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ORIGINAL PAPER

Description of two new genera, *Santelmoa* and *Bentartia* and two new species of Zoarcidae (Teleostei, Perciformes) from the Southern Ocean

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Abstract Two new genera of lycodine zoarcid fish, *Santelmoa* and *Bentartia*, and two new species, *Santelmoa carmenae* and *Bentartia cinerea*, are described from 13 specimens collected from the Gerlache Strait, Southern Ocean, at 1,056-m depth. *Santelmoa* can be distinguished from all other lycodine genera by the combination of the following characters: anterior portion of frontals fused; scapular foramen open; ceratohyal–epihyal articulation interdigitating; cranium narrowed; supratemporal commissure and occipital pores absent; intercalar reaching the prootic; parasphenoid wing well developed; palatal arch well developed; posterior hyomandibular ramus short; post-temporal ventral ramus well developed; six branchiostegal rays; vertebrae asymmetrical; pelvic fin rays ensheathed; scales, lateral line, pyloric caeca, palatine and vomerine teeth present. *Bentartia* differs from the remaining lycodine genera by the following combination of characters: basioccipital and exoccipitals fused; supraoccipital–exoccipital articulation broadly contacting; ceratohyal–epihyal articulation interdigitating; post-temporal ventral ramus weak; two posterior nasal pores; cranium narrowed; supratemporal commissure and occipital pores absent; intercalar set posteriorly; palatal arch well developed; posterior hyomandibular ramus not elongate; parasphenoid wing high; six branchiostegal rays; vertebrae asymmetrical; pelvic fin rays ensheathed; scales, lateral line, pyloric caeca, palatine and vomerine teeth present. The relationships of the two new genera are discussed.

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Introduction

The eelpouts (family Zoarcidae) inhabit primarily the outer shelves to upper slopes of the North Atlantic and North Pacific, but there have been significant radiations into the Arctic, southern South America and Antarctica and a few genera have abyssal benthic species (Anderson and Fedorov 2004). The family includes more than 240 species belonging to 51 genera (Anderson and Fedorov 2004; Shinohara et al. 2004; Shinohara and Sakurai 2006; Matallanas 2008; Mincarone and Anderson 2008; Matallanas 2009b).

The fish faunas of the Bellingshausen Sea, Peter I Island and West Antarctic Peninsula (Gerlache Strait mainly), a very poorly known area, were studied as part of the Spanish Bentart Research Programmes. During the Bentart-03 Expedition, carried out on board the RV *Hespérides* from 24 January to 3 March 2003, many zoarcids were captured with baited traps, mainly from the Bellingshausen Sea where they predominate both in number and biomass in waters deeper than 550 m (Matallanas and Olaso 2007).

According to recent revisions and descriptions (Eastman 2005; Moeller and Stewart 2006; Anderson 2006; Matallanas 2008, 2009a, 2009b), Zoarcidae is one of the most speciose benthic fish families in Antarctic waters, containing 30 species in 12 genera. Four genera (*Lycodichthys*, *Seleniolycus*, *Gosztonyia* and *Bellingshausenia*) and 26 species are endemic to the Antarctic region (Anderson 1990, 1991, 2006; Anderson and Gosztonyi 1991; Moeller and Stewart 2006; Matallanas 2008, 2009a, 2009b).

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The study by Anderson (1994), reconstructing the phylogeny of zoarcids and establishing their generic limits, remains the keystone work on the systematics of this family, since it provides a firm basis for pursuing further research. In the present report, two new genera (*Santelmoa* and *Bentartia*), as well as two new species (*Santelmoa carmenae* and *Bentartia cinerea*), are described.

Materials and methods

All type specimens were collected in the Gerlache Strait during the Spanish expedition Bentart 03 on the R/V *Hespérides*, from 30 January to 20 February 2003 (Matallanas and Olaso 2007) and deposited at the UAB fish collection (Zoología, Universidad Autónoma de Barcelona).

Counts, measurements and general terminology follow Gosztonyi (1977, 1988) and Anderson (1982). Pore terminology follows Gosztonyi (1977) and Anderson (1982). Measurements were made with ocular micrometer or dial calipers to the nearest 0.1 mm. Specimens were X-rayed to record both shape and meristics of axial skeleton and vertical fins. Osteological observations were made on stained specimens. The definitions of the character states in this paper follow those of Anderson (1994).

The phylogenetical position of the two new genera were analysed cladistically by PAUP* version 4.0 (Swofford 2002), based on 44 transformation series (TS; Anderson 1994), all of which are informative for the intergeneric relationships in the subfamily (Table 3).

Comparative material examined

Gosztonyia antarctica (holotype: UAB:B03BSZ2, 285 mm SL, Bellingshausen Sea, 69°49′S, 77°44′W, 615 m, 14 February 2003; paratypes: UAB:B03BSZ3, 291 mm SL, UAB:B03BSZ4, 300 mm SL and UAB:B03BSZ2B, used for anatomical analysis, captured with the holotype; UAB:B03GSZ1, 242 mm SL, Gerlache Strait, 64°32′S, 61°97′W, 1,056 m, 26 February 2003). *Bellingshausenia olasoi* (Holotype: UAB:B03BSZ14, 254 mm SL, Bellingshausen Sea, 69°49′S, 77°49′W, 602 m, 15 February 2003; Paratypes: UAB:B03BSZ22, 297 mm SL and UAB:B03BSZ14B, used for anatomical analysis, collected with the holotype; UAB:B03BSZ40, 286 mm SL and UAB:B03BSZ41, 280 mm SL, Bellingshausen Sea, 69°49′S, 77°44′W, 615 m, 14 February 2003).

Results

Santelmoa gen. nov

Type species *Santelmoa carmenae* sp. nov

Etymology

The genus is named after the Spanish ship San Telmo lost in the "Terra Australis Incognita" (in Cape Shirreff, Livingston Island, according to Pinochet de la Barra 1993) on 2–4 September 1819, in honour of the 644 Spanish shipwrecked. If somebody survived, they would be the first men in history to walk on Antarctic land. Gender is feminine.

Diagnosis

Santelmoa is a lycodine zoarcid, as defined by Anderson (1994), with the following combination of characters: anterior portion of frontals fused with no trace of a suture; scapular foramen open; ceratohyal–epihyal articulation interdigitating; cranium narrowed; supratemporal commissure and occipital pores absent; intercalar reaching the prootic; parasphenoid wing well developed; palatal arch well developed; posterior hyomandibular ramus short; post-temporal ventral ramus well developed; branchiostegal rays six; vertebrae asymmetrical; pelvic fin rays ensheathed; scales, lateral line, pyloric caeca, palatine and vomerine teeth present.

Santelmoa carmenae sp. nov.
(Figs. 1–4).

Material examined

Holotype

UAB:B03GSZ51, 264 mm SL, Gerlache Strait, Station 24°N, 64°32′58″S 61°97′38″W, 1,056 m depth, baited traps, 26 February 2003.

Paratypes

UAB:B03GSZ33, 234 mm SL; UAB:B03GSZ42, 277 mm SL; UAB:B03GSZ52, 247 mm SL; UAB:B03GSZ59, 238 mm SL, UAB:B03GSZ60, 241 mm SL and UAB:B03GSZ344, 246 mm SL. UAB:B03GSZ43, 260 mm SL and UAB:B03GSZ44, 242 mm SL (used for anatomical analysis: cranium, palatal series, hyoid arch, branchiostegals and pectoral girdle) and UAB:B03GSZ34, 248 mm SL (used for anatomical analysis: suspensorium and pectoral girdle). All specimens captured with the holotype.

