkayi</i>	Apparently at Peter I Island (compare Arana and Retamal 1999 with Klages et al. 1995)	622–1,696 m	Adult specimens	Associated with capture of <i>Paralomis birsteini</i>	Arana and Retamal (1999)
Anomura	Lithodidae	<i>Neolithodes domedeae</i>	Peter I Island, Bellingshausen Sea (68°42.1'S, 90°54.9'W)	1,129 m	1 adult specimen	Associated with capture of <i>Paralomis birsteini</i>	Arana and Retamal (1999)
Anomura	Lithodidae	<i>Paralomis birsteini</i>	Peter I Island, Bellingshausen Sea (68°42.1'S, 90°54.9'W), Gerlache sea mount (65°25.6'S, 90°38.96'W), Scotia Sea (59°24.39'S, 44°24.02'W) Antarctic Ocean off Ross Sea, Scott Island (67°29'S, 179°55'W)	660–1,876 m	A total of 88 adult specimens (77 males and 11 females of which 10 were ovigerous)	For further station data in the vicinity of indicated stations see Arana and Retamal (1999)	Arana and Retamal (1999)
Anomura	Lithodidae	<i>Paralomis birsteini</i>		500–1,080 m	Adult specimens, 1 female, 4 males, carapace length from 55 to 68 mm		Macpherson (1988b)
Anomura	Lithodidae	<i>Paralomis spectabilis</i>	Antarctic Ocean off Ross Sea, Scott Island (67°23'S, 179°53'W)	1,470–2,075 m	Adult specimens		Macpherson (1988a); Zaklan (2002)
Anomura	Lithodidae	<i>Paralomis spectabilis</i>	Scotia Sea (59°58.6'S, 32°24.6'W)	563–605 m	1 adult male		Birstein and Vinogradov (1972)
Anomura	Lithodidae	<i>Paralomis formosa</i>	Scotia Sea (59°53.1'S, 32°19.5'W; 59°58.6'S, 32°24.6'W)	523–671 m, 536–605, respectively	1 male, 2 males		Macpherson (1988a)
Anomura	Lithodidae	<i>Lithodes</i> sp.	Peter I Island, (68°83.5'S, 90°82.2'W; 68°70.2'S, 90°68.9'W)	218 m, 375 m	2 specimens, 1 female	From trap and Agassiz trawl	García-Raso et al. (2004)
Anomura	Lithodidae	<i>Paralomis</i> sp.	Bellingshausen Sea, 68°9.5.2'S, 78°23.3'W	1,408–1,947 m	1 male, 1 female	From Agassiz trawl	García-Raso et al. (2004)

tebrate faunas in both Antarctic and Subantarctic waters can be traced back as far as the Early Cretaceous, about 130 million years ago when the break-up of the Gondwana continent first became evident, and eastern Gondwana became isolated in the high southern latitudes (Lawver et al. 1992; Crame 1999). At the Late Cretaceous-Early Cenozoic boundary, the Austral Province showed temperate aspects in its marine invertebrate fauna, as evidenced by the rich decapod fossil record (Feldmann et al. 1997; Crame 1999). Antarctic cooling may have started as late as 35 million years ago as a result of ongoing continental drift and the establishment of the Antarctic Circum-polar Current (Barker et al. 1991), leading to an isolation of the Antarctic marine realm from surrounding seas (Clarke 1990). Faunal impoverishment and, particularly, the final extinction of reptants until approximately 15 million years ago, as evidenced by the fossil record, were not abrupt but gradual (Forster et al. 1987; Clarke and Crame 1989; Feldmann et al. 1997, 2003). In addition, an important hint of substantial lack of benthic predators as early as the Eocene is the undamaged and well-preserved asteroid and ophiuroid fossil record without indication of regenerated arms from Seymour Island (Blake and Zinsmeister 1988; Aronson and Blake 1997, 2001). Lack of physiological adaptations to low temperatures during the warm Cretaceous period when, for example, brachyuran crabs showed a high level of radiation (Schram 1982), may have contributed to extinction of reptant crabs during later Antarctic cooling (Clarke 1990; Frederich et al. 2001; Pörtner 2002). Ecological competition with better-adapted groups such as peracarid crustaceans, which flourished and radiated during this period, may have contributed to the disappearance of many decapod species, also (Crame 1999; De Broyer et al. 2003). Furthermore, glaciation events of the Antarctic continental shelf may have affected especially those reptant crab species with a limited bathymetric distribution range (Gorny 1999). Eurybathic species with a refuge in deeper waters, such as many recent caridean shrimps of the Southern Ocean, may have been able to re-colonise the shelf (Gorny 1999). This may explain why Antarctic invertebrates, in general, show a wider bathymetric distribution than species from other regions (Brey et al. 1996).

#### Reptant decapods in the Southern Ocean

Of about 115 decapod species known from the antipodal region of South America and around the Subantarctic islands, the reptant infraorders Brachyura and Anomura compose more than 20 and 40%, respectively (for review, see Gorny 1999). The debate regarding whether at least some reptant species are present in the Antarctic (Yaldwyn 1965; Dell 1972; Gorny 1999; Frederich et al. 2001; Thatje 2004, and references therein) resulted from Stebbing's (1914) record of the brachyuran crab *Halicarcinus planatus* from Macdougall

