Taxonomy and Phylogeny of Lycodinae (Teleostei: Zoarcidae) from the Southern Ocean and Magellan Province

Doctoral thesis

Cecília Corbella i Felip

2013

Universitat Autònoma de Barcelona
Facultat de Biociències
Departament de Biologia Animal, Biologia Vegetal i Ecologia
Unitat de Zoologia

Taxonomy and Phylogeny of Lycodinae (Teleostei: Zoarcidae) from the Southern Ocean and Magellan Province

Tesi doctoral

Cecília Corbella i Felip

Bellaterra, gener 2013

Il·lustracions i disseny de les portades: Oriol Martínez Canas

Aquest treball ha estat possible gràcies a la concessió d'una beca predoctoral PIF (beques per a personal investigador en formació per a departaments de la Universitat Autònoma de Barcelona). La recerca ha estat parcialment finançada per l'acció complementaria del "Ministerio de Educación y Ciencia" CTM 2009-07583-E/ANT, per les beques de curta durada fora de Catalunya pel becaris de les convocatòries PIF de la UAB i per les beques de "Synthesys Project".

El material estudiat en aquesta tesi ha estat obtingut durant la campanya espanyola Bentart 2003-2006 (Jesús Matallanas i Ignacio Olaso); la campanya danesa Galathea 3 (Peter Rask Møller i Steen Knudsen) i la campanya Atlantis 2009-2010 del Centro Oceanográfico de Vigo (Instituto Español de Oceanografía).

Universitat Autònoma de Barcelona
Facultat de Biociències
Departament de Biologia Animal, Biologia Vegetal i Ecologia
Unitat de Zoologia

Tesi doctoral

Taxonomy and Phylogeny of Lycodinae (Teleostei:Zoarcidae) from the Southern Ocean and Magellan Province

Memòria de tesi doctoral presentada per:

Cecília Corbella i Felip

Per a optar al grau de Doctora en Biologia Animal.

Amb el vist-i-plau dels directors de la tesi:

Dr. Jesús Matallanas García
Universitat Autònoma de Barcelona

Dra. Montserrat Pérez Rodríguez
Instituto Español de Oceanografía

Bellaterra, gener 2013

AGRAÏMENTS

Bé!, si estic escrivint els agraïments és que això ja va en serio i ja estic acabant!!!. No m'ho acabo de creure, sembla que fa dos dies que m'hi vaig posar. Mirant endarrere i analitzant el camí fet, me n'adono que va ser un gran encert acceptar aquesta aventura. He tingut moments de tot. De molta feina i d'estrès però també moments divertits, emocionants i especials. Gràcies a tots els que d'una manera o d'una altra m'heu fet aquest camí més agradable.

En primer lloc, voldria donar les gràcies als meus directors, al Jesús Matallanas i a la Montse. El Jesús per donar-me la oportunitat d'embarcar-me en aquest projecte i encomanar-me la passió per l'anatomia d'aquests peixets tant especials. Y a Montse por acogerme en su laboratorio y enseñarme todo lo que se sobre la biología molecular. Muchas gracias a los dos por la paciencia, la dedicación y los consejos que me habéis dado.

Gràcies també a tots els companys de la unitat de zoologia que en algun moment m'heu ajudat i aconsellat. Especialment a les Laies (la Laia aranya i la Laieta) i la Núria, les quatre ens vam embarcat a la vegada en els nostres projectes i ens hem anat acompanyant durant tot el procés. I també a la Carolina que s'ha incorporar una mica més tard al grup de les doctorandes de Zoologia. I l'Anna, el salvavides de totes nosaltres ajudant-nos en els problemes i dubtes, ens has ajudat moltíssim i gràcies també pel teu bon humor! i al Francesc pels cafès imprescindibles de bon matí i els dinars que hem compartit juntament amb la Sandra, la Marta, el Nitu, el Marco, l'Emili, l'Abel i la Cristina.

Durant el doctorat he tingut la oportunitat de fer algunes estades fora de Catalunya. Gracias a Pablo Presa de la Universidad de Vigo por acogerme en tu laboratorio así como a Alfonso por las horas compartidas en el laboratorio y a Yassine por los partidos del Barça! También a Ana y a Núria por la ayuda que me disteis y por las charlas! Also I would like to gratefully acknowledge Peter Møller for helping me so much during my visit in Denmark.

I perquè hi ha molt més a part de la feina. Gràcies a les amigues de la universitat. La Silvia, l'Agnès, la Laura, la Mireia, la Gina, la Mònica i la Maria. Tot hi que ens veiem poc, quan ens retrobem sembla que no hagi passat el temps.

Especialment a l'Agnès, gràcies per les xerrades de bon matí que han sigut imprescindibles per començar amb bon peu cada dia i a la Silvia que dia rere dia ha estat allà per tot el que he necessitat. Joan per a tu també! perquè cada vegada que ens veiem em recordes per què vaig decidir ser Biòloga. M'encomanes el teu entusiasme i la teva energia. Marta i què dir! La meva gran amiga de l'institut, gràcies per estar sempre amb mi.

I a tot al grup Mediterrània. Tots compartim un mateix sentiment cap a les tradicions catalanes, sobretot per les danses. Però som molt més que un grup de dansa, som un grup d'amics. Hem compartit molts sopars, viatges, converses i festes. Tots en algun moment m'heu fet passar bones estones. Moltes gràcies!!

I finalment! Però no menys important! Vull agrair a la meva família, al meu pare, la meva mare i al Martí. Gràcies pel suport que m'heu donat amb tot el que he volgut fer. Sé que sempre puc comptar amb vosaltres. Moltes gràcies per tot!!! I també al resta de la meva família, als meus tiets i als meus cosins, especialment a la meva àvia i a la nane.

I a tu Ori, mil gràcies! gràcies per suportar aquests últims mesos el tema estrella de les nostres converses la tesi! Gràcies per aquesta magnífica tapa i el format en general! I gràcies pel teu optimisme, pel teu bon humor, pel suport i pels ànims que m'has donat.

I ara ànims per llegir tot el que us queda!!!!

TABLE OF CONTENTS

ABSTRACT

Family Zoarcidae (eelpouts) is the largest family of the suborder Zoarcoidei (Perciformes), including 4 subfamilies (Lycozoarcinae, Zoarcinae, Gymnelinae and Lycodinae) and about 240 species in 54 genera. This family has a wide distribution and it is found in all oceans and seas of the world; it primarily inhabits mud bottoms of the continental shelves and the slopes of boreal seas, but some species are known from the abyssal zone. Species of Lycodinae are abundant in the North Pacific and North Atlantic seas but there has been some radiation into the Arctic, South America and Antarctic waters. The origin of eelpouts was probably in the North Pacific (Okhotsk Sea); this is evidenced by a very high diversity and a higher number of endemisms, and by the fact that there are representatives of all the 4 subfamilies of Zoarcidae.

This thesis is focused on the taxonomic and phylogeny of Lycodinae. Subfamily Lycodinae is the largest subfamily within Zoarcidae and it includes 38 genera and about 190 species. It is a fish group little known; in the last few years, 5 new genera have been described (*Leucogrammolycus*, *Gosztonyia*, *Bellingshausenia*, *Santelmoa* and *Bentartia*) and there are probably still many species and genera which remain undescribed. The systematic of Lycodinae has been widely discussed by many authors, and although molecular data has been added in the last few years, there are some points that are still unclear.

The aim of this thesis is to contribute to the knowledge of the diversity and the phylogeny of subfamily Lycodinae. To achieve the objectives, four studies have been carried out.

Specimens from Magellan province, the Southern Ocean and the Solomon Sea (Western South Pacific) have been studied. As a result, 2 new genera, *Patagolycus* and *Argentinolycus,* have been described and a third genus (*Iluocoetes*) has been redescribed. Two new species of *Santelmoa* (*S. fusca* and *S. antarctica*) have been described from the Southern Ocean and a new species (*Pachycara matallanasi*) from the Solomon Sea has been described.

The last study is a phylogenetic analysis of some genera of Lycodinae. It has been carried out using molecular data (Cytochrome Oxidase I and Control Region) and anatomical data.

Resulting trees show that, *Lycodapus* is separated from all other genera and that the remaining genera are divided into Antarctic and Magellanic genera. *Pachycara brachycephalum* appeared in a separated clade of *Pachycara priedei* and *Pachycara matallanasi*. The same result is found in species of *Lycenchelys* (*L.bachmanni* and *L. wilkesi*) which are separated. These two cases show that a complete review using anatomic and molecular data is required in some genera of Lycodinae.

RESUM

La família zoarcidae, és una de les més diverses del subordre Zoarcoidei (Perciformes), comprèn 4 subfamílies (Lycozoarcinae, Zoarcinae, Gymnelinae i Lycodinae) i inclou més de 240 espècies en 54 gèneres. Aquesta família té una distribució molt àmplia ja que es troba a quasi tots els mars i oceans del món, la majoria de les espècies habiten a les zones litorals, a la plataforma continental i a la meitat superior del talús continental però algunes habiten a la zona abissal. Les espècies de la família Zoarcidae són molt abundants al Pacífic Nord i a l'Atlàntic Nord tot hi que també hi ha gèneres que es distribueixen pel sud de l'oceà Atlàntic, l'Àrtic, l'oceà Pacífic i per l'oceà Antàrctic. Probablement, l'origen dels zoàrcids va ser al nord-oest de l'oceà Pacífic, concretament al mar de Okhotsk. En aquesta zona, hi habiten representants de les 4 subfamílies, hi ha una gran diversitat d'espècies i un gran nombre d'endemismes.

Aquesta tesi, està centrada en l'estudi de la subfamília Lycodinae. Aquesta subfamília és la més diversa dintre dels Zoarcidae i presenta 38 gèneres i més de 190 espècies. És un grup de peixos força desconegut com queda palès en el fet que en els últims anys s'han descrit 5 gèneres nous (*Leucogrammolycus*, *Gosztonyia*, *Bellingshausenia*, *Santelmoa* i *Bentartia*) i de ben segur que en queden molts més per descriure. La sistemàtica d'aquesta subfamília ha estat discutida per molts autors, i tot hi que recentment s'hi han incorporat les dades moleculars, encara hi ha alguns punts de la seva sistemàtica que no han quedat resolts.

El principal objectiu d'aquesta tesi és contribuir en el coneixement de la diversitat i de la filogènia de la subfamília Lycodinae. Per tal d'assolir aquest objectiu, s'han realitzat quatre estudis.

S'han estudiat exemplars de la subfamília Lycodinae procedents de la província de Magallanes, de l'oceà Antàrtic i del mar de Solomon (sud-oest de l'oceà Pacífic). Com a resultat d'aquest treball, s'han descrit 2 gèneres nous (*Patagolycus* i *Argentinolycus*) i un tercer gènere, el gènere *Iluocoetes* s'ha descrit de nou. Per altra banda, s'han descrit dues espècies noves del gènere *Santelmoa* (*S. fusca* i *S. antarctica*) de l'oceà Antàrtic i una nova espècie (*Pachycara matallanasi*) del mar de Solomon.

L'últim treball, és una anàlisi filogenètica d'alguns gèneres de la subfamília Lycodinae realitzat mitjançant dades moleculars (Citocrom Oxidasa I i Regió Control) i

dades anatòmiques. L'arbre filogenètic ens mostra que el gènere *Lycodapus* es troba a la base de l'arbre clarament separat de tots els altres gèneres. Els gèneres restants es troben dividits principalment en dos grups, per una banda els gèneres Antàrtics i per l'altra els gèneres Magallànics. *Pachycara brachycephalum* apareix clarament separat de les altres espècies de *Pachycara* (*P. priedei* i *P. matallanasi*). El mateix resultat el trobem a les espècies del gènere *Lycenchelys* (*L. bachmanni* i *L. wilkesi*) que també es troben separades. Aquests dos casos mostren la necessitat de realitzar una revisió completa d'alguns gèneres de la subfamília Lycodinae mitjançant dades anatòmiques i moleculars.

Aiakas kreffti
Aiakas zinorum
Austrolycus depressiceps
Austrolycus laticinctus
Bellingshausenia olasoi
Bentartia cinerea
Bothrocara brunneum
Bothrocara elongatum
Bothrocara hollandi
Bothrocara molle
Bothrocara pusillum
Bothrocara soldatovi
Bothrocara zestum
Bothrocarina microcephala
Bothrocarina nigrocaudata
Crossostomus chilensis
Crossostomus fasciatus
Dadyanos insignis
Derepodichthys alepidotus
Eucryphycus californicus
Exechodontes daidaleus
Gosztonyia antarctica
Hadropogonichthys lindbergi
Iluocoetes elongatus
Iluocoetes fimbriatus

INTRODUCTION

Japonolycodes abei
Letholycus magellanicus
Letholycus microphthalmus
Lycenchelys alba
Lycenchelys albeola
Lycenchelys albomaculata
Lycenchelys alta
Lycenchelys antarctica
Lycenchelys aratrirostris
Lycenchelys argentina
Lycenchelys aurantiaca
Lycenchelys bachmanni
Lycenchelys bellingshauseni
Lycenchelys brevimaxillaris
Lycenchelys bullisi
Lycenchelys callista
Lycenchelys camchatica
Lycenchelys chauliodus
Lycenchelys cicatrifer
Lycenchelys crotalinus
Lycenchelys fedorovi
Lycenchelys folletti
Lycenchelys hadrogeneia
Lycenchelys hippopotamus
Lycenchelys hureaui

1 INTRODUCTION

1.1 FAMILY ZOARCIDAE: GENERAL ASPECTS

The family Zoarcidae is the most diverse family of the suborder Zoarcoidei, and is divided into four subfamilies: Lycozoarcinae, Zoarcinae, Gymnelinae and Lycodinae, with about 250 currently recognized species in 54 genera (Anderson and Fedorov, 2004; Shinohara *et al*., 2004; Shinohara and Sakurai, 2006; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2009c, 2010, 2011a, 2011b) (table 1). This family has a wide distribution and is found in all oceans and seas of the world; it primarily inhabits mud bottoms of the continental shelves and the slopes of boreal seas, although some species are known from abyssal zone. Most of the currently recognized genera are from North Pacific and North Atlantic, although there has been some radiation into the Arctic, South America and Antarctic waters (Weitzman, 1997; Anderson and Fedorov, 2004).

Diagnostic characters for family Zoarcidae are the following: body elongate, dorsal and anal fins confluent with caudal. Basisphenoid bone, swim bladder, posterior nostrils and supramaxilla absent. Pelvic fins, lateral lines, pseudobranchia and pyloric caeca rudimentary or absent. Scales minute, imbedded, cycloid; or absent. Branchiostegal rays 4-8, usually 6. Ovary single. Vertebrae 58-150. Maximum adult size range about 12-110 cm total length (Anderson, 1994; Anderson and Fedorov, 2004).

1.1.1 Family name and systematic position

Zoarcidae is a difficult group for several reasons, including extremely similar morphology between species, which is reflected in its systematic that has been hotly debated.

For many years, the eelpout has been allied with other fish families. For a short time, it was associated with Gadiformes and Ophidioides (Reinhardt, 1838; Yarrell, 1841, 1859; Müller, 1846; Kaup, 1856; Greenwood *et al*., 1966; Rosen and Patterson, 1969; Lauder and Liem, 1983) but this association was rejected by other

authors (Marshall and Cohen, 1973; Anderson and Hubbs, 1981; Shaklee and Whitt, 1981).

However, the eelpouts have most often been linked with the suborder Blennioidei (Cuvier, 1829; Gill, 1862; Regan, 1912; Hubbs, 1952; Makushok, 1958; Gosline, 1968; Gosztonyi, 1977). *Blennius viviparus* (Linnaeus, 1758) was the first species described of the current family Zoarcidae (fig. 1). This species were placed in a group known by different names. Gronow (1760) described *Enchelyopus*, the type species of which was *Blennius viviparus* (Linnaeus, 1758). Cuvier (1829) used the term "Les Zoarcès" for the first time to name a group which included species of *Blennius*, the type species of which was *Blennius viviparus* (Linnaeus, 1758).