Diagnosis, as for the genus

Counts and proportional measurements are presented in Table 1. Body, laterally compressed; tail, relatively short and laterally compressed, especially posteriorly. Head, slightly depressed in males and ovoid in females; mouth, subterminal; end of maxilla extending to the posterior

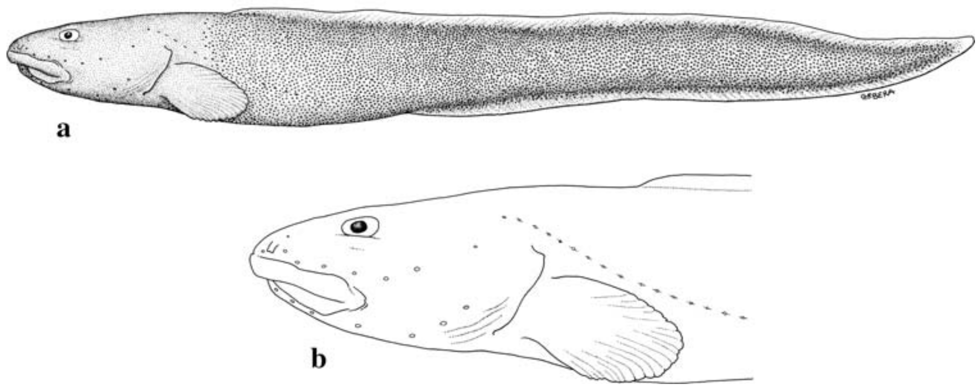

Fig. 1 *Santelmoa carmenae* gen. et sp. nov., UAB:B03GSZ51 (holotype), 264 mm SL male, from Gerlache Strait. **a** Left lateral view, **b** left lateral view of head showing pore pattern

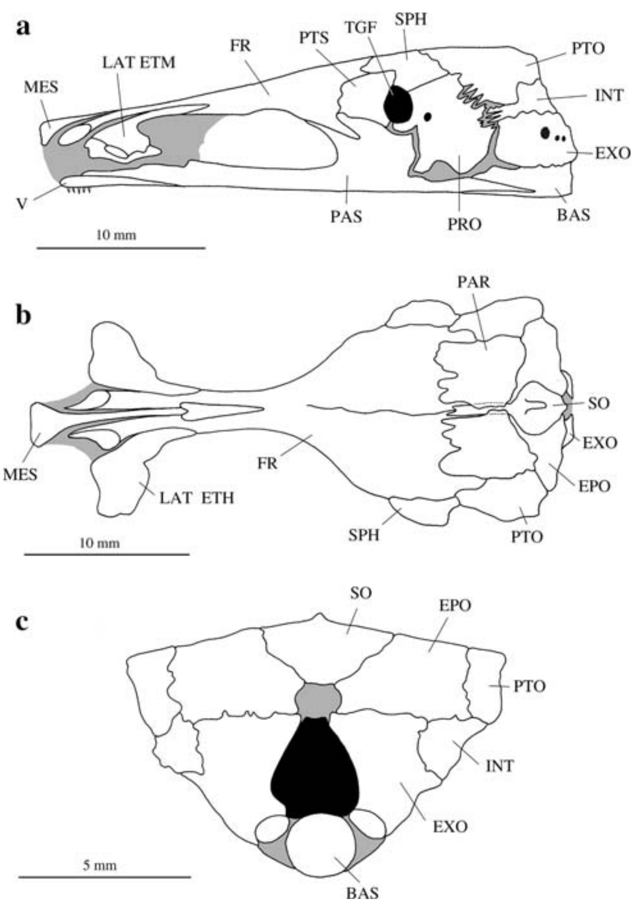

Fig. 2 Cranium of *Santelmoa carmenae* gen. et sp. nov. *Lateral view* (**a**), *dorsal view* (**b**) and *posterior view* (**c**). *BAS* basioccipital, *EPO* epioccipital, *EXO* exoccipital, *FR* frontal, *INT* intercalar, *LAT ETM* lateral ethmoid, *MES* mesethmoid, *PAR* parietal, *PAS* parasphenoid, *PRO* prootic, *PTO* pterotic, *PTS* pterosphenoid, *SO* supraoccipital, *SPH* sphenotic, *TGF* trigeminofacialis foramen, *V* vomer

margin of eye in males and to middle of pupil in females. Lower lip with a small posterior lobe; small prickles on lips and snout. Nasal tube short, pigmented and not reaching the upper lip. Gill slit extending ventrally to just the ventral edge of the pectoral fin base. Opercular lobe, small (Fig. 1a, b).

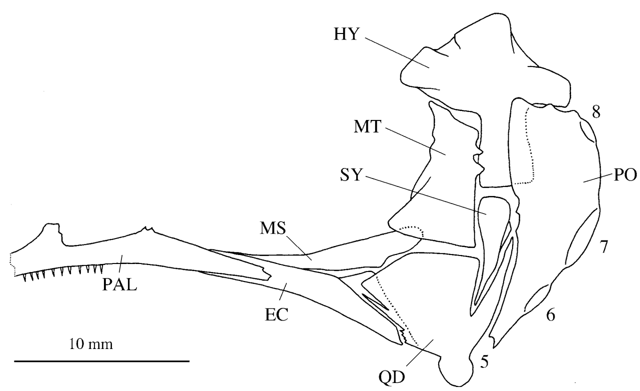

Fig. 3 Left suspensorium and preopercle (PO) of *Santelmoa carmenae* gen. et sp. nov. *EC* ectopterygoid, *HY* hyomandibula, *MS* mesopterygoid, *MT* metapterygoid, *PAL* palatine, *QD* quadrate, *SY* symplectic, *6*, *7* and *8* preopercular pores

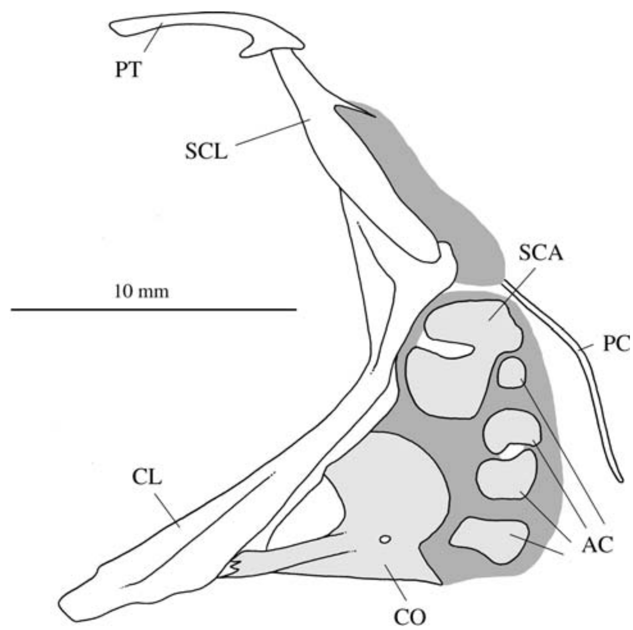

Fig. 4 Left lateral view of pectoral girdle of *Santelmoa carmenae* gen. et sp. nov. *AC* actinosts, *CL* cleithrum, *CO* coracoid, *PC* postcleithrum, *PT* post-temporal, *SCA* scapula, *SCL* supracleithrum