Bay, South Orkney Islands (Fig. 1). This material was probably collected during the Scottish National Antarctic Expedition in 1903, and Stebbing's record was based on museum material only. Yaldwyn (1965) was the first to doubt that the occurrence of *H. planatus* at the South Orkney Islands was possible. Although this species is very common in intertidal to shallow subtidal waters in the Magellan region, including the Falkland Islands, and the genus has a circum-polar Subantarctic distribution (Gorny 1999), it has never been found at South Georgia, which has been particularly well studied. Frederich (1999) supposed *H. planatus* to be a potential invader of the Antarctic, due to low  $[Mg^{2+}]$  contents in its haemolymph, which is atypical of crabs (Frederich et al. 2001). *H. planatus* has extended larval development through completely planktotrophic stages which, in combination with low starvation resistance, should select against this species in the Antarctic environment (compare Boschi et al. 1969; for discussion see Thatje et al. 2003a; Thatje 2004). This may also have impeded the occurrence of *H. planatus* at South Georgia, although a colonisation through larvae by means of currents should be, theoretically, possible. On the basis of our recent knowledge, we seriously doubt the record of *H. planatus* from the South Orkney Islands (Stebbing 1914), and suspect it may have been due to mislabelled museum material (see also Yaldwyn 1965).

Larvae of benthic reptants were first reported by Tiefenbacher (1994), who found five mesopelagic larvae of the palinurid *Stereomastis suhmi* (Bate, 1878) between 400 and 800 m sampling depth. Tiefenbacher supposed the occurrence of palinurid larvae suggested an adult population in the deep waters of the sampling area (Drake Passage, 57°08.5'S; 55°0.60'W), although this remains uncertain. However, larvae and adults of *S. suhmi* have been reported from elsewhere in the Magellanic region (Arntz et al. 1999; Thatje et al. 2003b) and at about 2,100 m depth on the continental slope south of the Beagle Channel (Arntz et al. 1999). These records suggest that adult *S. suhmi* may occur in the deep of the Drake Passage and even further south.

Recently, reptant larvae of the genus *Pinnotheres* (Brachyura) and the mole crab *Emerita* sp. (Anomura) have been recorded in Maxwell Bay (King George Island, 62°14'33S; 58°43'81 W) at the tip of the Antarctic Peninsula (Thatje and Fuentes 2003), representing the first records of reptant larvae south of the Polar Front. These records may have been due to the intrusion of Subantarctic water masses into the Antarctic regime, as evidenced by the accompanying Subantarctic copepods (genus *Acartia*), and do not necessarily imply adult populations in the Antarctic (for discussion see Thatje and Fuentes 2003).

#### Lithodid crabs in the Southern Ocean

Lithodid crabs are typical representatives of high latitudes and have a high diversity in Subantarctic waters

(Zaklan 2002). The first certain record of an adult reptant decapod from the high-Antarctic marine realm, a lithodid from the South Pacific side of the Antarctic, was published by Birstein and Vinogradov (1967). This first find of *Paralomis spectabilis* Hansen, off Scott Island (67°23'S; 179°53'E) occurred during the Russian expedition on board the oceanographic vessel "Ob" to the Southern Ocean in summer 1957–1958. Although Hale (1941) had found *Lithodes murrayi* Henderson, 1888 off Macquarie Island some years earlier, this was at a much lower latitude (58°28'S; 158°53'E). Later, three individual lithodids from the Southern Pacific (about 67°29'S; 179°55'W), at about 1,080 m water depth, were described as *P. birsteini* by Macpherson (1988b).

The various records of lithodid crabs from the Southern Ocean (Table 1) raised fishery expectations, as lithodids were known as a fishery resource around the Subantarctic island of South Georgia (Collins et al. 2002; Otto and Macintosh 1996; Thatje 2004; Fig. 1). However, until recently, ecologists regarded the scant records as exceptional, and not indicative of exploitable populations. The catch of 88 specimens of *P. birsteini* along the Antarctic Peninsula to the Bellingshausen Sea (Fig. 1; Arana and Retamal 1999), and the records of *L. murrayi* off Peter I Island (180–260 m water depth, Klages et al. 1995) clearly demonstrate the existence of lithodid anomuran populations in the Antarctic. The potential value of these populations as fishery resources is considered to be low due to delayed first maturity and slow growth, in comparison with shrimp populations in the Antarctic (Arntz et al. 1992). A curious find is the low proportion of females within the catches (although based on relatively few specimens); 11 out of 88 specimens *P. birsteini* (Arana and Retamal 1999). Over 90% of these were ovigerous ( $N=10$ ), indicating a reproductively active population existed in Antarctic waters, rather than a group of adult lithodids that had migrated south and were not able to reproduce (and moult) successfully. Nevertheless, there is still a lack of records of smaller juveniles and/or larvae from Antarctic waters.

The taxonomic status of *P. birsteini* in the work by Arana and Retamal (1999) remains uncertain, since both authors confused this species with *P. anamerae* in their Table 1 (Arana and Retamal 1999). However, M.A. Retamal (personal communication) confirmed the species identification as *P. birsteini*. *L. turkayi* was also found associated with captures of *P. birsteini* in the Bellingshausen Sea (apparently at Peter I Island), but exact station data for this species are lacking (Arana and Retamal 1999). The lithodid record by Klages et al. (1995) suggested their occurrence was related to temperatures above 0°C at the seafloor (+1.8°C in their study), and this might explain the absence of records of lithodid anomurans from the colder Weddell and Lazarev Sea shelves, where temperatures are usually below 0°C (see Seabrooke et al. 1971; Arntz et al. 1992; see also Anger et al. 2003, 2004).

## Conclusions

Lithodid anomurans are the only reptant decapods presently known to include adult populations in the Antarctic. These crabs have not been recorded from the high-Antarctic continental shelf (Weddell and Ross Seas), and this may be related to the permanent low temperatures on those shelves.

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