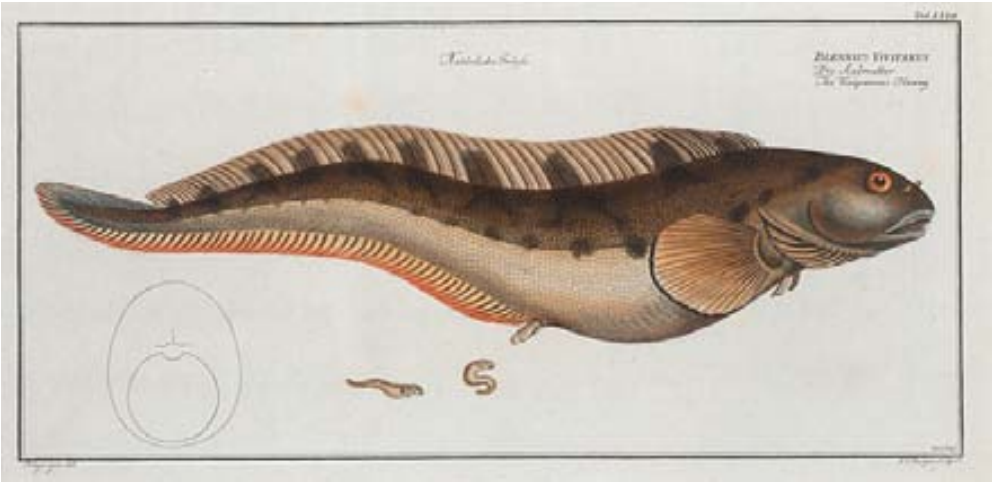


Figure 1. *Blennius viviparus* Linnaeus, 1758 (Bloch, 1785)

Based on the name "Les Zoarcès" proposed by Cuvier (1829), Nilsson (1832) did the first attempt to latinize the generic name for eelpouts and proposed the name Zoarcaeus (Norman, 1966; Gosline, 1968). Then, other authors suggested other possible names: Zoarchidae (Swainson, 1839); Zoarceoidae (Gosline, 1968) and Zoarcidae (Jordan and Gilbert, 1883; Gill, 1893; Gosline, 1968; Lahille, 1908). Currently, Zoarcidae is considered the correct name for the family. However, the systematic of the eelpouts was still unclear and many authors attempted to classify this family.

Table 1. Subfamilies and genera of Zoarcidae (Anderson and Fedorov, 2004; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2010, 2011a, 2011b)

Family	Subfamily	Genus
Zoarcidae	Lycozoarcinae	*Lycozoarces* Andriashev, 1939
	Zoarcinae	*Zoarces* Cuvier, 1829
	Gymnelinae	*Andriashevia* Fedorov and Neyelov, 1978 *Bilabria* Schmidt, 1936 *Davidijordania* Popov, 1931 *Ericandersonia* Shinohara and Sakurai, 2006 *Gymnelopsis* Soldatov, 1922 *Gymnelus* Reinhardt, 1834 *Hadropareia* Schmidt, 1904 *Krusensterniella* Schmidt, 1904 *Magadania* Shinohara, Nazarkin and Chereshnev, 2004 *Melanostigma* Günther, 1881 *Nalbantichthys* Schultz, 1967 *Opaeophacus* Bond and Stein, 1984 *Puzanovia* Fedorov, 1975 *Seleniolycus* Anderson, 1988
	Lycodinae	*Aiakas* Gosztonyi, 1977 *Austrolycus* Regan, 1913 *Bellingshausenia* Matallanas, 2009 *Bentartia* Matallanas, 2010 *Bothrocara* Bean, 1890 *Bothrocarina* Suvorov, 1935 *Crossostomus* Lahille, 1908 *Dadyanos* Whitley, 1951 *Derepodichthys* Gilbert, 1896 *Dieidolycus* Anderson, 1988 *Eucryphycus* Anderson, 1988 *Exechodontes* DeWitt, 1977 *Gosztonyia* Matallanas, 2008 *Hadropogonichthys* Fedorov, 1982 *Iluocoetes* Jenyns, 1842 *Japonolycodes* Shinohara, Sakurai and Machida, 2002 *Letholycus* Anderson, 1988 *Leucogrammolycus* Mincarone and Anderson, 2008 *Lycenchelys* Gill, 1884 *Lycodapus* Gilbert, 1890 *Lycodes* Reinhardt, 1831 *Lycodichthys* Pappenheim, 1911 *Lycodonus* Goode and Bean, 1883 *Lycogrammoides* Soldatov and Lindberg, 1929 *Lyconema* Gilbert, 1896 *Maynea* Cunningham, 1871 *Notolycodes* Gosztonyi, 1977 *Oidiphorus* McAllister and Rees, 1964 *Ophthalmolycus* Regan, 1913 *Pachycara* Zugmayer, 1911 *Phucocoetes* Jenyns, 1842 *Piedrabuenia* Gosztonyi, 1977 *Plesienchelys* Anderson, 1988 *Pogonolycus* Norman, 1937 *Pyrolycus* Machida and Hashimoto, 2002 *Santelmoa* Matallanas, 2010 *Taranetzella* Andriashev, 1952 *Thermarces* Rosenblatt and Cohen, 1986

Lahille (1908) divided the family Zoarcidae into three subfamilies: Zoarcinae Swainson, 1839; Lycodinae Gill, 1862 and Gymnelinae Gill, 1863. Hubbs (1952) recognized two superfamilies within Blennioidei: Zoarcicae (northern blennies) and Blenniicae (tropical blennies). This classification was revised by Makushok (1958) and he reaffirmed the classification proposed by Hubbs (1952), but he divided the northern blennies into three superfamilies: Stichaeoidae, Cryptacanthodoidae and Zoarceoidae. Gosline (1968) made a critical review of the classification of the Perciformes and studied the systematic of the suborder Blennioidei. He recognized 5 superfamilies within Blennioidei: Notothenioidae, Trachinoidae, Congrogadoidae, Zoarceoidae and Blennioidae (that included Blenniicae or tropical blennies from Hubbs (1952) and Makushok (1958).

Finally, Nelson (1994) proposed 4 suborders (Blennioidei, Zoarcoidei, Notothenioidei and Trachinoidei). At the same time, Anderson (1994) continued Gosline´s study (1968) and performed a complete revision of zoarcids. As a result of his thorough work, he recognized 8 families within suborder Zoarcoidei: Bathymasteridae, Ptilichthyidae, Zaproridae, Anarhichadidae, Stichaeidae, Pholidae, Scytalinidae and Zoarcidae. And the family Zoarcidae was divided into four subfamilies: Lycozoarcinae Andriashev, 1939; Zoarcinae Gill, 1862; Gymnelinae Gill, 1863 and Lycodinae Gill, 1862 (Table 1).

Currently, the family Zoarcidae is placed within Perciformes, in the suborder Zoarcoidei (Nelson, 2006) with the four subfamilies proposed by Anderson (1984, 1994) (Table 1).

1.1.2 Origin of the zoarcids

It is widely accepted that Zoarcidae dominated deep-sea habitats in high latitudes of the north hemisphere, and they dispersed throughout the Southern Ocean (Regan, 1914; Norman, 1937, 1938; Andriashev, 1953, 1965, 1979, 1987; DeWitt, 1971; Gosztonyi, 1977; Anderson, 1984), but the authors disagree with regard to when this happened (fig.2).

Schmidt (1950) suggested that both family Zoarcidae and closely related families of eelpouts (Stichaeidae and Pholidae) emerged during the Miocene in the north of the Okhotsk Sea and at the same time, differentiation of families began and

modern species appeared during the Pliocene and Pleistocene. It is believed that western North Pacific is the center of eelpout speciation (Anderson, 1994; Nelson, 1994), which is evidenced by a very high diversity and a higher number of endemic genus and species (Schmidt, 1950; Briggs, 1974), and by the fact that there are representatives of all the 4 subfamilies of the family Zoarcidae (Fedorov *et al*., 2003; Fedorov, 2004; Chereshnev *et al*., 2005).

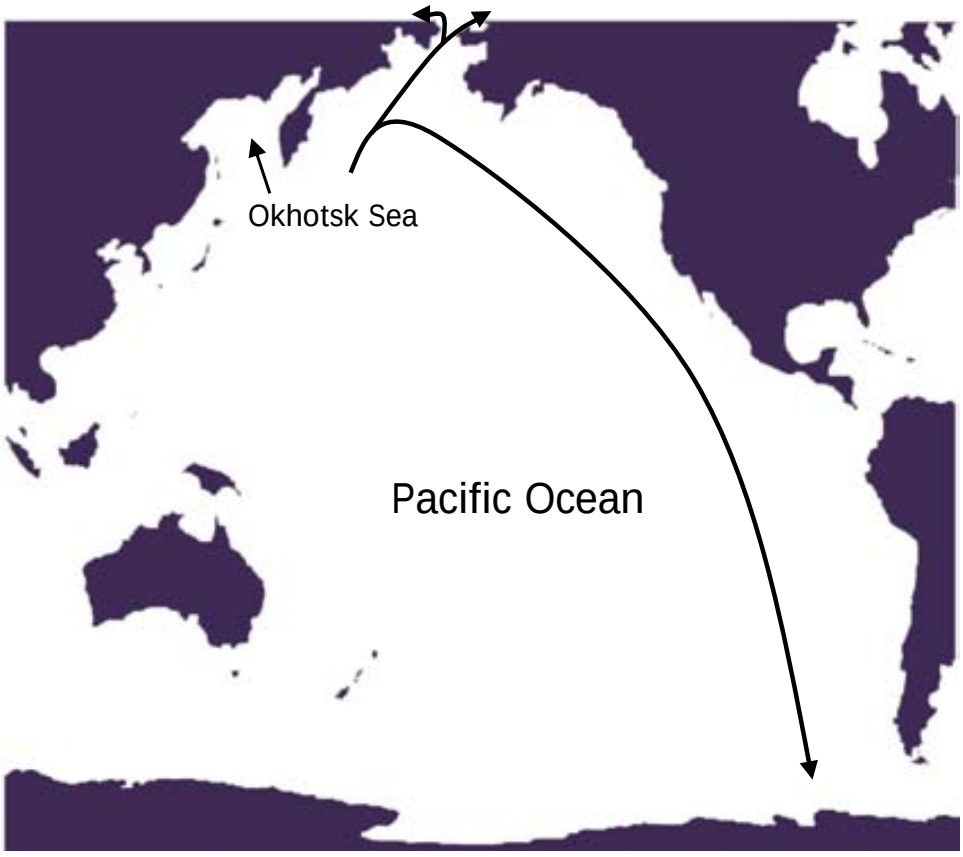


Figure 2. Distribution of family Zoarcidae.

Anderson (1988a) also mentioned that the origin of zoarcids was in the northern part of the Pacific Ocean but originated sometime during the Eocene. Then, during the Miocene period Zoarcidae and Liparidae began to disperse in the Southern Ocean with invasions from the North Pacific to the southern hemisphere moving down to the west coast of America and across the Scotia Ridge, and eventually colonizing the Antarctic waters (Andriashev, 1991; Anderson, 1994) (fig. 2). In the Southern Ocean there was a second speciation center of the family Zoarcidae (Andriashev, 1965, 1987; Briggs,

2000) which is reflected in 5 endemic genera in this place (*Lycodichthy* Pappenheim, 1911; *Gosztonyia* Matallanas, 2009a; *Bellingshausenia* Matallanas, 2009b*; Bentartia* Matallanas, 2010 and *Santelmoa* Matallanas, 2010). After the opening of the Drake Passage (20-22 million years ago), zoarcids and liparids could penetrate into the South Atlantic (Andriashev, 1998). The Pacific origin of Zoarcidae suggested by Schmidt (1950), Briggs (1974) and Anderson (1994) was supported later by Møller and Gravlund (2003) basing himself on *Lycodes.*

Radiation towards other places of the northern hemisphere happened during the Pliocene and Pleistocene periods during the many glacial and interglacial periods, with repeated opening and closing of the Bering Strait (Anderson, 1982, 1994; Herman and Hubkins, 1980) (fig. 2).

Molecular data makes possible to date the time of divergence between taxa using sequences (Zuckerkandl and Pauling, 1965). This method was called “molecular clock” and assumes that the substitution rate is the same in all branches of the phylogenetic tree; however, there is increasing evidence that the rate constancy is often violated (Bromham and Penny, 2003; Wu and Li, 1985).

“Molecular clock” method has been widely used to estimate the timing of family Lycodinae diversification (Stepien *et al*., 1997, Møller and Gravlund, 2003; Radchenko *et al*., 2009), assuming a substitution rate for fish mitochondrial DNA of 1-2% nucleotide mutation during 1 million years. Stephien *et al*., (1997) estimates the time of mitochondrial divergence between the suborder Zoarcoidei and Notothenioidei that resulted in a diverged about 20.5 ± 2.5 million years ago (Miocene) and modern zoarcids may have diversified about 10.0 ± 0.5 million years (Miocene) assuming a 1% substitution rate. Within family Zoarcidae the time of divergence of the families Lycodinae and Gymnelinae comprises 9.0-11.2 million year (Radchenko *et al*., 2009)

The method based on rates of divergence (“Molecular clock”) has been improved with the incorporation of calibration points. Biogeographic and fossil data are among the main sources of information for dating phylogenetic nodes. The problem is that no Lycodinae fossils exist and only some fossils of closer groups of Zoarcidae have been found. A nototheniid fossil from La Meseta Formation on Seymour Island (Antarctic Peninsula) is estimated at 38 million years ago (late Eocene) (Eastman and Grande, 1991; Balushkin, 1994). Estimated divergence times of notothenioid are studied and a controversial result was found between “molecular clock” analysis and

fossil calibration (Near, 2004). Previous studies placed the divergence of Antarctic notothenioid at 7-15 million years (late Miocene) (Kennett, 1982; Eastman and McCune, 2000; Poulin *et al*., 2002) but the age resulting from the fossil calibrate indicated an early divergence at 24.1±0.5 million years (Oligocene-Miocene) (Near, 2004). Some results under 1% mutation for 1 million years conditions, show that the divergence time between family Lycodinae and Stichaeidae was approximately 12.1 - 11 million years ago in subfamilies Lycodinae and Gymnelinae (Radchenko *et al*., 2009).

Fossils of closely related families of the suborder Zoarcoidei (Stichaeidae and Pholidade) estimated at 11.6-12.25 million years ago (middle Miocene) were found in Agnev deposits of Sakhalin with some present day genera (Nazarkin, 2000). These fossil records indicate the possibility of an early time of divergence within Zoarcoidei (Radchenko *et al*., 2009).

The lack of calibration points hampers this method and for this reason, the time of divergence of eelpouts is still unclear.

1.2 BACKGROUND STUDIES

1.2.1 Anatomic studies

Since the first specimen of the subfamily Lycodinae was described, most of the studies have been about new species or systematic revisions. Initially, these descriptions were only about external anatomy and colour. In the course of time, measurements protocol (Gill, 1884; Gosztonyi, 1977, 1988; Anderson, 1981) and osteologic description (Lahille, 1908; Regan, 1912; Gosline, 1968) were incorporated. But, the most important work is the “Systematic and Osteology of the Zoarcidae (Teleostei: Perciformes)” (Anderson, 1994). Anderson performed a detailed, systematical revision of the family on the basis of comparative anatomical study of genera. He incorporated a complete description of each genus which included information about neurocranium, suspensorium, pectoral girdle and hyoid bar (fig. 3). This study is the basis of all posterior studies and descriptions of new genera and new species of Zoarcidae (a thorough explanation of methods used are in Chapter 1-3).