Table 1 Counts and Measurements of *Santelmoa carmenae* gen. et sp. nov

SL (mm)	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB-B03GSZ51	UAB-B03GSZ33	UAB-B03GSZ42	UAB-B03GSZ52	UAB-B03GSZ59	UAB-B03GSZ60	UAB-B03GSZ344	
	264	234	277	247	238	241	246	234–277
Sex	Male	Female	Male	Male	Female	Female	Female	
Meristic characters								
Dorsal fin rays	92	93	94	93	94	95	91	91–95
Anal fin rays	75	78	78	78	79	79	77	75–79
Caudal fin rays	10	10	10	11	10	10	10	10–11
Pectoral fin rays	16	16	16	16	16	16	16	16
Precaudal vertebrae	24	25	24	25	24	25	25	24–25
Caudal vertebrae	75	76	77	76	78	79	75	75–79
Total vertebrae	99	101	101	101	102	104	100	99–104
1st D fin pterygiophore with Vert.	6	7	7	7	6	7	8	6–8
Gill rakers	3 + 11	2 + 12	3 + 11	3 + 11	3 + 10	3 + 11	3 + 12	2–3 + 10–12
Pseudobranchiae	5	4	4	3	3	3	4	3–5
Morphometric characters (% SL)								
Head length	17.5	15.0	18.5	15.4	13.9	15.1	15.6	13.9–18.5
Head width	9.6	7.6	10.6	9.1	7.7	8.2	8.3	7.7–10.6
Head height	8.5	8.3	8.9	8.6	8.2	8.2	8.8	8.2–8.9
Snout length	5.3	3.7	5.6	3.9	3.6	3.7	3.5	3.5–5.6
Nostril tube length	0.6	0.8	0.6	0.6	0.6	0.8	0.8	0.6–0.8
Eye diameter	2.5	2.8	2.8	2.3	2.5	2.5	2.7	2.3–2.8
Interorbital width (hard)	1.2	1.2	1.1	1.2	1.0	1.0	1.1	1.0–1.2
Upper jaw length	9.5	6.1	9.8	6.9	5.6	5.5	5.9	5.5–9.8
Lower jaw length	10.2	7.2	10.5	8.4	6.9	6.8	7.4	6.8–10.5
Predorsal length	23.1	21.3	23.4	23.1	17.6	19.1	22.3	17.6–23.4
Preanal length	41.6	40.1	40.4	40.5	40.3	40.2	41.4	40.1–41.6
Tail length	58.3	59.8	59.5	59.5	59.6	59.7	58.5	58.3–59.8
D fin height above A fin origin	2.4	2.5	2.5	2.4	2.5	2.4	2.4	2.4-2.5
Body height at A fin origin	8.7	8.8	9.2	8.2	9.7	9.4	9.6	8.2–9.7
Pectoral fin length	8.5	9.1	7.2	7.4	8.6	8.2	8.3	7.2–9.1
Pectoral fin base height	3.9	4.0	3.9	4.1	4.2	4.3	4.2	3.9–4.2

Table 1 continued

SL (mm)	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB-B03GSZ51	UAB-B03GSZ33	UAB-B03GSZ42	UAB-B03GSZ52	UAB-B03GSZ59	UAB-B03GSZ60	UAB-B03GSZ344	
	264	234	277	247	238	241	246	234–277
Sex	Male	Female	Male	Male	Female	Female	Female	
P fin base/P fin length ratio	45.7	44.1	51.4	55.2	48.5	53.0	50.9	44.1–55.2
Pelvic fin length	0.9	1.1	0.7	0.9	1.2	0.8	1.0	0.7–1.2
Caudal fin length	2.6	2.9	2.1	2.4	2.5	2.5	2.8	2.1–2.9
Gill slit length	5.2	5.3	5.8	5.6	5.2	5.6	5.9	5.2–5.9
Opercular lobe length	0.7	0.6	0.9	0.7	0.6	0.7	0.6	0.6–0.9
Isthmus width	4.4	4.6	5.0	5.5	5.4	4.9	4.4	4.4–5.5
Morphometric characters (% HL)								
Head width	54.7	50.7	57.4	59.2	55.6	54.4	55.1	50.7–59.2
Head height	48.7	55.5	48.0	55.7	59.5	54.6	58.6	48.0–59.5
Upper jaw length	54.5	40.5	52.9	45.2	40.4	36.8	39.7	36.8–54.5
Pectoral fin length	48.7	60.3	40.8	48.1	62.2	54.4	52.9	40.8–62.2
Snout length	30.3	24.6	30.5	25.2	26.2	24.7	23.5	23.5–30.5
Eye diameter	14.5	18.6	15.3	15.2	18.4	16.4	18.1	14.5–18.6
Interorbital (hard)	7.3	7.9	6.2	8.1	7.2	6.8	7.5	6.2–8.1
Pelvic fin length	5.2	7.6	4.1	6.3	8.7	5.4	6.2	4.1–8.7

Teeth on jaws, vomer and palate conical. Premaxilla with two or three rows anteriorly and single row posteriorly. Dentary with three or four irregular rows anteriorly and single row posteriorly. Vomerine teeth 15 in the holotype, 8–16 in the paratypes. Palatine with two irregular rows anteriorly and single row posteriorly; palatine teeth (left/right) 16/13 in the holotype, 10–17/12–18 in the paratypes. Oral valve overlapping anterior margin of vomer and well separated from the palate laterally. Pyloric caeca, two small nubs. Gill rakers 2–3 + 10–12, stout and forked with 2–4 cusps except the lowermost, which is triangular. Pseudobranch filaments 3–5, elongated.

Cephalic lateralis pore system with pores moderately large excepting the posterior nasal, the eighth preoperculomandibular and the first postorbital, when present. Two nasal pores, one located anteromesial to nasal tube and the other posterior to it. Postorbital pore 4 present in all specimens; postorbital pore 1 present in both sides of paratype UAB:B03GSZ344 and on the left side of paratypes UAB:B03GSZ59 and UAB:B03GSZ60, absent in the other specimens. Suborbital pores 6 + 0 in all; preoperculomandibular pores 8 in all. Interorbital pore absent (Fig. 1b). Supratemporal commissure and occipital pores absent. Suborbital bones in a reversed L-shaped pattern. Lateral line configuration with three branches (Fig. 1a). Ventral branch beginning just behind the fourth postorbital pore and coursing just above the anal fin to the end of the tail; mediolateral branch, with more scattered neuromasts, originating before the anal fin origin, extending to the end of tail; dorsolateral branch beginning behind the anal fin origin and coursing well below the dorsal fin to the tail tip. Flesh and skin firm; scales extend completely across the body to vertical through the mid-pectoral fin, on the ventral surface of the abdomen, between the ventral fins and on the vertical fins to about two-thirds their length; pectoral fin base and axil with scattered scales in some specimens; caudal fin naked.

Neurocranium narrowed (Fig. 2a, b). Parasphenoid wing forked, reaching mid-height of the trigeminofacialis foramen and broadly articulated with the pterosphenoid; frontal and parasphenoid not separated by pterosphenoid. Prootic and pterotic juncture strongly interdigitating. Intercalar longitudinally elongated, excluding exoccipital and pterotic articulation, and articulated with the prootic with interdigitated suture. Frontal ramus long with an anterior foramen in the interorbital space; anterior portion of frontals fused with no trace of a suture, posterior portion separate showing a complete suture; frontal descending wing as a prong; frontal corner squared; sphenotic and parietal separated by frontal. Parietals enlarged and nearly meeting in the cranial midline posteriorly (Fig. 2b). Supraoccipital small, with a slender anterior blade partially overlapped by parietals, and with a well-developed median crest posteriorly; supraoccipital excluded from exoccipital by epiotic (Fig. 2c); no supratemporal commissure across parietals. Ethmoid cartilage protruding well into the orbital fenestra.

Palatopterygoid series well developed, with mesopterygoid and ectopterygoid overlapping more than half the dorsal and anterior surface of quadrate (Fig. 3). Anterior surface of quadrate serrated. Metapterygoid large. Posterior ramus of hyomandibula short. Symplectic with a posterior strut. Hyoid bar with ceratohyal–epihyal joint strongly serrated along the whole length. Six branchiostegal rays.

Pectoral girdle (Fig. 4) with a strong post-temporal bearing a well-developed ventral ramus. Supracleithrum with small posteriorly directed prong and an ovoid cartilaginous lamina. Scapular foramen open anteriorly; prominent postero-dorsal scapular strut. Coracoid with a well-developed posterior strut and a small foramen. Actinosts 4, the uppermost smaller, with a foramen in the cartilaginous basal plate between the two centrals. Postcleithrum present. Pelvic fin rays joined, ensheathed by the dermis.

Vertebrae asymmetrical, 24–25 + 75–79 = 99–104. Last precaudal vertebra associated with dorsal fin rays 18–20. Dorsal fin origin associated with vertebrae 6–8, with no free pterygiophores. Terminal dorsal fin ray associated with second or third preural vertebra. Two anal fin pterygiophores, with two anal fin rays inserted anterior to the haemal spine of the first caudal vertebra. Terminal anal fin ray associated with second preural vertebra. One epural. First preural centrum, ural centrum, parhypural and hypurals fused into one element. Caudal fin rays 10–11, with two epural, four upper hypural and four or five lower hypural rays.

Colour in alcohol. Tail and dorso-lateral part of body, mid-brown uniform; abdomen, dark grey; cheek and branchiostegal membrane, blackish; fins, ash coloured; lips and posterior margin of gill cover, light; oral cavity greyish, peritoneum black.

Etymology

The specific name, *carmenae*, is after Carmen Benito (manageress, Servei de Radiosòtops, Facultat de Biologia, Universitat de Barcelona, Spain) for helping me with the X-rays of the Antarctic zoarcids.

Bentartia gen. nov

Type species *Bentartia cinerea* sp. nov.

Etymology

The genus is named after BENTART, the Antarctic Spanish expeditions during which the material was collected. Gender is feminine.

Diagnosis

Bentartia is a lycodine zoarcid, as defined by Anderson (1994), with the following characters: basioccipital and exoccipitals fused; supraoccipital–exoccipital articulation broadly contacting; ceratohyal–epihyal articulation interdigitating; post-temporal ventral ramus short; posterior nasal pores two; cranium narrowed; supratemporal commissure and occipital pores absent; intercalar set posteriorly; palatal arch well developed; posterior hyomandibular ramus not elongate; parasphenoid wing high; branchiostegal rays six; vertebrae asymmetrical; pelvic fin rays ensheathed; scales, lateral line, pyloric caeca, palatine and vomerine teeth present.

Bentartia cinerea sp. nov
(Figs. 5–8).

Material examined

Holotype

UAB:B03GSZ11, 324 mm SL, Gerlache Strait, Station 24°N, 64°32′58″S, 61°97′38″W, 1,056 m depth, baited traps, 26 February 2003.

Paratypes

UAB:B03GSZ30, 325 mm SL; UAB:B03GSZ47, 332 mm SL (used for anatomical analysis: cranium, palatal series, hyoid arch, branchiostegals and pectoral girdle), captured with the holotype.

Diagnosis, as for the genus

Description

Counts and proportional measurements presented in Table 2. Body ovoid in cross section; tail elongate and laterally compressed. Head globular, interorbital space weakly concave; mouth slightly oblique, subterminal, end of maxilla extending to the posterior margin of the eye. Small prickles on lips and snout. Eye round, small and entering the dorsal profile of head. Nasal tube unpigmented, reaching the upper lip when depressed forward. Gill slit extending ventrally to just the lower edge of the pectoral fin base. Opercular lobe relatively well developed (Fig. 5a, b).

All teeth conical. Teeth on premaxilla arranged in two or three rows near symphysis and single row laterally and posteriorly; teeth of outer row longer. Teeth on dentary in three or four rows near symphysis and single row posteriorly. Vomerine teeth eight in the holotype and six in the paratypes. Palatine teeth strong, in two irregular rows anteriorly and single row posteriorly; palatine teeth (left/right) 9/12 in the holotype, 9/9 in the paratypes. Oral valve well developed, papillose, its posterior end reaching the head of vomer and well separated from the palate laterally. Two nub-like pyloric caeca. Gill rakers 3 + 10, forked with 3–5 cusps, except the lowermost, which is triangular. Pseudobranch filaments four, elongated.

Cephalic lateralis pore system with pores moderate in size. Nasal pores three, one located anteromesial to the nasal tube, two others posterodorsal to the nasal tube and the posterior one smaller. Postorbital pores 1 and 4 present in all. Suborbital pores 6 + 0 arranged in reversed L-shaped pattern; preoperculomandibular pores 8. Interorbital pore absent (Fig. 5b). Supratemporal commissure and occipital pores absent. Lateral line configuration with two branches (Fig. 5a). Ventral branch, with neuromasts closely set, beginning just behind the fourth postorbital pore and coursing just above the anal fin to the end of the tail; mediolateral branch, with more scattered neuromasts, originating between pectoral fin tip and anal fin origin, coursing at mid-body to the tail tip. Flesh and skin firm; head and anterior body naked; posterior half covered by scales in a wedge-shaped pattern. Vertical fins naked anteriorly, scaled posteriorly to about half its length; caudal fin naked.

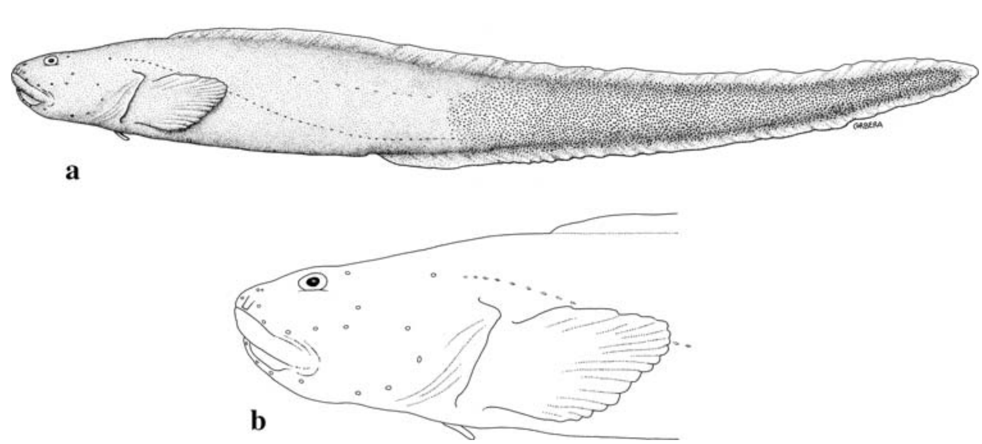

Fig. 5 *Bentartia cinerea* gen. et sp. nov., UAB:B03GSZ11 (holotype), 324 SL male, from Gerlache Strait. **a** left lateral view, **b** left lateral view of head showing pore pattern