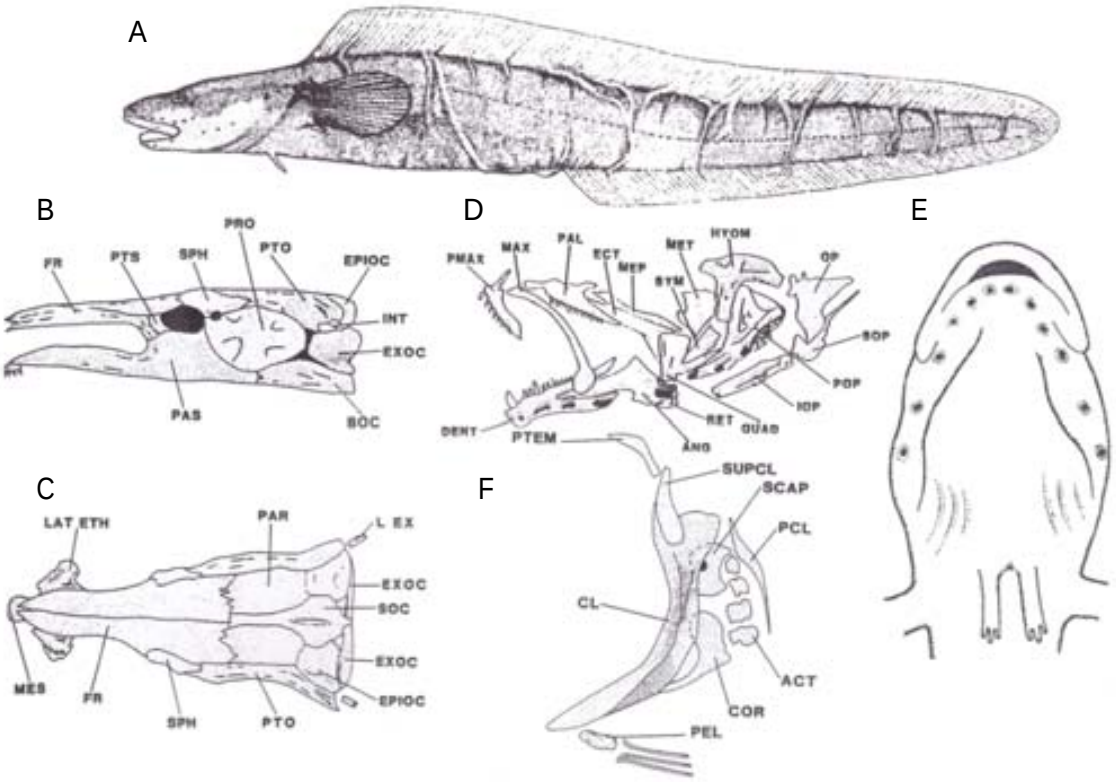


Figure 3. Complete description of *Austrolycus depressiceps* (Anderson, 1994). General view **(A)**, neurocranium, left lateral view **(B)** and dorsal view **(C)**, left splanchnocranium and opercular bones **(D)**, ventral view of head region **(E)** and left pectoral girdle **(F)**. ACT, actinost; ANG, anguloarticular; BOC, basioccipital; CL, cleithrum; COR, coracoid; DENT, dentary; ECT, ectopterygoid; EPIOC, epioccipital; EXOC, exoccipital; FR, frontal; HYOM, hyomandibula; INT, intercalary; IOP, interopercle; L EX, lateral extrascapular; LAT ETH, lateral ethmoid; MAX, maxilla; MEP, mesopterygoid; MES, mesethmoid; MET, metapterygoid; OP, opercle; PAL, palatine; PAR, parietal; PAS, parasphenoid; PCL, postcleithrum; PEL, pelvic bone; PMAX, premaxilla; POP, preopercle; PRO, prootic; PTEM, posttemporal; PTO, pterotic; PTS, pterosphenoid; QUAD, quadrate; RET, retroarticular; SCAP, scapula; SOC, supraoccipital; SOP, subopercle; SPH, sphenotic; SUPCL, spracleithrum; SYM, symplectic.

1.2.2 Phylogenetic studies

The first approximation to the study of the relationships between families was made by Gosline (1968). At that time, the family Zoarcidae was placed within Blennioidei and he studied the relationships between groups of Blennioidei. But a first phylogenetic study was made by Anderson (1994), he studied the relationships between subfamilies of Zoarcidae. The phylogenetic hypothesis was carried out through a character matrix with 76 characters. Each character was polarized with the following code: "0" for the plesiomorphous state and "1" or higher for the apomorphous state. As a result of the study, he determined the relationships between endemic Magellan Province genera (*Aiakas*, *Iluocoetes*, *Notolycodes*, *Pogonolycus*, *Maynea*, *Phucocoetes*, *Austrolycus*, *Crossostomus* and *Dadyanos*) with the exception of a genus *Oidiphorus* that was not added because Anderson considered that it was a problematic genus. He determined that *Aiakas* was separated from all the other genera (*Notolycodes*, *Pogonolycus*, *Maynea*, *Phucocoetes*, *Austrolycus*, *Crossostomus* and *Dadyanos* (fig. 4). Within this group, *Pogonolycus* was separated from the other genera and the rest of genera formed two groups closely related (*Maynea* and *Phucocoetes* and *Austrolycus*, *Crossostomus* and *Dadyanos*). However, the resolution of the subfamily Lycodinae is very poor in Anderson (1994), who accepted that zoarcids are affected by homoplasy in anatomical characters.

In recent years, the outstanding advances in both, molecular biology and bioinformatics have supplied taxonomists with powerful tools to solve systematic and phylogenetic problems. The use of DNA sequences has several advantages over traditional morphological approaches. For example, molecular data gives a high number of characters available for analyses, universality of characters and high degree of substitution (Hillis and Wiens, 2000). However, molecular data is not free of problems. One of the major criticisms is the fact that molecular data possess low character state, and therefore a high saturation probability during the substitution process. Consequently, in this case molecular and morphological data have the same problem: the acquisition of the same anatomical trait in diverse organisms with not common ancestry, a process called convergence. This is one of the oldest and most important issues in phylogenetic reconstructions (Darwin, 1859; Henning, 1966).

Sometimes, we found conflict between morphological and molecular phylogenies reconstruction, and convergence could be an explanation for these incongruences (e.g. Hedges and Sibley, 1994; Hollar and Springer, 1997; McCracken and Sheldon, 1998; McCracken *et al*., 1999; Teeling *et al*., 2002). Often, the convergence is used as a reason to reject morphological data in favour of molecular data for the reconstruction of phylogenies (Hedges and Maxson, 1996; Givnish and Sytsma, 1997) but actually, as mentioned above convergence may also be problematic for phylogenetic analysis of molecular data (Bull *et al*., 1997; Wiens *et al*., 2003).

Another important issue in molecular data is that, in general, the phylogenetic inferences are carried out with few genes and the gene-phylogenies do not necessarily explain the same history as the organisms. For this reason, both data are useful and necessary to systematic and phylogenetic analysis but we have to use both data with caution (Wiens *et al*., 2003) and must take into account the specific restrictions of each method.

As mentioned above, molecular genetic methods have many advantages and these methods are widely used for the determination of the relationships of taxa and help to solve systematic problems in many groups, but it has recently started being used in Zoarcids.

In the last few years, some authors have attempted to study the relationships among suborders, families and genera. But the studies do not include all genera because it is a large family with a wide distribution, and some genera inhabit in remote sites, making it difficult to get samples. For this reason, the authors have studied the relationships among species within the same genus or few genera, usually addressed to specific taxonomy problems. For example, the study of nucleotic sequence variation of the mitochondrial COI gene in *Zoarces* (Radchenko *et al*., 2008a); phylogeny of the genus *Lycodes* (Møller and Gravlund, 2003); relationships among some species of the subfamily Gymnelinae (Radchenko *et al*., 2008b); phylogenetic relationships between some genera of the family Zoarcidae (Radchenko *et al*., 2008c), relations of some taxa of the subfamily Lycodinae (Radchenko *et al*., 2009) and relationships among *Ophthalmolycus amberensis* and *Pachycara sp.* from the Ross Sea (Smith, 2012).

Other authors studied teleostean phylogenies including a large number of taxa, but usually only one or two sequences from family Zoarcidae. These studies are

interesting to search eelpouts relatives (Chen *et al*., 2003; Miya *et al*., 2003; Dettaï and Lecointre, 2004, 2005; Li *et al*., 2009; Dettaï *et al*., 2011). Zoarcoidei has been allied with Blennioidei (Stepien *et al*., 1997), Notothenioidei (Stepien, 1997), Trachinoidei and Cottoidei (Chen *et al*., 2003, Dettaï and Lecointre, 2004, 2005), Gasterosteoidei (Miya *et al*., 2003, Kawahara, 2008, Li *et al*., 2009). Different sequences have been used for these studies: cytochrome b, cytochrome oxidase I, 12S, 16S, 28S and rhodopsin, but the closest group of Zoarcidae is still unclear and more molecular and morphological data are required.

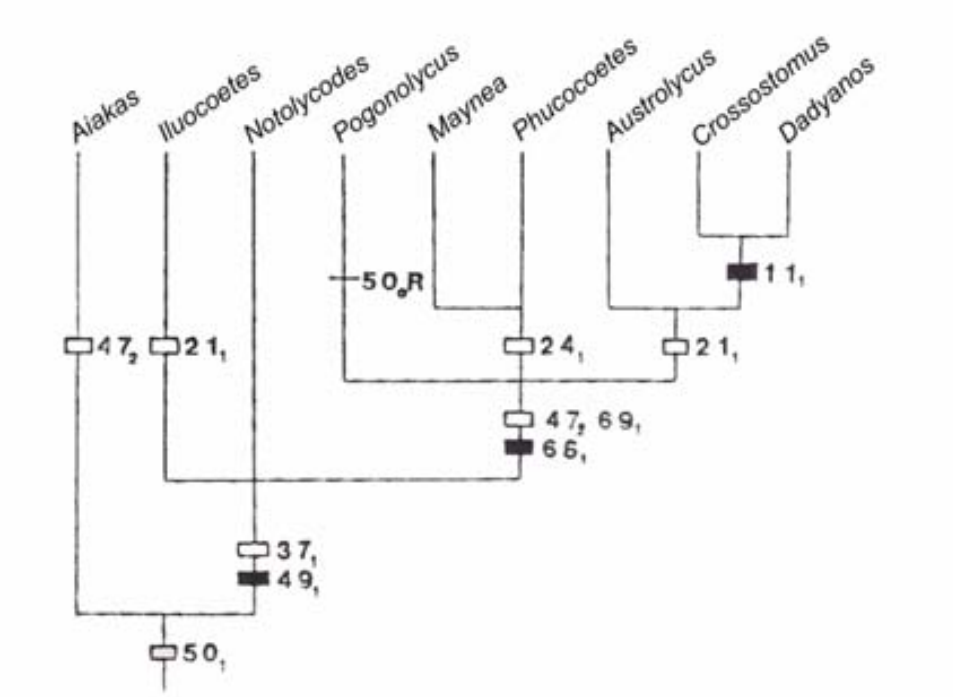


Figure 4. Phylogenetic hypothesis of the relationships among the endemic Magellan Province genera (Anderson, 1994). Black bars, synapomorphies; open bars, homoplastic. Character numbers listed in chapter 1, 2 and 4.

1.3 OBJECTIVES

1.3.1 Taxonomic and phylogenetical study of Lycodinae

This PhD thesis is focused on the study of the subfamily Lycodinae. This subfamily was described for the first time as Lycodoida by Gill (1862), and it was placed within family Blennioidae that contained four subfamilies. Two of these subfamilies (Zoarcinae Gill, 1862 and Lycodinae Gill, 1862) are still valid today.

Subfamily Lycodinae is a very successful and highly diversified group distributed throughout most oceans and seas of the world, including Arctic and Southern Ocean. It is the largest subfamily of family Zoarcidae and it includes 38 genera (table 1) and around 190 species (Anderson, 1994; Anderson and Fedorov, 2004; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2009c, 2010, 2011a, 2011b). It is worth mentioning that several new genera have been recently described *Leucogrammolycus* Mincarone and Anderson, 2008 from Brazil and *Gosztonyia* Matallanas, 2009a; *Bellingshausenia* Matallanas, 2009b; *Santelmoa* Matallanas, 2010 and *Bentartia* Matallanas, 2010 from Southern Ocean. Other genera (*Patagolycus* Matallanas and Corbella, 2012 and *Argentinolycus* Matallanas and Corbella, 2012) are described in this thesis jointly with a redescription of *Iluocoetes* (see Chapter 1).

Subfamily Lycodinae is defined on the basis of two synapomorphies: the reduction of the oral valve and the suborbital bone chain in a reversed L-shaped pattern (fig.5). Other important characters are the following: Body and tail elongate, vertebrae 58–144. Branchiostegal membranes attached to isthmus except free posteriorly in *Lycodapus* ; gill slit usually broad, restricted in a few species. Interorbital pore usually absent. Single epural with 1–2 rays. Caudal fin rays 6–12. Suborbital bones 4–9, usually 6–8. No fin spines except a fused pelvic splint formed in a few species (Anderson and Fedorov, 2004).

The genus *Lycodes* is the largest group of zoarcid fishes including 62 species (Anderson, 1994; Møller, 2000a, 2000b, 2001a, 2001b). This genus inhabits only in the northern hemisphere and morphology phylogenetic analyses establish that *Lycodes* is the most primitive genus of the subfamily Lycodinae based on one plesiomorphic character: parasphenoid wing height is high (above mid-height of trigeminofacialis foramen) whereas it is low in all other Lycodinae (Anderson, 1984,

1994). Monophyly of the group is generally accepted based on one autapomorphic character, the submental crest (Anderson, 1994; Andriashev, 1954; Møller and Anderson, 2000).

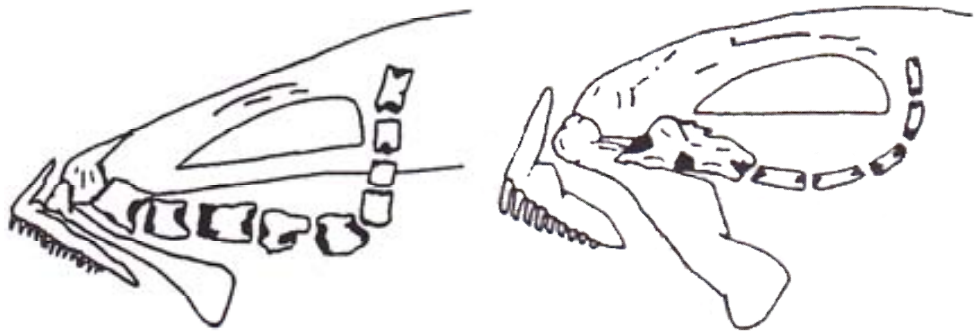


Figure 5. Suborbital bone configuration. Subfamily Lycodinae (*Bothrocara tanakae*) **(A)** and Subfamily Zoarcinae (*Zoarces gilli*) **(B)** (Anderson, 1994)

1.3.2 Area of the study

The specimens studied in this thesis are from SW Atlantic Ocean (Falkland/Malvinas Islands), Gerlache Strait (Southern Ocean) and Solomon Sea (Pacific Ocean).

In SW Atlantic Ocean (Magellan province) subfamily Lycodinae is represented by 14 genera, 12 of these are endemic of this area (*Aiakas*, *Austrolycus*, *Crossostomus*, *Dadyanos*, *Iluocoetes*, *Letholycus*, *Maynea*, *Notolycodes*, *Phucocoetes*, *Piedrabuenia*, *Plesienchelys and Pogonolycus*), and in the last year two new endemic genera have been added to the list (*Patagolycus* and *Argentinolycus*) as a result of this thesis (see Chapter 1) (fig. 6).

Figure 6. Distribution of endemic Magellan Lycodinae

The Southern Ocean has different characteristics from the rest of the world's oceans. It is the youngest ocean and it is the major connection among the Atlantic Ocean, the Pacific Ocean and the Indic Ocean and is generally considered to extend from Antarctic continent in the south, to the Subtropical Convergence in the north (Foster and Middleton, 1984). The Southern Ocean was formed between Eocene and Oligocene when Gondwana fragmented and Antartica broke away from South America with the subsequent creation of the Drake Passage (Loeb *et al*., 1993). As a consequence, the Antarctic Circumpolar Current appeared (Barmes and Conlan, 2007).

The circulation of the Southern Ocean is dominated by three main circumpolar fronts: from north to south, these are the Sub-Antarctic Front (SAF), the Antarctic Polar Front (APF) (Emery, 1977; Whitworth, 1980) and the Antarctic Circumpolar Current (ACC). The ACC is the most important current in the Southern Ocean; the ACC eastward flow is driven by strong westerly winds. These fronts are known as Polar Frontal Zone (Hanson and Gordon, 1998) (fig. 7).