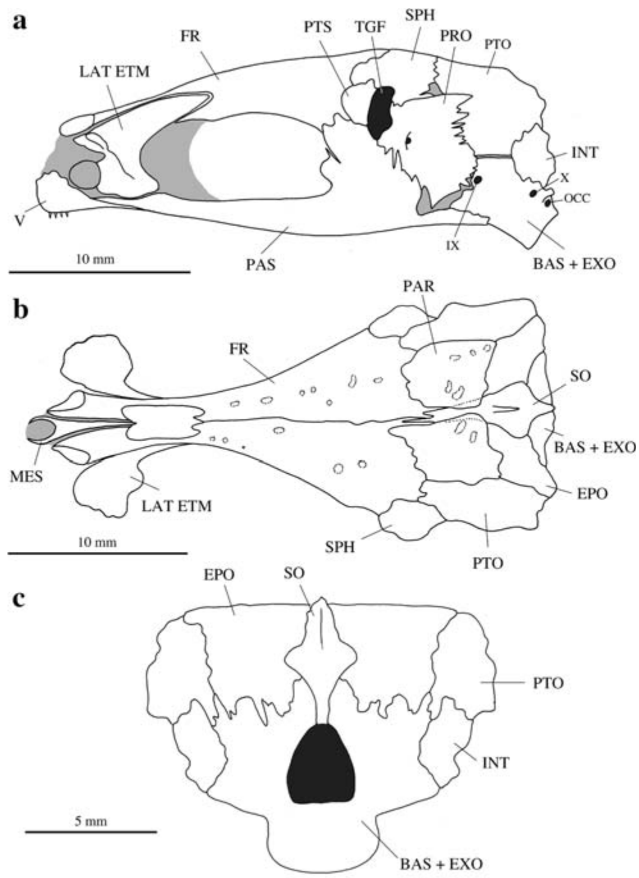

Fig. 6 Cranium of *Bentartia cinerea* gen. et sp. nov. *Lateral view* (**a**), *dorsal view* (**b**) and *posterior view* (**c**). *BAS + EXO* basioccipital and exoccipital fused, *EPO* epioccipital, *FR* frontal, *INT* intercalar, *LAT ETM* lateral ethmoid, *MES* mesethmoid, *PAR* parietal, *PAS* parasphenoid, *PRO* prootic, *PTO* pterotic, *PTS* pterosphenoid, *SO* supraoccipital, *SPH* sphenotic, *TGF* trigeminofacialis foramen, *V* vomer, *IX* glossopharyngeal foramen, *X* vagus foramen, *OCC* occipitospinal foramen

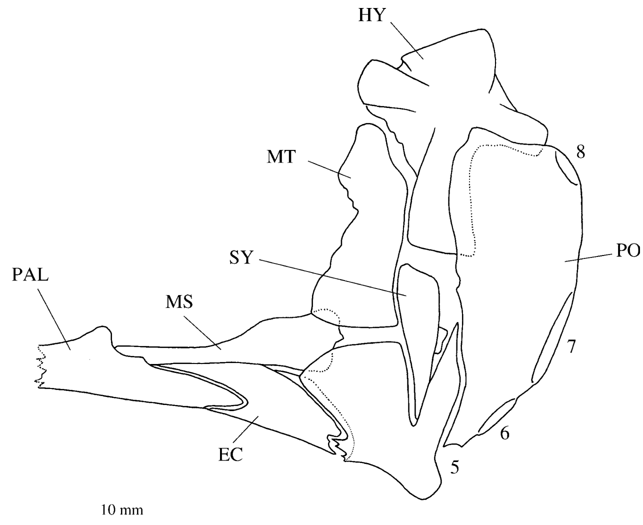

Fig. 7 Left suspensorium and preopercle (PO) of *Bentartia cinerea* gen. et sp. nov. *EC* ectopterygoid, *HY* hyomandibula, *MS* mesopterygoid, *MT* metapterygoid, *PAL* palatine, *QD* quadrate, *SY* symplectic, *6*, *7* and *8* preopercular pores

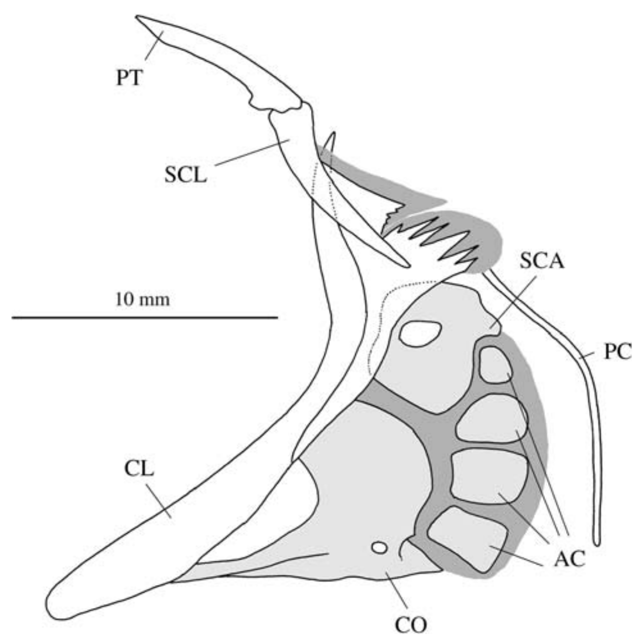

Fig. 8 Left lateral view of pectoral girdle of *Bentartia cinerea* gen. et sp. nov. *AC* actinosts, *CL* cleithrum, *CO* coracoid, *PC* postcleithrum, *PT* post-temporal, *SCA* scapula, *SCL* supracleithrum

Neurocranium narrowed and cavernous, laterally ovoid (Fig. 6a, b). Basioccipital and exoccipitals fused, with no trace of a suture and join the prootic through an interdigitating suture. Three foramina present in the exoccipital portion of this bone: glossopharyngeal foramen (IX), vagus foramen (X) and, in a thickened notch, occipitospinal foramen. Parasphenoid wing reaching mid-height of the trigeminofacialis foramen and articulating with the pterosphenoid; parasphenoid and prootic juncture interdigitating. Frontal and parasphenoid not separated by pterosphenoid. Prootic and pterotic juncture strongly interdigitating. Intercalar well developed, set posteriorly. Frontal ramus long with an anterior foramen in the interorbital space; frontal bones separate, with a complete suture; frontal corner squared; sphenotic and parietal separated by frontal and pterotic. Parietals enlarged and closely set in cranial midline. Supraoccipital small, with a slender anterior blade partially covered by the parietals and a well-developed median crest; supraoccipital and exoccipital part of the basioccipital–exoccipital broadly articulating posteriorly (Fig. 6c); no supratemporal commissure across parietals. Ethmoid cartilage extensive, protruding well into the orbital fenestra.