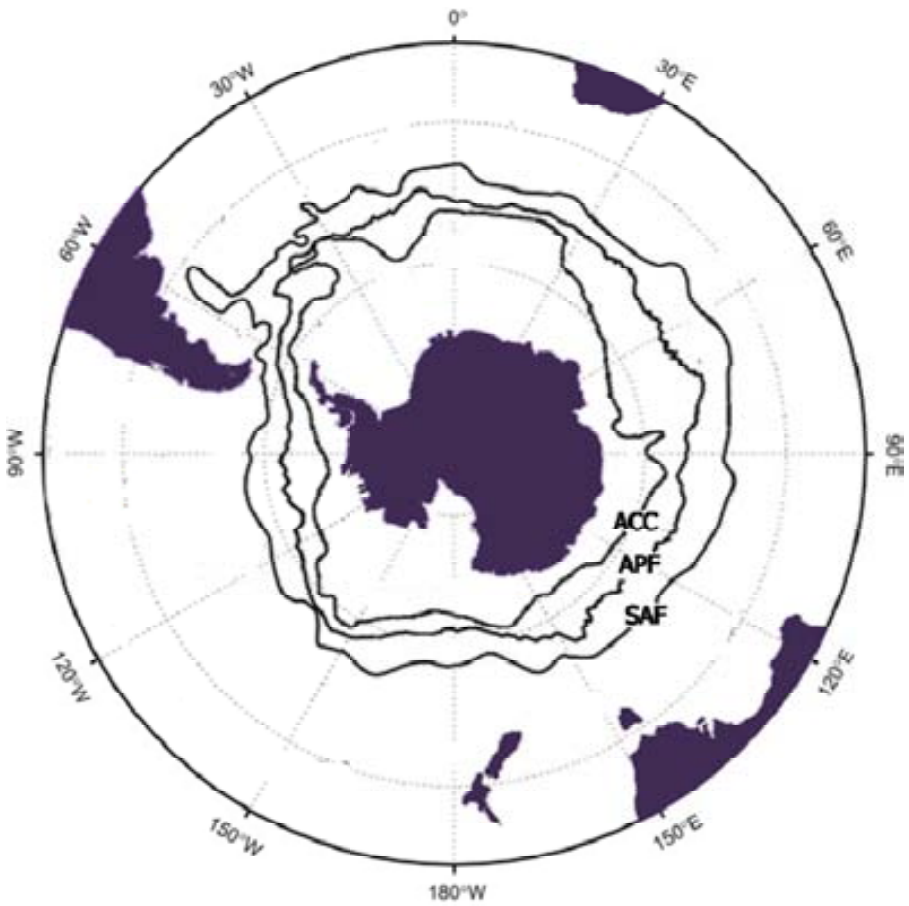


Figure 7. The three main circumpolar fronts from Southern Ocean. SAF, Sub-Antarctic Front; APF, Antarctic Polar Front; ACC, Antarctic Circumpolar Current. (Orsi *et al*., 1995).

The Antarctic characteristic led to a speciation process and it has become a place with a rich biota with endemic taxa, the fauna distinctiveness of the Antarctic Region is almost incredible. A high level of endemism is a distinguishing feature of the Antarctic fish fauna (Eastman, 2005), among the benthic fishes the endemism fauna rate rises to 88% for species and 76% for genera (Andriashev, 1987), and species level endemism rate for invertebrates is also high (51% to 91% depending on the group) (Arntz *et al*., 1997; Brandt, 1999).

Zoarcidae is one of the largest taxa in the Southern Ocean (Eastman, 2005), 12 genera are known from this Ocean, 5 of these are endemic (*Lycodichthys*, *Gosztonyia*, *Bellingshausenia*, *Bentartia* and *Santelmoa*) (Gill, 1884; Matallanas, 2009a, 2009b, 2010). Only 2 genera *(Lycenchelys* and *Oidiophorus*) are common in the

Southern Ocean and the South Atlantic Ocean. The specimens studied are from Pacific waters of Antarctic Peninsula and from the Bellingshausen Sea (fig. 8).

Figure 8. The area where the specimens studied were collected.

Finally, some specimens were collected in Western South Pacific Ocean. Particularly, in the Solomon Sea which is bounded by New Guinea on the west and Solomon Islands on the east and lies between the New Britain on the north and the Louisiade Archipelago on the south (fig. 9). Few genera and species of Lycodinae are known in Western Pacific Ocean.

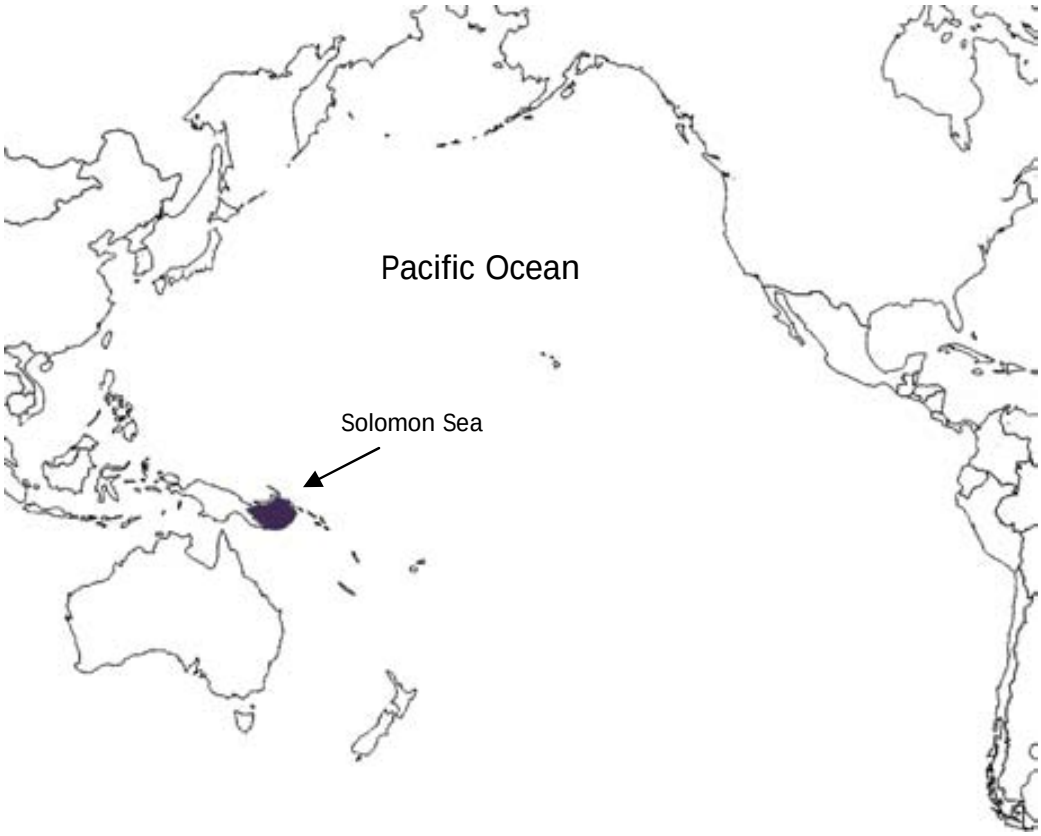


Figure 9. Location of Solomon Sea

1.3.3 Specific objectives

This thesis aims to contribute to the improvement of knowledge about the Lycodinae (Zoarcidae), a peculiar group of fishes little known. Until relatively recently, this subfamily has been carefully studied, but its systematic is still unclear and there are aspects that are unknown and it is highly probable that many species and genera will remain undescribed. The main aims of this PhD are to review specimens of subfamily Lycodinae of the above mentioned regions and identify and classify them at the species level, as well as perform a phylogenetic study with molecular and morphologic data.

The specific targets of this thesis are the following:

1. To make an anatomical study of specimens of Lycodinae, allowing the taxonomic identification of the collected material.

2. To describe new species found in the reviewed material through anatomical characters.

3. To obtain genetic information about species and genera that have been recently described, and investigate the genetic diversity among some genera of subfamily Lycodinae.

4. To evaluate different genes that may be useful to establish the phylogenetic relationships subfamily Lycodinae genera.

5. To obtain mitochondrial sequences of representative genera of subfamily Lycodinae and to use it to reconstruct a phylogeny of the group.

To achieve the aforementioned objectives, the following works have been undertaken:

CHAPTER 1:

Matallanas, J and Corbella, C. (2012) Redescription of *Iluocoetes* Jenyns, 1842, proposal of a new genus, *Argentinolycus*, for *Iluocoetes elongatus* (Smitt, 1898) and description of *Patagolycus melastomus*, gen. et sp. nov. (Teleostei, Zoarcidae). *Zootaxa*, 3296:1-18.

CHAPTER 2:

Matallanas, J., Corbella, C. and Møller, P.R. (2012) Description of two new species of *Santelmoa*, *Santelmoa fusca* sp. nov. and *Santelmoa antarctica* sp. nov. (Teleostei, Zoarcidae) from the Southern Ocean. *Polar Biology*, 9:1395-1405.

CHAPTER 3:

Corbella, C. and Møller, P.R. Description of *Pachycara matallanasi* sp.nov. from Solomon Sea (Western South Pacific Ocean).

CHAPTER 4:

Corbella, C., Pérez, M., Møller, P.R. and Matallanas, J. Molecular and morphological phylogenies of some genera of subfamily Lycodinae (Teleostei, Zoarcidae).

CHAPTER 1

Redescription of *Iluocoetes* Jenyns, 1842; proposal of a new genus, *Argentinolycus*, for *Iluocoetes elongatus* (Smitt, 1898), and description of *Patagolycus melastomus* gen. et sp. nov. (Teleostei: Zoarcidae)

2 Redescription of ***Iluocoetes*** Jenyns, 1842, proposal of a new genus, ***Argentinolycus***, for ***Iluocoetes elongatus*** (Smitt, 1898) and description of ***Patagolycus melastomus***, gen. et sp. nov. (Teleostei, Zoarcidae).

2.1 ABSTRACT

The osteological characters of the two nominal species of *Iluocoetes*, *I. fimbriatus* and *I. elongatus* are quite different. The present definition of *Iluocoetes* based on osteological characters is not valid since it was based on characters found in *I. elongatus* but not in *I. fimbriatus*, the type species of the genus. In this chapter, *Iluocoetes* is redefined on the basis of osteological characters found in the holotype of *Iluocoetes fimbriatus* and other specimens of the species, and *Iluocoetes elongatus* is placed in another genus: *Argentinolycus* gen. nov. Besides, a new genus and species, *Patagolycus melastomus*, is described on the basis of fourteen specimens, 94-437 mm TL, collected from SW Atlantic Ocean, at depths of 164-489 m. The similarities found between *Patagolycus melastomus* sp. nov. and *Iluocoetes fimbriatus* in body colour as well as in many meristic and morphometric characters, represent a remarkable example of how challenging zoarcid taxonomy can be. The differences between these two species are highlighted. A tree showing interrelationships among the Magellanic endemic lycodine genera is included.

2.2 INTRODUCTION

The family Zoarcidae is one of the best represented in number of genera and species in the marine fish fauna of the southern tip of South America; these fish can be found from the intertidal zone to deep waters of the continental slope (Gosztonyi, 1977). Gosztonyi's (1977) review of the Zoarcidae of temperate South America (Magellan Province: Briggs, 1974), the first since Norman (1937), added three new genera and species and two new species to this area. Gosztonyi (1981) added a new species and Anderson (1988b) added two new genera and one new species to the Magellan Province zoarcid fauna. Twelve genera are endemics of this province of the Southern South America Region (Anderson and Gosztonyi, 1991).

Although there have been numerous systematic works on zoarcids of this area, many earlier genera and species have been inadequately described using characters of questionable value, causing misinterpretations among some workers (Anderson, 1994). The majority of recent systematic problems stem from the use of traditional morphometric characters that Anderson (1988b, 1994) found to be sexually dimorphic or allometric in several species of this family. Gosztonyi (1977, 1984) found ontogenic changes and sexual dimorphism in jaw dentition in some South American species.

Anderson (1994) found a consistent set of osteological, internal and external anatomical features in a systematic study of this family, redefining each genus and providing a phylogenetic hypothesis of the relationships of most of the endemic Magellan Province genera. Matallanas (2010) provides cladograms showing the interrelationships amongst the Antarctic and Magellanic lycodine genera, including four new Antarctic genera recently described (Matallanas, 2009a, 2009b, 2010).

Iluocoetes was established by Jenyns (1842) as monotypyc for *Iluocoetes fimbriatus*. Smitt (1898) described *Phucocoetes variegatus* with four forms: *elongatus*, *effusus*, *micropus*, and *macropus.* According to Regan (1913) only *P. variegatus elongatus* seems to be a distinct species, placing *P. v. efusus* and *P. v. micropus* within *Iluocoetes fimbriatus* Jenyns, 1842. Norman (1937) placed *P. v. elongatus* within *Iluocoetes* as *I. elongatus* (Smitt, 1898) and the other three forms of Smitt within *I. fimbriatus*. Gosztonyi (1977) re-examined in the NMR of Stockholm all Smitt's types, concluding that *P. v. macropus* is a junior synonym of *I. fimbriatus* while *P. v. effusus*

and *P. v. micropus* are identical with *I. elongatus* (Smitt, 1898). At present, according to Gosztonyi (1977), Anderson (1994) and Anderson and Fedorov (2004), *Iluocoetes* is represented by two species, *I. fimbriatus* and *I. elongatus.*

Anderson (1994) redefined *Iluocoetes* based on osteological characters obtained not from specimens of *Iluocoetes fimbriatus*, the type species of *Iluocoetes*, but from a 147 mm SL specimen of *Iluocoetes elongatus* (CAS 53297): cranium (8, fig. 3D, dorsal view of neurocranium; 62, fig. 112, left lateral view of neurocranium; fig. 113, bones of left side of head showing suborbital configuration; fig. 114, left splachnocranium and opercular bones), pectoral girdle (62, fig.115, left pectoral girdle) and caudal skeleton (63, fig. 116, two specimens, 147 and 131 mm SL; both CAS 53297). Although Anderson (1994) include as material examined a cleared and stained specimen of *I. fimbriatus* (ZMH 104782, former ISH 1401-1966), and another superficially dissected (ZMH 104500, former ISH 1359-1966) no osteological characters of those specimens were described by the author. At present the osteological characters of *I. fimbriatus*, the type species of *Iluocoetes*, remain unknown.

The anatomical study of a lot of eelpouts captured in Argentinian waters (SW Atlanctic Ocean) by the Instituto Español de Oceanografía, and assigned to *Iluocoetes fimbriatus* Jenyns, 1842 following Gosztonyi's (1977) key and description, revealed that they do not agree with the osteological characters found by Anderson (1994) in *I.elongatus* and used by this author to redefine *Iluocoetes*. Thus, the osteological characters of the two nominal species of *Iluocoetes*, *I. fimbriatus*, described herein, and those of *I. elongatus*, described by Anderson (1994), are quite different. Consequently, the present redefinition of *Iluocoetes* by Anderson (1994) is not valid since it was based on osteological characters found in *I. elongatus* but not in *I. fimbriatus*, the type species of the genus.

In this chapter, *Iluocoetes* is redefined on the basis of osteological characters found in the holotype of *Iluocoetes fimbriatus* and in other specimens of the species; *Iluocoetes elongatus* is placed in another genus: *Argentinolycus* gen. nov. Furthermore, the anatomical study of some specimens from the SW Atlantic Ocean, that are similar to *I.fimbriatus* in general body colour as well as in many meristic and morphometric characters, but differs from it in having a black orobranchial cavity, scales on head and in pectoral fin base and axil, a different head colour and two

posterior nasal pores amongst other, revealed that such specimens differ from *I. fimbriatus* not only in the characters listed before, but also in many osteological characters of generic range. Consequently, a new genus and species, *Patagolycus melastomus*, is described. The relationships of the three monotypic genera are discussed.

2.3 MATERIALS AND METHODS

2.3.1 Material examined

Iluocoetes fimbriatus Jenyns, 1842: 166, Pl. 29 (figs. 2-2a):

HOLOTYPE (unique): BMNH 1917.7.14.69, Chiloé Archipelago, Chile. BMNH 1912.7.1.84, 140 mm TL, SW Atlantic Ocean, Port Stanley, Falkland (Malvinas) Islands. BMNH 1936.8.26.984-987, 122 mm TL, SW Atlantic Ocean, R.R.S. William Scoresby Cruise, 49º78'33''S, 61º11'66'' W, Falkland (Malvinas) Islands, 5 December 1931. BMNH 1936.8.26.962-973: 77, 102, 147 and 155 mm TL, SW Atlantic Ocean, R.R.S. William Scoresby Cruise, Bahía Grande, Argentina, 51º17'S, 68º50'W, 10 January 1932. BMNH 1936.8.26.988-991, 132 and 203 mm TL, SW Atlantic Ocean, Patagonian Shelf, 50º28'S, 60º10'W , 28 April 1928. BMNH 1842.2.12.1, 101 and 122 mm TL (syntypes of *Lycodes variegatus* Günther, 1862), SW Atlantic Ocean, Falkland (Malvinas) Islands. UAB.P44, 113 mm TL juvenile; UAB.P46 (damaged), 200 mm TL male; UAB.P25, 210 mm TL; UAB.P45, 218 mm TL and UAB.P47, 224 mm TL, used for anatomical analysis (cranium, suspensorium, pectoral girdle) all five specimens from the SW Atlantic Ocean, Atlantis-09 campaign, stn 7, 45º24'95"S, 60º01'21"W, 350-360 m, 3 March 2009). ZMH 104782 (former ISH 1401-1966), 302 mm SL; Burdwood Bank, South Atlantic, FRV "Walther Herwig", stn 337/66: 54º00'S, 58º21'W, 200 m, 1 July 1966. *Iluocoetes facali* Lloris and Rucabado, 1987: IIPB 114/1987. Holotype, 105 mm TL, intertidal, Tierra del Fuego (Argentina), 54º52'S 67º20'W, 1976 (fig.10).