Palatopterygoid series well developed, with mesopterygoid and ectopterygoid overlapping more than half the dorsal and the anterior surface of quadrate; anterior surface of quadrate serrated (Fig. 7). Metapterygoid, large. Posterior ramus of hyomandibula about the same length as the anterior

Table 2 Counts and Measurements of *Bentartia cinerea* gen. et sp. nov

	Holotype	Paratype
	UAB-B03GSZ11	UAB-B03GSZ30
SL (mm)	324	325
Sex	Male	Female
Meristic characters		
Dorsal fin rays	114	113
Anal fin rays	96	92
Caudal fin rays	9	11
Pectoral fin rays	17	16
Precaudal vertebrae	27	29
Caudal vertebrae	94	89
Total vertebrae	121	118
1st D fin pterygiophore with Vert.	5	6
Gill rakers	3 + 10	3 + 10
Pseudobranchiae	4	Damaged
Morphometric characters (% SL)		
Head length	13.3	12.1
Head width	8.7	6.7
Head height	7.4	6.6
Snout length	3.0	2.7
Nostril tube length	0.7	0.9
Eye diameter	1.6	1.9
Interorbital width (hard)	1.0	0.9
Upper jaw length	6.3	4.6
Lower jaw length	7.2	5.5
Predorsal length	16.9	16.0
Preanal length	34.8	37.5
Tail length	65.1	62.4
D fin height above A fin origin	2.4	2.4
Body height at A fin origin	8.7	8.7
Pectoral fin length	7.9	8.0
Pectoral fin base height	4.0	3.4
P fin base/P fin length ratio	50.9	42.3
Pelvic fin length	1.2	1.3
Caudal fin length	2.4	3.0
Gill slit length	5.1	4.4
Opercular lobe length	1.1	0.8
Isthmus width	5.6	4.7
Morphometric characters (% HL)		
Head width	65.8	55.3
Head height	55.4	54.8
Upper jaw length	47.5	38.5
Pectoral fin length	59.6	66.0
Snout length	22.7	22.8
Eye diameter	12.5	16.2
Interorbital (hard)	8.1	8.1
Pelvic fin length	9.5	10.6

ramus. Symplectic with a posterior strut. Hyoid bar with ceratohyal–epihyal joint strongly serrated along whole length. Six branchiostegal rays.

Post-temporal ventral ramus weak (Fig. 8). Supracleithrum with a posterior triangular prong surrounded by a cartilaginous lamina. Cleithrum with a posteriorly directed lamina with several prongs and an oval cartilaginous lamina. Scapular foramen enclosed by bone; prominent postero-dorsal scapular strut. Coracoid with a well-developed posterior strut and a small foramen. Actinosts 4, the uppermost smaller. Postcleithrum present.

Vertebrae 27–29 + 89–94 = 118–121. Precaudal vertebrae asymmetrical; caudal vertebrae and posteriormost precaudal symmetrical. Last precaudal vertebra associated with dorsal fin rays 24–25. Dorsal fin origin associated with vertebrae 5–6, with no free pterygiophores. Terminal dorsal fin ray associated with second preural vertebrae. Four anal fin pterygiophores anterior to haemal spine of first caudal vertebrae. Terminal anal fin ray associated with second preural vertebra; one epural. First preural centrum, ural centrum, parhypural and hypurals fused into one element. Second preural centrum formed by two vertebrae fused, with two complete neural arches pierced by one lateral foramen. Caudal fin rays 9–11, with two epural, three or four upper hypural and four lower hypural rays. Pelvic fin rays joined, ensheathed.

Colour in alcohol. Head and body, uniform ash colour. Oral cavity, light; peritoneum, black.

Etymology

The specific name *cinerea* is derived from the Latin word *cinereus* (ash-coloured) in reference to its body colour.

Discussion

Santelmoa and *Bentartia* are included in the subfamily Lycodinae (*sensu* Anderson 1994; Anderson and Fedorov 2004) by the suborbital bone chain in a reversed L-shaped pattern and the loss of the interorbital pore.

Santelmoa can be distinguished from all lycodine genera mainly by the following combination of derived characters: frontals fused anteriorly, scapular foramen open, cranium narrowed and ceratohyal–epihyal articulation interdigitating.

The complete fusion of frontal bones is an autapomorphic state found only in *Notolycodes* (Anderson and Gosztonyi 1991; Anderson 1994). The frontal bones are fused anteriorly with no trace of a suture in *Santelmoa*. A similar fusion can be found in only two genera, the lycodine *Pyrolycus* Machida and Hashimoto, 2001 and the gymneline *Ericandersonia* Shinohara and Sakurai, 2006. This

Table 3 Character matrix for estimating the phylogenetic relationships between *Santelmoa* and *Bentartia* and other Antarctic and/or Magellanic lycodine genera

TS numbers	3	4	5	9	10	11	12	14	16	17	18	20	21	22	23	24	25	26	27	29	33	35	37	40	44	45	46	47	48	49	50	51	52	56	57	59	63	64	65	67	69	74	75	76	77
Aiakas	0	0	0	1	0	0	2	0	1	0	1	1	0	0	0	0	0	0	?	0	1	0	1	0	0	1	1	2	0	0	1	0	0	1	1	0	0	1	?	1	0	1	1	1	0
Austrolycus	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	1	0	0	0	1	2	1	1	1	1	0
Bothrocara	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	1	?	2	0	1	1	1	0
Crossostomus	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2	0	1	1	0	0	1	1	0	0	0	1	1	1	1	1	2	0
Dadyanos	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	2	0	1	1	0	0	1	1	0	0	0	1	2	1	1	1	1	0
Iluocoetes	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0	1	0	1	1	2	0
Lycenchelys	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	2	0	1	1	1	0
Lycodapus	0	1	1	0	0	0	2	0	1	0	0	1	1	1	0	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	?	1	0	1	1	1	0
Lycodichthys	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0
Maynea	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	2	0	1	1	1	0	1	0	0	0	1	?	2	1	1	1	2	0
Notolycodes	0	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0
Ophthalmolycus	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	1	0
Pachycara	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	0	1	1	1	0
Phucocoetes	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	1	1	0	0	1	0	0	0	0	1	1	1	1	1	1	0
Pogonolycus	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	0	1	0	1	1	0	0	0	1	1	1	1	1	2	0
Gosztonyia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0
Bellingshausenia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	1	1	1	0
Santelmoa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	1	0
Bentartia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	2	0	1	1	1	1
Lycozoarces	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

type of fusion is thought to be an intermediate apomorphic state. In future studies, polarisation of frontal fusion could be considered as multi-state and include the anterior fusion of the frontals. The posterior part of the frontal bones in *Santelmoa* is separate, showing a complete suture. The character state of the enlarged parietal bones of *Santelmoa* is difficult to establish; however, although very close to the cranial midline, the parietals are not in contact.

The scapulae and scapular foramen are very similar in *Santelmoa* and *Bellingshausenia*, but both are quite different from those of *Derepodichthys* in which the opercular foramen is a V-shaped slit between the dorsal and anterior scapular rami (Anderson and Hubbs 1981). *Santelmoa* and *Bellingshausenia* agree also in having neurocranium narrowed, the parasphenoid wing high, palatal arch well developed and the posterior hyomandibular ramus short. However, the two genera differ, respectively, by the number of branchiostegal rays (6 vs. 7), ceratohyal–epihyal articulation (interdigitated vs. smooth), post-temporal ventral ramus (well developed vs. weak) and intercalar development (reaching the prootic vs. reduced and posteriorly displaced).

Santelmoa agrees with *Gosztonyia* mainly in the ceratohyal–epihyal articulation interdigitating, neurocranium narrowed and intercalar reaching the prootic. However, the two genera differ, respectively, in: the number of branchiostegal (6 vs. 7), palatopterygoid development (well developed vs. weak), posterior ramus of hyomandibula (short vs. elongate), post-temporal ventral ramus (well developed vs. weak) and scapular foramen (open anteriorly vs. enclosed by bone).

Bentartia differs from all other lycodine genera in having the following combination of apomorphies: basioccipital–exoccipital fused, supraoccipital–exoccipital articulation broadly contacting, ceratohyal–epihyal articulation interdigitating, post-temporal ventral ramus weak, two posterior nasal pores and cranium narrowed.

The broad and posteriorly set intercalar of *Bentartia* cannot be mistaken with the exoccipital. The intercalar is easy to identify since it acts as the attachment point of the intercalar–post-temporal ligament, joining the post-temporal ventral ramus to the hinder part of the skull (Makushok 1958; Gosztonyi 1988). The basioccipital and exoccipital fusion is confirmed by the unmistakable identification of the intercalar and also according to the "principle of connections" (Geoffroy Saint-Hilaire 1807): "homologous body parts might differ greatly in shape and even composition, but can be recognised by their topological connections to the body parts around them". In fact, three cranial foramina: glossopharingeal foramen (IX), vagus foramen (X) and occipitospinal foramen are pierced on the lateral sides of the basioccipital–exoccipital bone of *Bentartia*; these foramina are on the exoccipital when this bone is free (Devillers 1958; Anderson and Hubbs 1981; Gosztonyi 1988). This type of fusion has not been found yet in any zoarcid; this derived state is an autapomorphy of *Bentartia*.

The supraoccipital–exoccipital articulation broadly contacting can be found in only two gymneline genera, *Gymnelus* and *Gymnelopsis* (Anderson 1982, 1994). *Bentartia* is the only lycodine in which this derived state appears. The apomorphous twin posterior nasal pores of *Bentartia* has been found hitherto in only *Nalbantichthys* and a few species of *Lycodes* (Anderson 1994).

Bentartia is similar to *Gosztonyia* in having the ceratohyal–epihyal articulation interdigitating, cranium narrowed and post-temporal ventral ramus short. However, the two genera differ, respectively in: number of branchiostegal rays (6 vs. 7), basioccipital–exoccipital fusion (fused vs. separate), supraoccipital–exoccipital articulation (broadly contacting vs. excluded by epioccipitals), palatopterygoid development (well developed vs. weak), posterior hyomandibular ramus (not elongate vs. elongate), posterior nasal pores (two vs. one) amongst other characters.

Bentartia and *Santelmoa* agree mainly in having an interdigitating ceratohyal–epihyal articulation and neurocranium narrowed. However, the two genera differ, respectively, in: frontal fusion (frontal bones fused anteriorly vs. separate), scapular foramen (open anteriorly vs. enclosed by bone), basioccipital–exoccipital fusion (separate vs. fused), supraoccipital–exoccipital articulation (excluded by epioccipitals vs. broadly contacting), post-temporal ventral ramus (well developed vs. weak), intercalar (reaching the prootic vs. set posteriorly) amongst other characters.

The two new genera, *Santelmoa* and *Bentartia*, agree with the *Maynea* group clade (Anderson 1994): *Aiakas*, *Iluocoetes*, *Notolycodes*, *Pogonolycus*, *Maynea*, *Phucocoetes*, *Austrolycus*, *Crossostomus* and *Dadyanos*, by the serrated ceratohyal–epihyal juncture. However this character is homoplastic within zoarcids (Anderson 1994). The *Maynea* group, excluding *Aiakas*, is defined (Anderson 1994) by one synapomorphy: an elongated posterior hyomandibular ramus. In contrast with this group, the posterior hyomandibular ramus of both *Santelmoa* and *Bentartia* is short. Further, both genera differ from the *Maynea* group genera by having the parasphenoid wing high, and excepting *Maynea* and *Phucocoetes*, by its narrowed neurocranium amongst other characters. The two new genera differ from *Aiakas* by having vomerine and palatine teeth, oral valve and ventral fins. Finally, *Santelmoa* and *Bentartia* differ from the six most derived Magellanic genera (Anderson 1994): *Pogonolycus, Maynea, Phucocoetes, Austrolycus, Crossostomus and Dadyanos*), by having the pelvic fin rays ensheathed (*Maynea* lack pelvic fins).

Phylogenetic trees, estimated by using maximum parsimony analysis (MP) and neighbour-joining (NJ), resulted in an MP consensus tree (TL = 96; CI = 0.53; RI = 0.56;

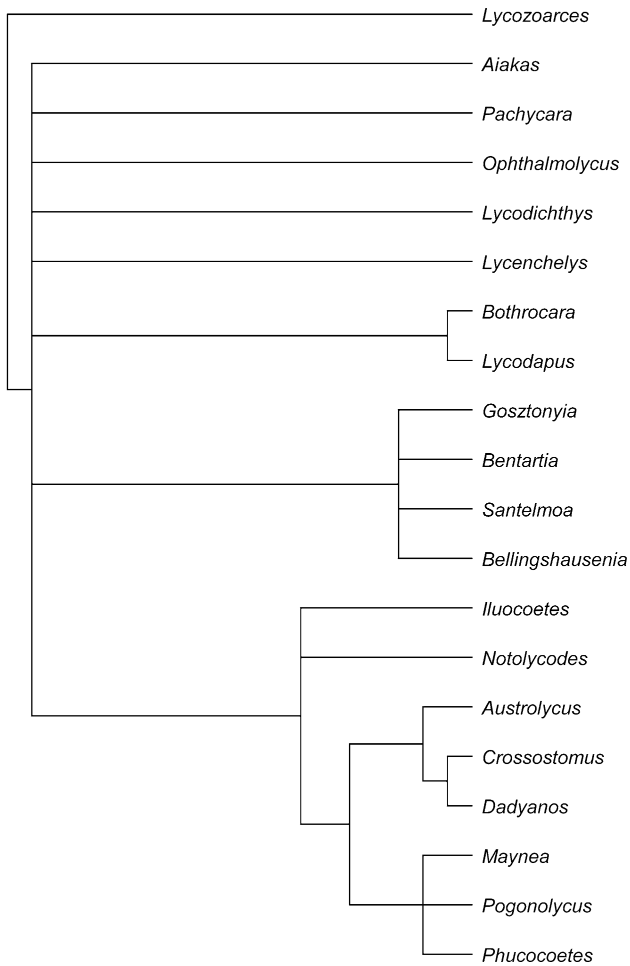

Fig. 9 Maximum parsimony tree (MP) showing interrelationships amongst the Antarctic and Magellanic lycodine genera, including *Santelmoa* gen. nov. and *Bentartia* gen. nov