Argentinolycus elongatus (Smitt, 1898):

ZMH 107650 (former ISH 25-1970), Puerto Deseado, Santa Cruz Province, Argentina, 47º45'S, 65º52'W, under stones in the intertidal zone, January 1971, 2 specimens, 139 and 156 mm TL. UAB.ZM41-42 (former CNPICT 1971/36), 150 mm TL mature female, and 147 mm TL mature male, sent to the first author by Dr. Atila E. Gosztonyi as a gift; same locality (fig.10).

Patagolycus melastomus gen. et sp. nov.:

HOLOTYPE: UAB.ZM2, 437 mm TL, male, SW Atlantic Ocean, Atlantis-2010 campaign, 46º26'50''S, 60º21'37''W, 253 m, 17 March 2010.
PARATYPES: UAB.ZM3, 355 mm TL, male, same collection data as holotype. UAB.ZM8, 385 mm TL, female, and UAB.ZM9, 288 mm TL, female, SW Atlantic Ocean, Atlantis-2010 campaign, 45º28'24''S, 60º02'66''W, 313 m, 11 March 2010. UAB.ZM14, 295 mm TL, male, SW Atlantic Ocean, Atlantis-2010 campaign, 45º05'92''S, 59º59' 46''W, 288 m, 9 March 2010. UAB.ZM22, 318 mm TL, female, SW Atlantic Ocean, Atlantis-2010 campaign, 46º05'77''S, 60º09'48''W, 319 m, 16 March 2010. UAB.ZM24, 322 mm TL female, SW Atlantic Ocean, Atlantis-2010 campaign, 46º39'39''S, 60º19'74''W, 457 m, 18 March 2010. UAB.ZM29, 178 mm TL, female, SW Atlantic Ocean, Atlantis-2010 campaign, 47º30'68''S, 60º29'38''W, 489 m, 23 March 2010. BMNH 1936.8.26.962-973 (212), 233 mm TL, male, SW Atlantic Ocean, R.R.S. William Scoresby Cruise, Bahía Grande, Argentina, 51º17'S, 68º50'W, 10 January 1932. BMNH 1936.8.26.984-987: (984.2), 107 mm TL, (984.3), 103 mm TL, (984.4), 95 mm TL, SW Atlantic Ocean, R.R.S. William Scoresby Cruise, 49º78'33''S, 61º11'66''W, Falkland (Malvinas) Islands, 5 December 1931. UAB.P24, 395 mm TL, male, and UAB.P25, 246 mm TL, female, SW Atlantic Ocean, Atlantis-2009 campaign, 45º24'95''S, 60º01'21''W, 350 m, 3 March 2009 (used for anatomical analysis)(fig.10).

Additional material examined:

ZMH 104500 (former ISH 1359-1966), 328 mm SL, Burdwood Bank, South Atlantic, FRV "Walther Herwig", stn 317/66, 48º16'S, 60º12'W, 400 m, 26 June 1966 (figured in Anderson 1994, 61, fig. 111 as *Iluocoetes fimbriatus* Jenyns, 1842, is actually a

Patagolycus melastomus). *Notolycodes schmidti* Gosztonyi, 1977 (ZMH 115857, former ISH 391-1978), 386 mm SL, South Atlantic, FRV "Walther Herwig", stn 926/78: 37º8'S, 54º14'W, 602 m, 28 September 1978.

Counts, measurements and general terminology follow Gosztonyi (1977, 1988) and Anderson (1982, 1994) (see annex 1 and 2). 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 (table 2).

Figure 10. Location of *Iluocoetes fimbriatus*, *Argentinolycus elongatus* and *Patagolycus melastomus*

Osteological observations were made on cleared and stained specimens. The definitions of the character states in this paper follow those of Anderson (1994) with some additions and modifications (Matallanas, 2010). Institutional abbreviations follow Leviton *et al.*, (1985). Abbreviations used in the text: TL, total length; SL, standard length.

Phylogenetical reconstruction was performed using PAUP (Swofford, 2002). It was analyzed based on 78 transformation series (TS) (76 from Anderson, 1994), all of which are informative for the intergeneric relationship in the subfamily. Monotypic *Lycozoarces* Popov, 1935 (Lycozoarcinae), primitive sister group of all other zoarcids (Anderson, 1994), was designed as outgroup taxa. Phylogenetic tree was calculated using maximum parsimony. Nodal support was calculated with 1000 bootstrap replicates. TS numbers used here are those assigned to each character by Anderson (1994), with the following modifications and additions: Frontal fusion (TS23) could be considered as multi-state (0, 1, 2) (Matallanas, 2010); TS77, basioccipital-exoccipital fusion, and TS78, intercalary development are added (table 3).

The TS series used are as follows. TS1, adult body form: body robust (0), body slender (1); TS2, tail length: relatively short (0), elongate (1); TS3, squamation: present (0), absent (1); TS4, condition of flesh: firm (0), gelatinous (1); TS5, lateral line: present (0), absent (1); TS6, lower jaw: not deep (0), deep (1); TS7, lip development: present (0), absent (1); TS8, upper lip attachment: free (0), adnate (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); TS13, oral valve enlargement: free edge extends to or before vomer (0), free edge greatly overlaps vomer (1); TS14, chin pad: absent (0), present (1); TS15, submental crests: 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); TS19, eye lens: normal (0), with opaque matter (1); TS20, parasphenoid wing height: ascending rami of parasphenoid wing reaches above the mid-height of the trigeminofacialis foramen (TGF) (0), parasphenoid wing broad, but without dorsal ramus projecting above ventral base of TGF (1); TS21, frontal corner: squared off (0), tapering (1); TS22, frontal ramus: long (0), shortened (1); TS23, frontal fusion: frontal bones 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 mid-line (0), in contact (1); TS28, supraoccipital blade: present (0), absent (1); TS29, supraoccipital–

exoccipital articulation: narrowly contacting or excluded by epioccipitals (0), broadly contacting (1); TS30, anterior section of pterotic: narrower than posterior section (0), wider than posterior section (1); TS31, head pores: present (0), absent (1); TS32, interorbital pores: present (0), absent (1); TS33, suborbital bone configuration: circular pattern (0), L-shaped pattern (1); TS34, dorsalmost preopercular foramina: foramen 7 at mid-height of preopercle, foramen 8 below dorsal edge (0), foramen 7 above mid-height of preopercle, foramen 8 at dorsal edge (1); TS35, preopercular and mandibular canals: continuous (0), separated (1); TS36, number of lateral extrascapulars: 2 (0), 0-1 (1); TS37, supratemporal commissure and occipital pores: present (0), absent (1); TS38, postorbital pores, present (0), absent (1); TS39, posterior nasal pores: present (0), absent (1); TS40, posterior nasal pore development: single (0), double (1); TS41, dentary foramina: foramina for preoperculomandibular pores 1-4 present (0), anterior foramina absent (1); TS42, pore from ventralmost preopercular foramen: absent (0), present (1); TS43, male caniniform dentition: absent (0), present (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 ventral edge of 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); TS53, lower pharyngeal teeth: present (0), absent (1); TS54, upper pharyngeals: 3 (0), 2 (1); TS55, shape of first epibranchial: rod-like (0), fan-shaped (1); TS56, postorbital canal passage: through lateral extrascapulars, posttemporal and supracleithrum (0), through lateral extrascapulars only (1); TS57, posttemporal ventral ramus: well developed (0), weak or absent (1); TS58, cleithrum ventral ramus: absent (0), present (1); TS59, scapular foramen: enclosed by bone (0), open (1); TS60, scapular strut: present (0), absent (1); TS61, postcleithrum: present (0), absent (1); TS62, number of pectoral actinosts (=radials): 4 (0), 2-3 (1), absent (2); 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); TS66, pelvic bone: present (0), absent (1); TS67, number of vertebrae: 58–71 (0); 72–105 (1), 109–134 (2), 134–150 (3); TS68, retrograde dorsal fin origin: first pterygiophore associated with vertebrae 1-2 (0), associate with vertebrae 3-17 (1); TS69, advanced dorsal fin origin: first pterygiophore associated with vertebrae 1 or greater (0), first pterygiophore anterior to first vertebrae (1); TS70, posterior dorsal-fin pungent spines: absent (0), present (1); TS71, middle-dorsal-fin elements: absent (0), present (1); TS72, free dorsal-fin pterygiophores: 0-2 (0), 3-14 (1); TS73, unpaired fin scutes: absent (0), present (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); TS78, intercalar development: reaching prootic and excluding exoccipital–pterotic articulation (0); not reaching prootic and more or less reduced (1).

2.4 RESULTS

The osteological characters of the two nominal species of *Iluocoetes*, *I. fimbriatus* and *I. elongatus* are quite different. The present redefinition of *Iluocoetes* by Anderson (1994) is not valid because it is based on osteological characters found in *I. elongatus* but not in *I. fimbriatus*, the type species of the genus. In this chapter, *Iluocoetes* is redefined on the basis of the examination of the holotype of *I. fimbriatus* (+radiographs), as well as on other specimens of the species. *Iluocoetes elongatus*, whose osteological characters differs from those of *I. fimbriatus*, is placed in another genus, *Argentinolycus* gen. nov. Besides, a new genus and species, *Patagolycus melastomus*, is described.

2.4.1 Genus *Iluocoetes* Jenyns, 1842

Iluocoetes Jenyns, 1842: 166. Type species: *Iluocoetes fimbriatus* Jenyns, 1842: 166, Pl. 29 (figs. 2-2a). Type by monotypy. *Paralycodes* Bleeker, 1874: 369. Type species *Lycodes variegatus* Günther, 1862. Type by original designation. Monotypyc.

Caneolepis Lahille, 1908: 431. Type species *Caneolepis acropterus* Lahille, 1908: 431-437, Pl. VII (figs. 1-10). Type by monotypy. No type material available (Gosztonyi, 1977:213; G. Chiaramonte, fish curator, MACN, 2011, in litt.) (fig. 11).

Figure 11. *Caneolepis*, Lahille 1908. Left lateral view

Redescription of *Iluocoetes* Jenyns, 1842

(Figs. 12, 13 and 21; tables 3-5)

Diagnostic characters found in the holotype (+radiographs): Submental crests present, not fused anteriorly; neurocranium elongate, narrowed; frontal bones fused totally with no trace of a suture; frontal corner squared; frontal ramus long; sphenotic and parietal separated by pterotic; parietal bones meeting in the mid-line; parasphenoid wing height high; ceratohyal-epihyal juncture smooth; five branchiostegal rays; posterior hyomandibular ramus elongate; palatal arch well developed; posttemporal ventral ramus well developed; scapular foramen enclosed by bone; scapular strut present; four notched radials (=actinosts); postcleithrum present; dorsal fin-rays 85 (last 7 counted from dorsal-fin pterygiophores); anal-fin rays, 71 (last 10 counted from anal-fin pterygiophores); pectoral fin rays 18; pelvic bone present; vertebrae asymmetrical (21+68=89); ribs on 4–21 abdominal vertebrae; one epural; dorsal-fin origin associated with vertebrae 4; oral valve well developed; gill slit extending ventrally to lower end of pectoral-fin base; gill rakers blunt; pyloric caeca nub-like; scales, palatine and vomerine teeth present; oral cavity pale; peritoneum, black; a blurred brown band between the anteroventral edge of the eye and the upper jaw.

All these characters are present also in the other specimens of *I. fimbriatus* examined, and additional diagnostic characters of *Iluocoetes* based on cleared and stained specimens of *I. fimbriatus* for anatomical study, are the following (fig. 13a, b): frontal and parasphenoid not separated by pterosphenoid; supraoccipital-exoccipital articulation excluded by epioccipitals (fig. 13b); supratemporal commissure and occipital pores absent; ascending rami of the parasphenoid reaches the upper margin of the trigeminofacialis foramen; intercalar well developed, not reaching prootic (fig. 13a); suborbital bones 8-9, canal with 7 pores; postorbital pores 1 and 4; posterior nasal pore single; cartilaginous basal plate of pectoral girdle with three foramina; vertebrae asymmetrical (19-21+64-77=83-97); dorsal-fin origin associated with vertebrae 2-4; oral valve well developed; gill rakers blunt; pelvic-fin rays ensheathed; squamation extensive, but head and pectoral-fin base and axil scaleless; lateral line mediolateral, palatine teeth 9-23; vomerine teeth 7-17.

Coloration in juvenile preserved specimens of *Iluocoetes fimbriatus* (UAB.P44, 113 mm TL; BMNH 1936.8.26.962-972: 77-155 mm TL; BMNH 1912.7.1.84, 140 mm TL; BMNH 1936.8.26.984-987, 122 mm TL). Head and body mid-brown coloured with dull white spots on both, head (nape, interorbital area, cheeks) and body,mainly in its dorsolateral part. A darker band on head between the anteroventral edge of the eye and the upper jaw. Ventrolateral part of both head and body light brown. Edge of dorsal fin with 5-6 darker bands. The character state of other diagnostic features of this genus are given in tables 2-5. Other descriptive characters of *I. fimbriatus* can be found in Gosztonyi (1977: 211-215). The general shape of *Iluocoetes fimbriatus* is in fig.12.

Figure 12. *Iluocoetes fimbriatus* BMNH 1936.2.26.988–991, 203 mm TL. Left lateral view showing a dark band between the antero-inferior edge of the eye and the upper jaw.

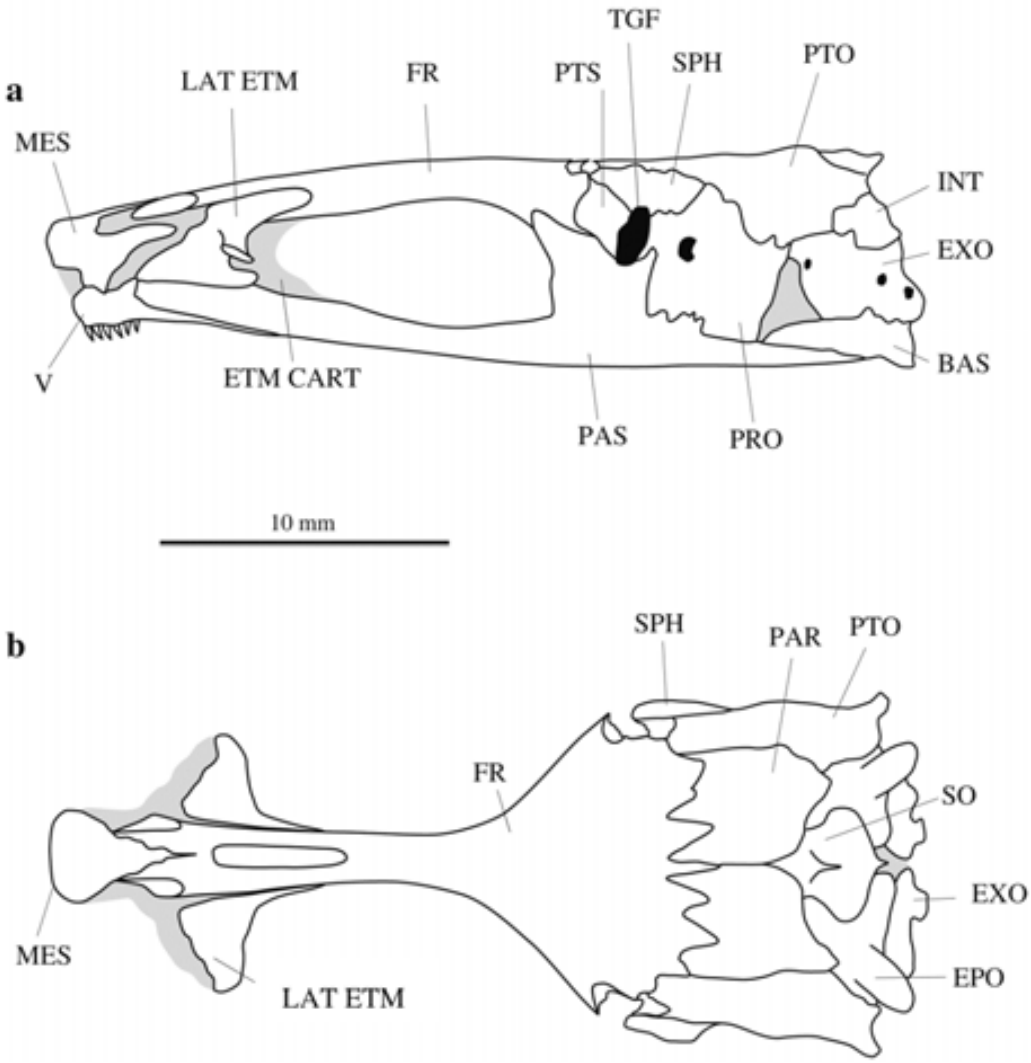


Figure 13. Neurocranium of *Iluocoetes fimbriatus* Jenyns, 1842. (UAB.P47, 224 mm TL). Lateral view **(a)** and dorsal view **(b).** BAS, basioccipital; EPO, epioccipital; ETM CART, ethmoid cartilage; EXO, exoccipital; FR, frontal; INT, intercalary; LAT ETM, lateral ethmoid; MES, mesethmoid; PAR, parietal; PAS, parasphenoid; PRO, prootic; PTO, pterotic; PTS, pterosphenoid; SO, supraoccipital; SPH, sphenotic; TGF, trigeminofacialis foramen; V, vomer.

2.4.2 *Argentinolycus* gen. nov.

(Fig. 14, 21; Tables 3-4)

Type species: *Phucocoetes variegatus elongatus* Smitt, 1898. A synonymy is found in Gosztonti (1977). Owing to misidentifications (Regan, 1913; Norman, 1937), the first available scientific name in print for this form is Smitt's (1898: 43) *Phucocoetes variegatus effusus*. As this name was not used until Anderson and Gosztonyi (1991: 2 in key only), the prevailing usage of *elongatus* is used here for nomenclatural stability.

The diagnosis given below is taken from the diagnosis and description of *Iluocoetes* given by Anderson (1994:61-63), based mainly on a 147 mm SL specimen of *Iluocoetes elongatus* (CAS 53295), and also from the description of *Iluocoetes elongatus* by Gosztonyi (1977). Skeletal structures are represented by Anderson (1994) cranium (8, fig. 3D: dorsal view of neurocranium; 62, fig. 112: left lateral view of neurocranium; fig. 113: bones of left side of head showing suborbital configuration; fig. 114: left splachnocranium and opercular bones), pectoral girdle (62, fig.115: left pectoral girdle) and caudal skeleton (63, fig. 116: two specimens, 147 and 131 mm SL, both CAS 53297) (fig. 14).

Diagnosis. Neurocranium elongate, depressed; parasphenoid wing broad, ut without dorsal ramus projecting above ventral base of trigeminofacialis foramen; frontal and parasphenoid articulating; pterosphenoid enlarged; intercalar very small, set posteriorly. Frontal bones separate; frontal corner tapering; parietals meeting in dorsal mid-line; supraoccipital small; supraoccipital and exoccipital narrowly articulating posteriorly; sphenotic excluded from parietal by frontal and pterotic.

Posterior ramus of hyomandibula elongate; palatopterygoid series well developed; ectopterygoid overlap both anterior and dorsal surface of quadrate. Ceratohyal-epihyal juncture with bone interdigitating along its entire length; branchiostegal rays 6. Suborbital bones 7-8, canal with 6 pores. Posttemporal ventral ramus absent; scapular foramen enclosed, scapula with well developed posterior strut; postcleithrum present. Vertebrae asymmetrical, 22-24+62-69 = 84-90.

Oral valve well developed; gill slit extending ventrally to slighly below lower end of pectoral-fin base; vertebrae asymmetrical; no interorbital or occipital pores and

no commissure across arietals; 6 suborbital pores along ventral ramus (6+0); two nasal pores; only postorbital pore 4; lateral line mediolateral complete; pyloric caeca absent; pelvic-fin membranes excised at tip; scales, palatine and vomerine teeth present. The character state of other diagnostic features of this genus can be observed in Tables 3 and 4.

Description. A complete description of *Argentinolycus elongatus* (Smitt, 1898), type species of the new genus, can be found under *Iluocoetes elongatus* (Smitt, 1898) in Gosztonyi (1977: 215-217); other data are in Gosztonyi (1984, 1988).

Etymology. From Argentina, as the species is known mainly from the Argentine Patagonia, and the Greek *lykos* (wolf), a commonly used suffix for southern hemisphere zoarcid genera. Gender: masculine.

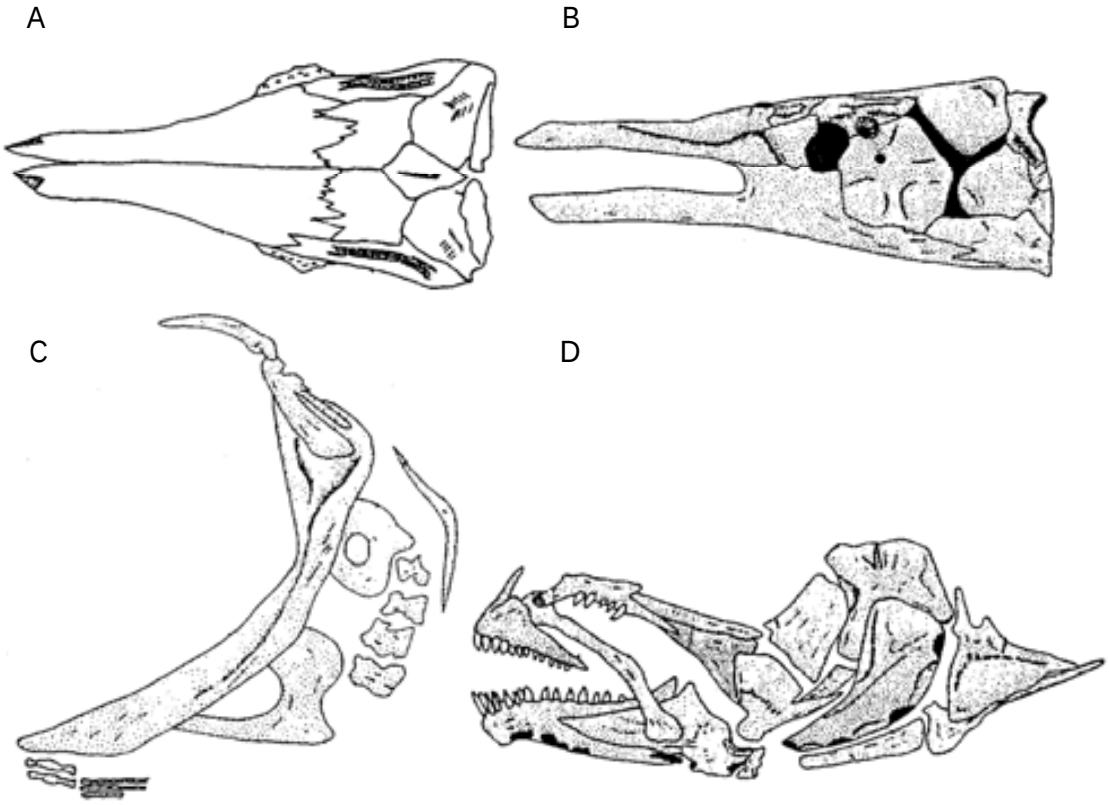


Figure 14. Skeletal structures of *Iluocoetes elongatus* actually *Argentinolycus elongatus* (Anderson, 1994). Dorsal view of neurocranium **(A)**; Left lateral view of neurocranium **(B)**; Pectoral girdle **(C)** and Left splachnocranium and opercular bones **(D)**.

2.4.3 *Patagolycus* gen. nov.

(Figs. 15-21; Tables 2, 3 and 5)

Type species: *Patagolycus melastomus* sp. nov.

Diagnosis. Submental crest present; neurocranium elongate, narrowed; frontals fused anteriorly with no trace of a suture; frontal corner squared; frontal ramus long; frontal and parasphenoid well separated by pterosphenoid; sphenotic and parietal in contact; parietals separated from mid-line; parasphenoid wing reaches the mid-height of the trigeminofacialis foramen; supraoccipital–exoccipìtal articulation excluded by epioccipital; supratemporal commissure and occipital pores absent; intercalar well developed; suborbital bones 8, canal with 7 pores; postorbital pores 1 and 4; ceratohyal–epihyal juncture interdigitating dorsally; five branchiostegal rays; posterior hyomandibular ramus elongate; palatal arch well developed; posttemporal ventral ramus well developed; scapular foramen enclosed by bone; scapular strut present; cartilaginous basal plate of pectoral girdle with four foramina; vertebrae asymmetrical; oral valve well developed; gill slit extending ventrally below lower end of pectoral-fin base; gillrakers scalloped; pelvic-fin rays ensheated; squamation extensive; lateral line, pyloric caeca, palatine and vomerine teeth present; oral cavity and peritoneum black.

Etymology. The generic name is composed of *Patago*, from Patagonia (the type species is found mainly in Patagonian waters) and the Greek *lykos* (wolf), a commonly used suffix for southern hemisphere zoarcid genera. Gender: masculine.

Patagolycus melastomus sp. nov.

Diagnosis. As for the genus.

Description. Body robust, short, ovoid in cross section. Tail laterally compressed especially posteriorly. Head robust, not depressed, as wide as high in both males and females; snout gently sloping. Mouth inferior; lips without lateral lobes.

Snout blunt, upper jaw slightly protruding, end of maxilla extending to posterior part of pupil in both males and females. Eyes slightly ellipsoid entering dorsal profile of head. Nasal tube pigmented at base, not reaching upper lip when depressed forward. Gill slit well developed, extending ventrally to below ventral edge of pectoral- fin base, but above pelvic fin insertion. Opercular lobe short, triangular (fig. 15 and 16).

Figure 15. *Patagolycus melastomus* gen. et sp. nov., UAB.ZM2 (holotype), 437 mm TL male, from SW Atlantic Ocean. Left lateral view showing general shape and body colour.

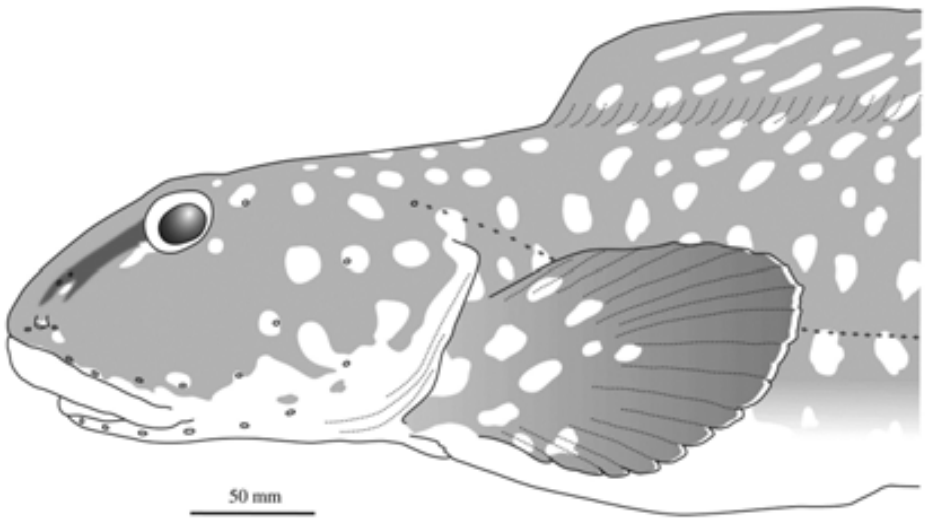


Figure 16. *Patagolycus melastomus* gen. et sp. nov., UAB.ZM2 (holotype), 437 mm TL male, from SW Atlantic Ocean. Left lateral view of head and trunk showing cephalic pore pattern, dark band between the anterior edge of the eye and the nostril tube, lateral line, and pectoral-fin shape.

Cephalic lateralis pore system with small pores. Nasal pores 3, one located anteromesial to nasal tube, two other posterodorsal to the nasal tube and the posterior one very small. Postorbital pores 1 and 4 present in all. Suborbital pores 6+1, in a reversed L-shaped pattern. Preoperculomandibular pores 8 (fig. 16). Interorbital pore absent. Supratemporal commissure and occipital pores absent. Lateral line mediolateral, extending from postorbital pore 4 to near tail tip.

Pectoral-fin origin at body midline; pectoral-fin base extending ventrally to abdomen; posterior margin of pectoral-fin ovoid; middle rays longest; 6-8 ventralmost rays thickened and exerted at tips (fig. 16). Flesh and skin firm; skin covering vertical fins. Scales relatively large, circular, non-overlapping, covering entire body, proximal two thirds of pectoral-fin base and axil, abdomen, tail, nape, posterior part of the interorbital space, cheeks, opercle, and vertical fins to nearly it margin. Two juvenile, BMNH 1936.8.26.984–987:(984.2), 107 mm TL and BMNH1936.8.26.984–987: (984.3), 103 mm TL, also have extensive squamation, including nape and upper part of opercle. The 94 mm TL specimen, BMNH 1936.8.26.984–987:(984.4), has scales throughout its body, but a scaleless head.

Neurocranium well ossified, narrowed. Frontal and parasphenoid well separated by pterosphenoid; sphenotic broadly articulating with parietal. Ascending rami of parasphenoid wing reaching mid-height of the trigeminofacialis foramen. Parasphenoid and prootic juncture, as well as prootic and pterotic juncture strongly interdigitating. Intercalar large, posteriorly set. Frontal ramus long, convex, with an anterior foramen in the interorbital space; frontal corner squared. Anterior portion of frontals fused with no trace of a suture, posterior portion showing a superficial suture; posterolateral edge of the frontals retreat. Supraoccipital wide, with a well developed median crest posteriorly; supraoccipital excluded from exoccipital by epioccipital; no supratemporal commissure across parietals. Ethmoid cartilage protruding well into orbital fenestra, with an anterior foramen (fig.17).

Teeth in jaws, vomer and palate conical. Upper jaw with 2-3 (in males), to 3-4 (in females) rows near symphysis merging into single posterior row; first premaxillary tooth is canine-like in adult males. Lower jaw with 3-4 (in males), to 4-5 (in females) irregular rows in the anterior part and single row in the posterior part; teeth of outermost rows larger than the inner rows ones. In the middle of the lower jaw, a tooth is distinctly enlarged in males (fig. 18a). A patch of 4–7 vomerine teeth.

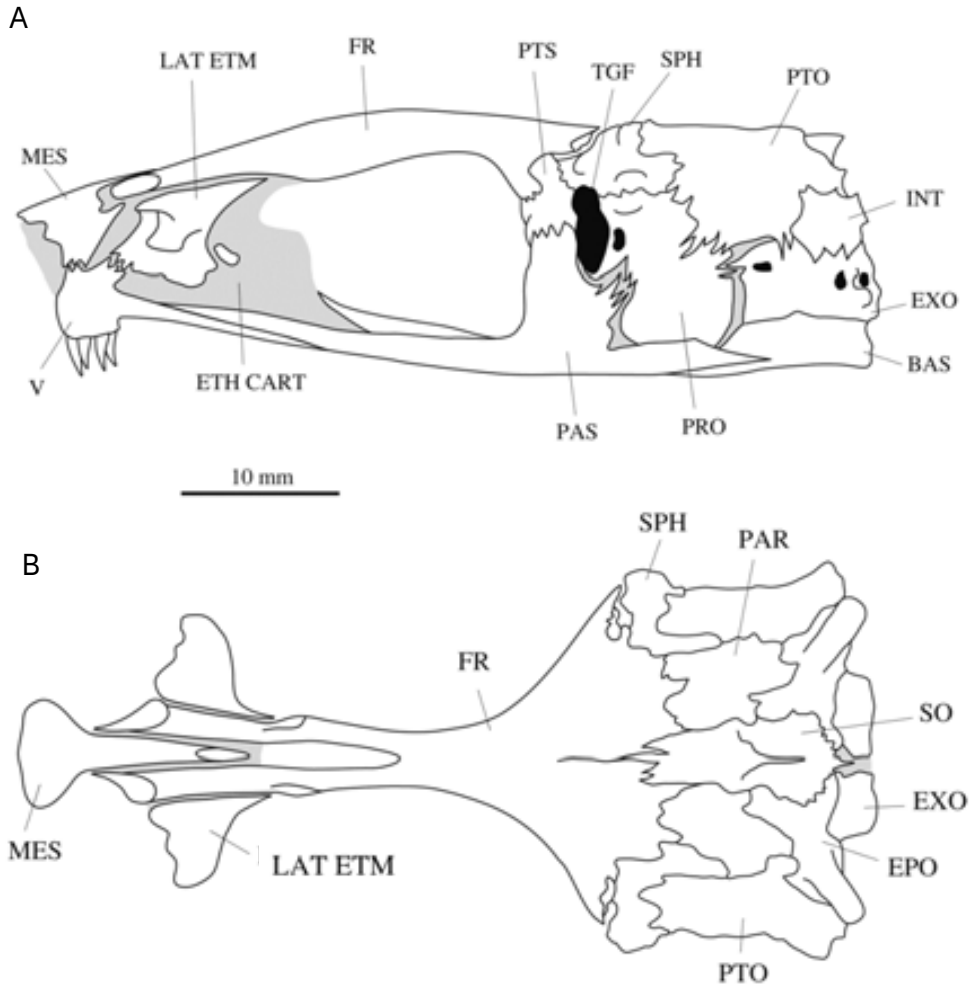


Figure 17. Neurocranium of *Patagolycus melastomus* gen. et sp. nov. (UAB.P24, 395 mm TL male). Lateral view **(A)** and dorsal view **(B).** BAS, basioccipital; EPO, epioccipital; ETH CART, ethmoid cartilage; EXO, exoccipital; FR, frontal; INT, intercalar; LAT ETM, lateral ethmoid; MES, mesethmoid; PAR, parietal; PAS, parasphenoid; PRO, prootic; PTO, pterotic; PTS, pterosphenoid; SO, supraoccipital; SPH, sphenotic; TGF, trigeminofacialis foramen; V, vomer.