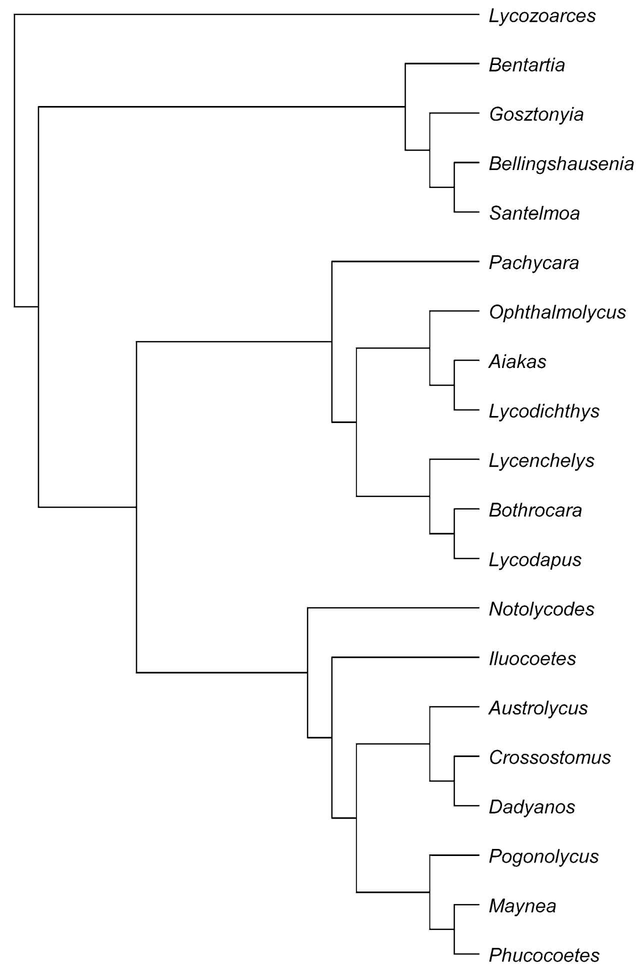

Fig. 10 Neighbour-joining tree (NJ) showing interrelationships amongst the Antarctic and Magellanic lycodine genera, including *Santelmoa* gen. nov. and *Bentartia* gen. nov

Fig. 9) and an NJ consensus tree (TL = 98; CI = 0.52; RI = 0.54; Fig. 10). In both cladograms (Figs. 9, 10), a group consisting of *Bentartia*, *Santelmoa*, *Gosztonyia* and *Bellingshausenia* is differentiated from both the Magellanic and the remaining lycodine genera. This *Bentartia* group of four genera is defined by one synapomorphy: a narrowed neurocranium (TS24), a state found only in the *Puzanovia* clade (Gymnelinae) and in the monotypic lycodine genera, *Maynea* and *Phucocoetes* (Anderson 1994). The *Bentartia* group is also characterised by the homoplastic loss of the supratemporal commissure and occipital pores (TS37), a derived state found also in *Aiakas*, *Lycodapus* and *Ophthalmolycus* (Anderson, 1994). The plesiomorphic state of the parasphenoid wing height (TS20) is retained by the four genera of the *Bentartia* group, in contrast with the remaining Antarctic and Magellanic zoarcid genera. This plesiomorphic state, common in the other zoarcid subfamilies, can be found in only the lycodine *Lycodes* (Anderson 1994). *Bentartia* differs from the other genera by one autapomorphy: basioccipital and exoccipitals fused (TS77) and one apomorphy: supraccipital–exoccipital articulation broadly contacting (TS29). *Santelmoa* and *Bellingshausenia* are united by one synapomorphy: scapular foramen open (TS59). The NJ tree (Fig. 10) closely supports Anderson's (1994) hypothesis on the relationships among the endemic Magellan Province genera, except for the position of *Aiakas*.

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Appendix 1

The monotypic *Lycozoarces* (Lycozoarcinae), primitive sister group of all other zoarcids (Anderson 1994), was designed as outgroup taxa. TS numbers used here are those assigned to each character by Anderson (1994), with the following additions: frontal fusion (TS 23) could be considered as multi-state (0, 1, 2); a new TS, number 77, is added. TS3, squamation: present (0), absent (1); TS4, condition of flesh: firm (0), gelatinous (1); TS5, lateral line: present (0), absent (1); TS9, lower lip attachment: adnate (0), free (1); TS10, lip grooves: absent (0), present (1); TS11, elongate facial papillae: absent (0), present (1); TS12, oral valve reduction: free edge extends to vomer (0), free edge well before vomer and valve laterally constricted (1), absent (2); TS14, chin pad: absent (0), present (1); TS16, pseudobranch filaments: 6–13 (0), 0–5 (1); TS17, pyloric caeca state: present (0), absent (1); TS18, pyloric caeca development: nubbins (0), elongate (1); TS20, parasphenoid wing height: high (0), reduced (1); TS21, frontal corner: squared off (0), tapering (1); TS22, frontal ramus: long (0), shortened (1); TS23, frontal fusion: separate (0), fused anteriorly (1), fused completely (2); TS24, cranium width: wide (0), narrowed (1); TS25, frontal–parasphenoid articulation: not separated by pterosphenoid (0), separated by pterosphenoid (1); TS26, sphenotic–parietal articulation: separated by frontals (0), in contact (1); TS27, parietal–parietal articulation: separated from midline (0), in contact (1); TS29, supraoccipital–exoccipital articulation: narrowly contacting or excluded by epioccipitals (0), broadly contacting (1); TS33, suborbital bone configuration: circular pattern (0), L-shaped pattern (1); TS35, preopercular and mandibular canals: continuous (0), separated (1); TS37, supratemporal commissure and occipital pores: present (0), absent (1); TS40, posterior nasal pore development: single (0), double (1); TS44, incisiform dentition: absent (0), present (1); TS45, palatine teeth: present (0), absent (1); TS46, vomerine teeth: present (0), absent (1); TS47, branchiostegal membrane: free of isthmus (0), attached to isthmus, with gill slit extending to or below the ventral edge of the pectoral fin base (1), attached to isthmus, with gill slit extending to about mid-pectoral base (2), gill slit above pectoral base, pore like (3); TS48, palatopterygoid series development: well developed (0), reduced (1); TS49, posterior ramus of hyomandibula: short (0), elongate (1); TS50, ceratohyal–epihyal articulation: smooth (0), interdigitating (1); TS51, branchiostegal ray reduction: rays 6 (0), rays 4–5 (1); TS52, branchiostegal ray addition: rays 6 (0), rays 7–8 (1); TS56, postorbital canal passage: through lateral extrascapulars, post-temporal and supracleithrum (0), through lateral extrascapulars only (1); TS57, post-temporal ventral ramus: well developed (0), weak or absent (1); TS59, scapular foramen: enclosed by bone (0), open (1); TS63, pectoral fin: well developed (0), reduced (1), minute, nub-like (2), absent (3); TS64, number of pelvic fin rays: 2–3 (0), absent (1); TS65, pelvic fin membranes: rays joined, ensheathed (0), rays exserted (1); TS67, number of vertebrae: 58–71 (0); 72–105 (1), 109–134 (2), 134–150 (3); TS69, advanced dorsal fin origin: first pterygiophore associated with vertebrae 1 or greater (0), first pterygiophore anterior to first vertebrae (1); TS74, number of epurals: 2 (0), 1 (1), absent (2); TS75, number of epural caudal fin rays: 3 (0); 1–2 (1); TS76, number of caudal fin rays: 13–15 (0), 9–12 (1), less than 9 (2); TS77, basioccipital–exoccipital fusion: separate (0), fused (1).

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