Palatine teeth in a single row of 3-7 teeth. Lower jaw with reduced submental cartilaginous crests, not fused anteriorly (fig. 18a). Oral valve nearly reaching anterior edge of vomer and well separated from the palate laterally. Pyloric caeca two small nubs. Gill rakers 2-3+11-13=13-15, stout and scalloped (fig. 18b); in specimens preserved for a long periode of time, the indentations are likely to get damaged. Pseudobranch filaments 6−7, elongate.

Palatopterygoid series well developed (fig. 19a), with mesopterygoid overlapping more than half dorsal surface of quadrate and ectopterygoid overlapping half anterior surface of quadrate. Metapterygoid large. Posterior ramus of hyomandibula elongate. Hyoid bar with ceratohyal–epihyal joint with bone interdigitating dorsally (fig. 19b). Five branchiostegal rays: first, slender, attached on medial side of ceratohyal; remainder four thickened, 2 articulating on outer side of ceratohyal and 2 on outer side of epihyal.

Pectoral girdle (fig. 20) with a strong posttemporal bearing a well-developed ventral ramus. Supracleithrum with a posteriorly-directed prong. Scapular foramen enclosed by bone; prominent postero-dorsal scapular strut. Coracoid with a well-developed posterior strut and a foramen. Radials (=actinosts) 4, the uppermost smaller. Four foramina in the cartilaginous basal plate: one between each two radials, and another between radial 1 and scapula. Postcleithrum present. Pelvic-fin rays joined, ensheathed by the dermis.

Vertebrae asymmetrical, 20-21+65-72=86-93. Last precaudal vertebra associated with dorsal-fin rays 18-20. Dorsal-fin origin associated with vertebra 4 with no free pterygiophores. Dorsal-fin rays 83-89. Anal-fin rays 67-73. Terminal dorsal-fin ray associated with second preural vertebra. Terminal anal-fin ray associated with second preural vertebra. One epural. Caudal-fin rays 9-11, with 1-2 epural, four upper hypural and four or five lower hypural rays.

Fresh colouration. Medium to dark brown ground colour with 4-5 wide and darker vertical cross-bars from dorsal profile to well below body mid-line. Numerous circular and subcircular white spots on head, body, tail and pectoral fins; suborbital area without spots. Dorsal-fin with some slightly elongated white blotches. Edge of vertical fins black; anal-fin edge white in the male holotype. Edge of pectoral fins, ventral part of head, opercular edge, ventral fins and abdomen, white or dull white. A darker band across the snout between the anterior edge of the eye and the nasal tube (figs. 15 and 16). Lips pale; orobranchial cavity and peritoneum black. Coloration in preserved juvenile specimens of *Patagolycus melastomus*. Dorsolateral part of body mid-brown with dull white rounded spots; ventrolateral part lighter; dorsolateral part of head uniform mid-brown except a darker band on snout between the anterior edge of the eye and the nasal tube; ventrolateral part light. Edge of dorsal fin with 3–4 darker spots on its anterior half.

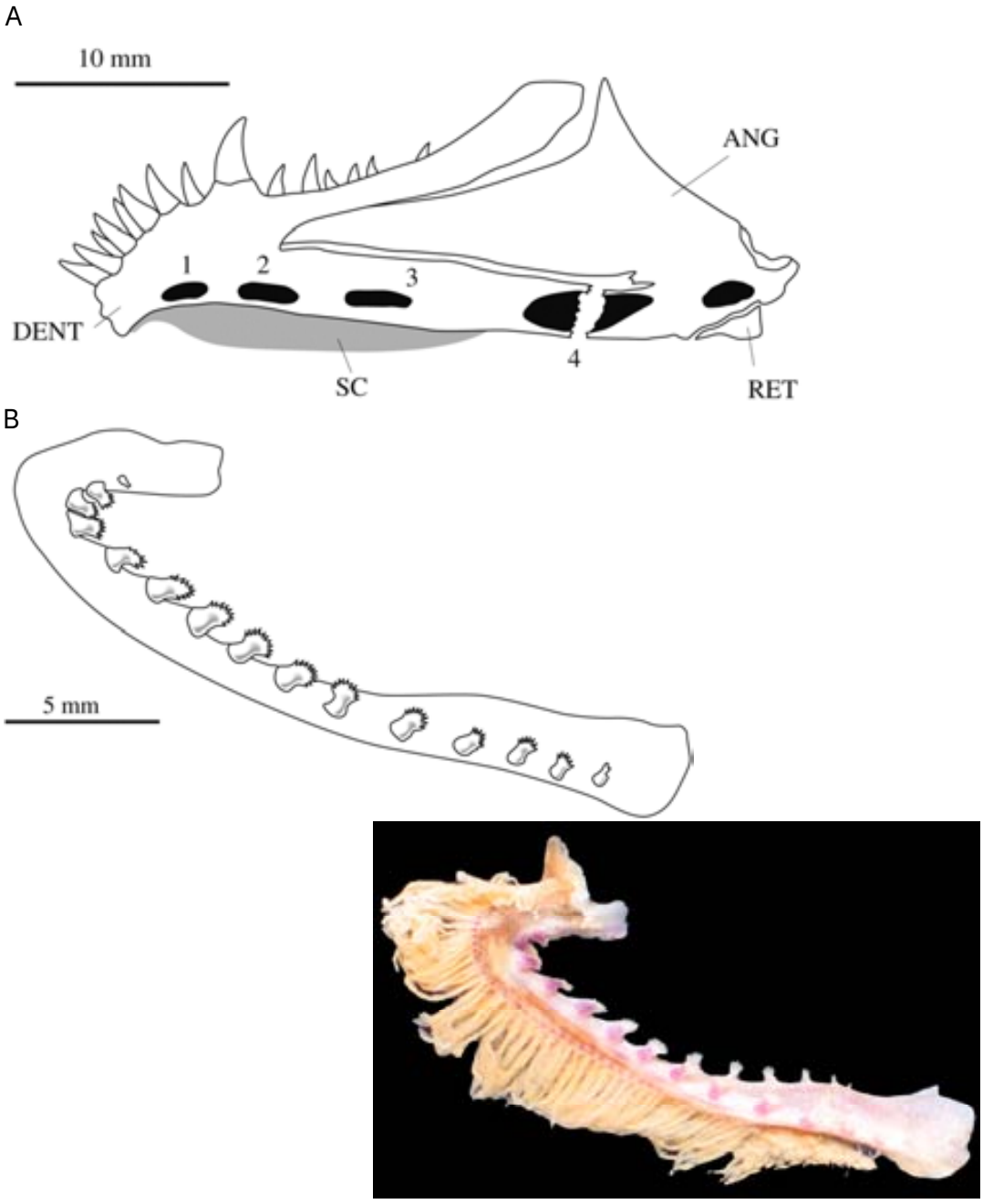


Figure 18. *Patagolycus melastomus* gen. et sp. nov. (UAB.P24, 395 mm TL male). Left lateral view of the lower jaw with submental crest **(A)**, First right gill arch with scalloped gill rakers **(B)**. ANG, angular; DENT, dentary; RET, retroarticular; SC, submental crest.

Table 2. Counts and Measurements of *Patagolycus melastomus* gen. et sp. nov. (see annex 1).

P. melastomus	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB.ZM2	UAB.ZM3	UAB.ZM8	UAB.ZM9	UAB. ZM14	UAB. ZM22	UAB. ZM24	UAB. ZM29	BMNH 1936.8.26 962-973 (212)	BMNH 1936.8.26 984-987 (984.2)	BMNH 1936.8.26 984-987 (984.3)	BMNH 1936.8.26 984-987 (984.4)	
Total length TL (mm)	437	355	385	288	295	318	322	178	233	107	103	94	94-437
Standard length SL (mm)	420	343	370	276	283	308	310	172	225	103	99	90	90-420
Sex	male	male	female	female	male	female	female	female	male	-	-	-	-
Meristic characters													
Dorsal-fin rays	83	86	87	88	88	88	84	85	86	89	85	84	83-89
Anal-fin rays	67	72	70	73	73	73	69	71	70	73	71	70	67-73
Caudal-fin rays	9	9	9	10	10	10	9	10	10	10	10	_	9-10
Pectoral-fin rays	18	18	18	18	18	18	19	18	18	18	17	18	17-19
Precaudal vertebrae	21	21	20	20	21	21	21	20	20	21	20	20	20-21
Caudal vertebrae	65	69	69	71	70	71	66	69	70	72	70	71	65-72
Total vertebrae	86	90	89	91	91	92	87	89	90	93	90	91	86-93
1st dorsal-fin pterygiophore with vertebrae	4	4	4	4	4	4	4	4	4	4	4	4	4
Palatine teeth (left/right)	5/5	5/5	6/6	7/6	7/7	6/5	7/6	5/6	6/6	5/6	5/5	3/4	3-7/4-7
Gill rakers	2+12	2+11	2+13	-	-	3+12	3+11	-	2+11	-	-	-	2-3+11-13
Pseudobranchiae	7	-	6	6	-	6	-	-	6	-	-	-	6-7
Morphometric characters (% TL)													
Head length (HL)	22.1	18.9	18.8	17.4	18.8	18.0	20.1	19.4	18.7	19.6	20.4	21.1	17.4-22.1
Head width	15.4	9.1	11.0	7.9	8.5	8.3	9.4	8.3	9.9	9.5	9.4	9.6	7.9-15.4
Head depth	15.1	9.5	11.6	9.9	10.0	10.0	10.8	10.0	11.0	10.7	10.6	10.7	9.5-15.1
Snout length	7.1	4.9	5.2	5.5	5.3	4.7	5.9	4.5	5.7	4.5	4.8	5.0	4.5-7.1
Nostril tube length	0.8	0.6	0.6	0.7	0.7	0.7	0.7	0.7	0.8	0.7	0.7	0.7	0.6-0.8
Eye diameter	3.2	3.6	3.4	3.5	4.0	3.6	4.1	4.7	4.3	5.3	5.6	5.9	3.2-5.9

Table 2. continued

P. melastomus	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB.ZM2	UAB.ZM3	UAB.ZM8	UAB.ZM9	UAB. ZM14	UAB. ZM22	UAB. ZM24	UAB. ZM29	BMNH 1936.8.26 962-973 (212)	BMNH 1936.8.26 984-987 (984.2)	BMNH 1936.8.26 984-987 (984.3)	BMNH 1936.8.26 984-987 (984.4)	
Interorbital (bony margin)	2.4	2.1	1.8	1.3	1.5	1.9	1.4	1.5	1.7	0.6	0.6	0.6	0.6-2.4
Upper jaw length	9.8	7.6	8.1	8.0	7.7	7.4	7.7	7.9	7.9	6.1	6.3	6.7	6.1-9.8
Lower jaw length	10.8	10.1	9.3	8.5	8.7	7.7	8.6	8.9	8.5	8.8	8.7	8.8	7.7-10.8
Predorsal length	24.0	19.4	21.3	23.9	17.2	20.0	21.1	20.2	20.1	20.5	20.3	22.3	17.2-24.0
Tail length	58.3	61.1	58.9	62.1	62.0	60.0	59.9	60.6	63.5	59.8	58.4	58.5	58.3-63.5
Dorsal-fin height above anal-fin origin	10.3	5.4	4.5	4.1	4.4	4.1	4.1	3.9	4.3	2.3	2.0	2.1	2.0-10.3
Body height at anal-fin origin	14.6	13.3	14.0	12.1	12.2	12.9	12.1	11.3	13.6	10.5	10.8	11.1	10.5-14.6
Pectoral-fin length	14.2	12.6	10.7	10.8	11.3	11.0	12.0	11.4	11.6	12.6	11.1	10.9	10.7-14.2
Pectoral-fin base height	6.5	5.3	6.3	5.0	5.0	5.4	5.1	4.6	5.3	4.3	4.6	4.4	4.3-6.5
Pelvic-fin length	4.0	3.1	3.1	3.1	3.5	2.9	3.7	3.6	3.7	4.5	4.0	3.9	2.9-4.5
Caudal-fin length	4.0	3.4	3.3	4.1	4.0	3.8	3.7	3.3	3.4	3.7	3.8	4.2	3.3-4.2
Gill slit length	9.3	7.7	8.8	6.8	7.1	8.3	7.4	7.4	7.2	7.1	7.2	7.9	6.8-9.3
Isthmus width	3.9	3.3	3.8	3.6	3.2	3.3	3.6	3.4	4.6	3.5	3.7	4.0	3.2-4.6
Morphometric characters (% HL)													
Head width	56.0	48.3	58.4	44.0	45.5	45.9	46.7	42.7	53.0	48.4	46.4	45.8	42.7-58.4
Head height	56.3	50.1	61.5	55.2	53.1	55.4	54.1	54.9	59.0	54.6	52.3	50.8	50.1-61.5
Upper jaw length	44.7	40.3	43.3	45.9	41.2	41.4	38.1	40.7	42.1	31.3	30.9	31.7	30.9-45.9
Pectoral-fin length	64.5	66.7	56.9	60.2	60.3	59.4	60.0	76.3	61.7	64.1	53.3	51.8	51.8-76.3
Snout length	32.1	26.2	28.0	30.8	28.2	26.3	29.7	23.1	30.6	23.2	23.7	24.0	23.1-32.1
Eye diameter	14.6	19.1	18.4	19.4	21.2	20.2	20.5	27.1	23.3	27.1	27.6	28.0	14.6-28.0
Interorbital (bony margin)	10.9	11.4	9.8	7.3	8.2	11.0	7.1	7.8	9.3	3.3	3.3	3.2	3.2-11.4
Pelvic-fin length	18.2	16.3	16.8	20.6	18.7	16.0	16.2	18.4	20.1	23.2	19.9	18.6	16.0-23.2

HL head length; SL standard length.

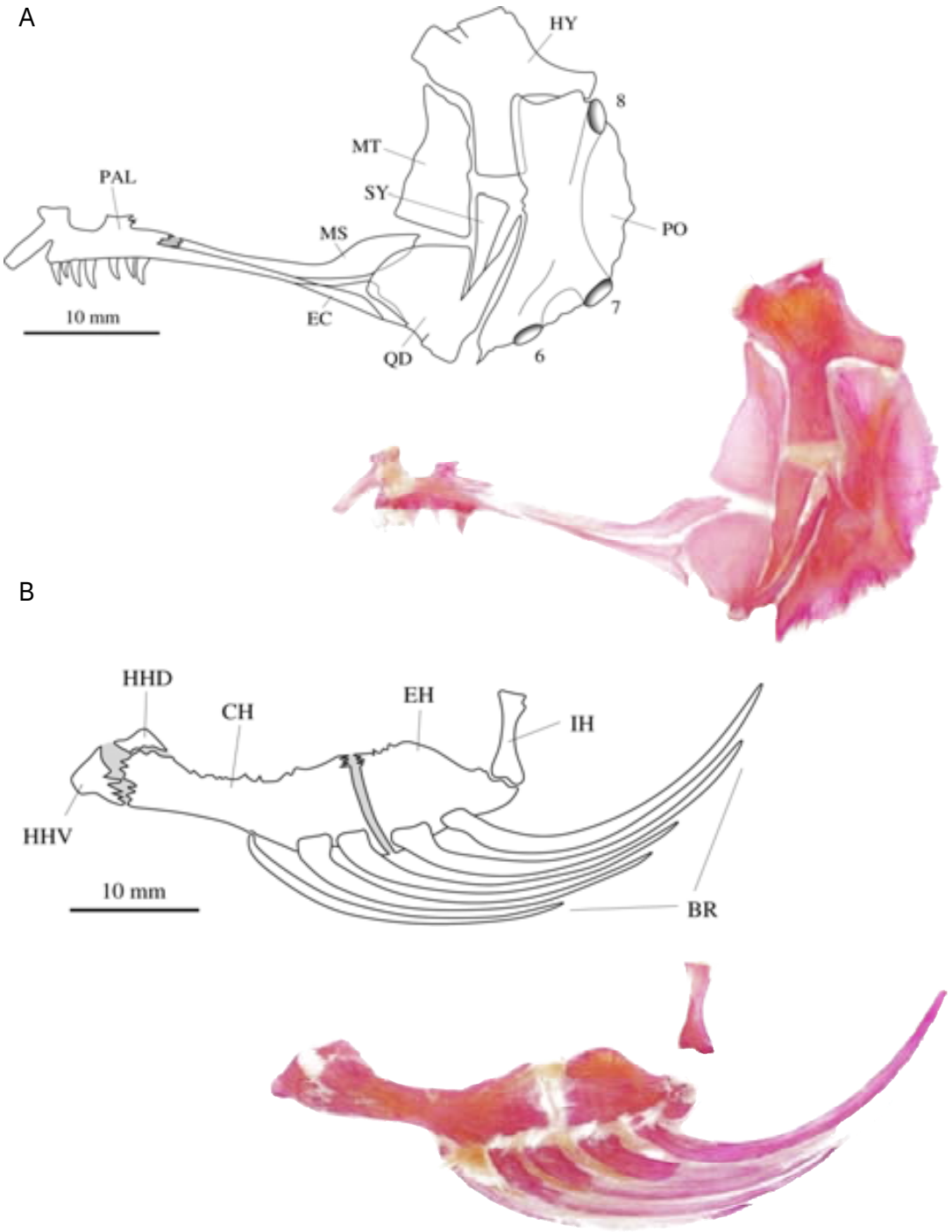


Figure 19. *Patagolycus melastomus* gen. et sp. nov. (UAB.P24, 395 mm TL male). Left suspensorium and preopercle **(A)** and Left hyoid bar **(B)**. BR, branchiostegal rays; CH, ceratohyal; EC, ectopterygoid; EH, epihyal; HHD, dorsal hypohyal; HHV, ventral hypohyal; HY, hyomandibula; IH, interhyal; MS, mesopterygoid; MT, metapterygoid; PAL, palatine; PO, 6, 7 and 8, preopercular pores; QD, quadrate; SY, symplectic.

Reproduction. Despite the reduced sample used, head length, head width, snout length as well as dorsal-fin height, are proportionally higher in the male holotype (the larger specimen) than in both male and females paratypes indicating both sexual dimorphism and ontogenic change (table 2). In the single ovary of three female paratypes two distinct clutches of oocytes can be distinguished: a large clutch of oocytes with a diameter between 1.33-1.42 mm, and another with a diameter of about 0.72 mm. The single ovary of *Patagolycus melastomus* sp. nov. belong to the cystovarian type, the most common type in Teleosts, according to the classification of Hoar (1969). Ovaries in the female specimens of the new species are unripe, they are in a maturing stage, with oocytes visible to the naked eye. It is known that, in general, mature zoarcid eggs are large, about 4-9 mm in diameter (Anderson, 1984) and those of the Patagonian species confirm this rule: Gosztonyi (1977) reports 5.0-5.5 mm in diameter for *Argentinolycus elongatus* (as *Iluocoetes elongatus*), 7.5-8.4 mm for *Austrolycus laticinctus*, 5.0 mm for *Dadyanos insignis* and 4.5 mm for *Phucocoetes latitans*; Matallanas *et al*., (1990) described a demersal egg cluster of *Austrolycus depressiceps*, obtained in the Beagle Channel, formed by 465 spherical eggs with 9.2-9.8 mm in diameter, the largest reported size for zoarcids.

Distribution. Southwest Atlantic Ocean between 45º28'- 51º27'S and 60º21' -68º50'W, at depths of 164-489 m.

Etymology. The specific name, *melastomus*, from the Greek *melas* (black, dark) and *stoma* (mouth), for the colour of its orobranchial cavity.

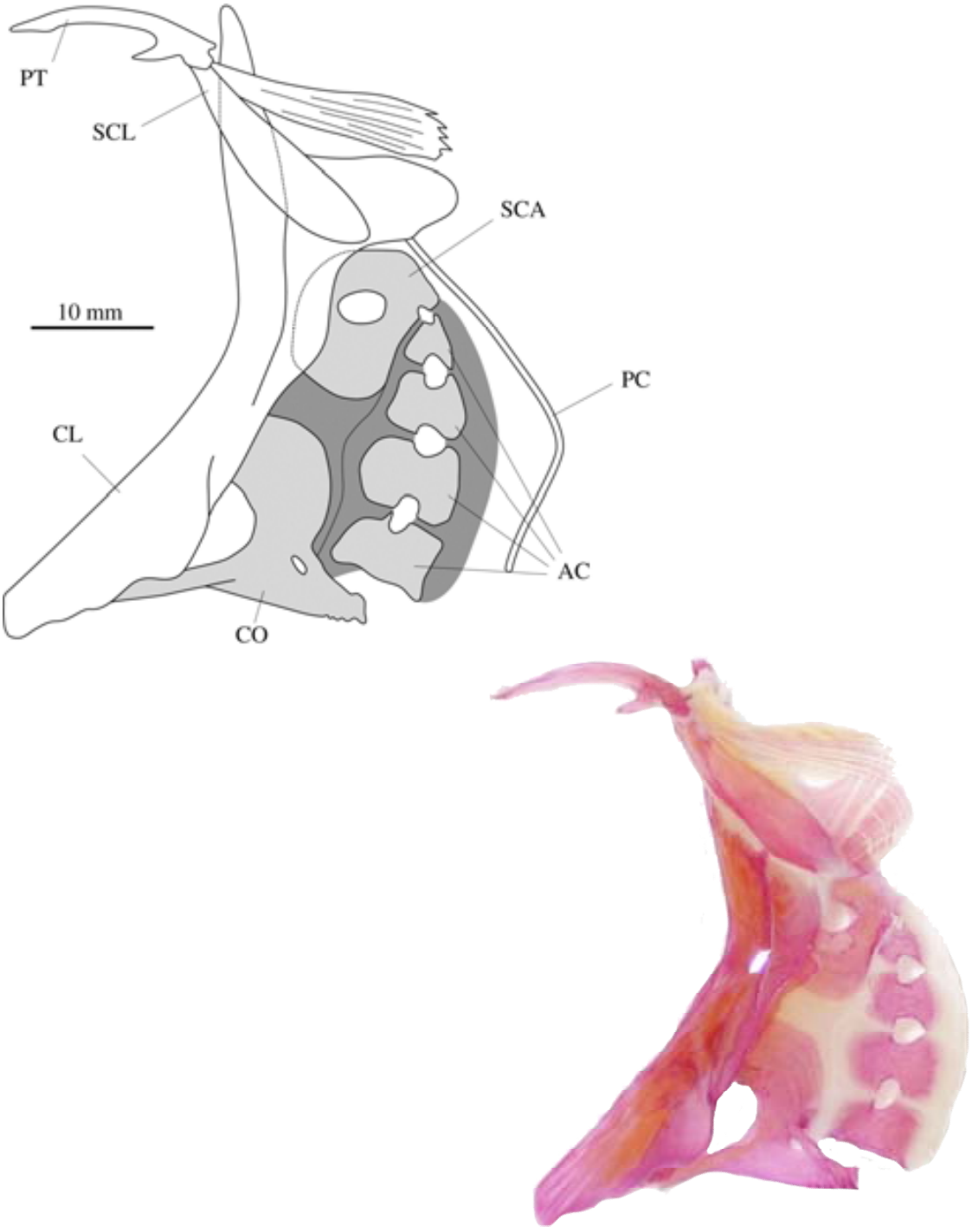


Figure 20. Left lateral view of the pectoral girdle of *Patagolycus melastomus* gen. et sp. nov. (UAB.P24, 395 mm TL male). AC, actinosts (=radials); CL, cleithrum; CO, coracoid; PC, postcleithrum; PT, posttemporal; SCA, scapula; SCL, supracleithrum.

Table 3. Character matrix for estimating the phylogenetic relationships between *Patagolycus, Iluocoetes* and *Argentinolycus* and the other Magellanic endemic Lycodine genera.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Aiakas	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	1	0	1	0	1	0	0	0	0	0	0	?	0	0	0	0	1	1	0	0	1	1	0	0	0
Argentinolycus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0
Austrolycus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Crossostomus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Dadyanos	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0
Iluocoetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	1	1	0	0	?	1	0	0	0
Letholycus	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Maynea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0
Notolycodes	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Oidiphorus	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
Patagolycus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	?	1	0	0	1
Phucocoetes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Piedrabuenia	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Plesienchelys	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0	0
Pogonolycus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Lycozoarces	0	0	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

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Aiakas	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	?	0	1	1	0	0	0	0	0	1	1	1	0	?
Argentinolycus	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	1	2	0	1
Austrolycus	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	-	1	0	0	0	0	1	1	1	0	1
Crossostomus	0	0	0	0	1	1	2	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	-	1	0	0	0	0	1	1	2	0	1
Dadyanos	0	0	0	1	1	1	2	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	-	1	0	0	0	0	1	1	1	0	1
Iluocoetes	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Letholycus	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	?	0	1	1	0	0	0	0	0	1	1	2	0	1
Maynea	0	0	0	0	0	0	2	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	?	0	2	-	1	0	0	0	0	1	1	2	0	1
Notolycodes	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Oidiphorus	0	0	1	0	0	0	2	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	1	1	2	0	1
Patagolycus	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Phucocoetes	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	0	0	1	1	1	0	1
Piedrabuenia	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	2	0	1
Plesienchelys	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1*
Pogonolycus	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	-	1	0	0	0	0	1	1	2	0	1
Lycozoarces	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

*Inadvertently not reported in Anderson,1994 (Anderson,pers.comm.)

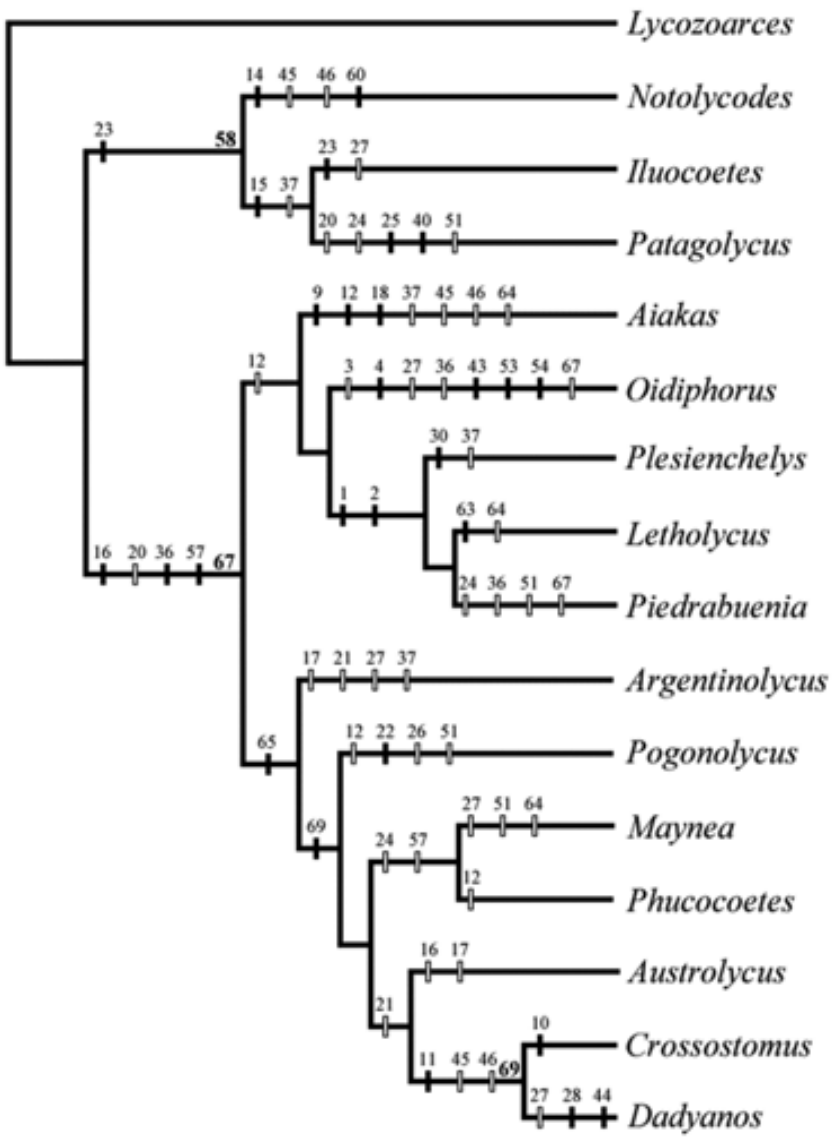


Figure 21. Interrelationships among the Magellanic endemic lycodine genera. Consensus tree resulting from the parsimony analysis of 78 morphological characters (Length=105; CI=0.53; RI=0.50). Bootstrap support values (rep=1000) are indicated on the nodes. White boxes on branches: homoplastic apomorphies; black boxes: synapomorphies.

2.5 DISCUSSION

Iluocoetes differs from *Argentinolycus* gen. nov. mainly in the following characters (*Iluocoetes* first): submental crests (present vs. absent); cranium width (narrowed vs. wide); frontal fusion (frontal bones fused totally vs. separate), frontal corner (squared-off vs. tapering); parasphenoid wing height (high vs. broad, without dorsal ramus); branchiostegal ray number (5 vs. 6); posttemporal ventral ramus (well developed vs. absent); ceratohyal–epihyal articulation (smooth vs. completely interdigitating along its entire length), pyloric caeca state (present vs. absent), and pelvic-fin membranes (ensheathed by dermis vs. rays exerted beyond membranes). Salient diagnostic characters of late juvenile and adult *Iluocoetes* and *Argentinolycus* are given in table 4.

Table 4. Salient diagnostic characters of late juvenile and adult *Iluocoetes* and *Argentinolycus*.

Character	*ILUOCOETES*	*ARGENTINOLYCUS*
Submental crests	present	absent
Pelvic-fin membranes	rays ensheathed	rays exerted
Postorbital pores	pores 1 and 4	pore 4
Branchiostegal ray number	5	6
Cranium width	wide	narrowed
Frontal fusion	frontal bones fused	separate
Frontal corner	squared off	tapering
Parasphenoid wing	high	low, broad
Pyloric caeca state	present	absent
Posttemporal ventral ramus	well-developed	absent
Ceratohyal-Epihyal articulation	smooth*	interdigitating along entire length

*Slightly serrated dorsally in ZMH104782, 302 mm SL. Gosztonyi (1977:214) says "serrated on its most dorsal portion".

The complete fusion of frontal bones is found only in *Notolycodes* (Anderson and Gosztonyi, 1991) and in *Iluocoetes* (this paper), but frontals fused anteriorly can be found in the gymneline *Ericandersonia* (Shinohara and Sakurai, 2006), as well as in the lycodines *Pyrolycus* (Machida and Hashimoto, 2002), *Santelmoa* (Matallanas, 2010), and in *Patagolycus* (this paper). In all specimens of *Iluocoetes fimbriatus* examined, 140−302 mm TL, the frontal bones are fused totally with no trace of a suture.

The submental crests can be found in only four genera, the gymneline *Ericandersonia* (Shinohara and Sakurai, 2006: figs. 6, 7A), and the lycodines *Lycodes* (Anderson, 1994: fig. 1A, B), *Iluocoetes* and *Patagolycus*.

From our consensus tree (fig. 21) *Iluocoetes* differs from its close congener *Notolycodes* in the following characters (*Iluocoetes* first): palatine and vomerine teeth (present vs. absent); chin pad at mandibular symphysis (absent vs. present); cartilaginous submental crests (present vs. absent), and parietal-parietal articulation (in contact vs. separate from mid-line). *Iluocoetes* differs from the remaining Patagonian lycodine genera by the characters given in its diagnosis, mainly in having frontal bones completely fused and, excluding *Patagolycus*, submental cartilaginous crests.

Patagolycus gen. nov. differs from *Notolycodes* in the following characters (*Patagolycus* first): palatine and vomerine teeth (present vs. absent); chin pad at mandibular symphysis (absent vs. present); submental crests (present vs. absent); frontal–parasphenoid articulation (separated by pterosphenoid vs. contacting); cranium width (narrowed vs. wide); frontal fusion (frontal bones fused anteriorly vs. fused totally); gill rakers shape (scalloped vs. blunt, triangular), and body colour. *Patagolycus* differs from the remaining Patagonian lycodine genera, excepting *Iluocoetes*, in having submental crests, frontals fused anteriorly, frontal and parasphenoid separated by pterosphenoid and, excluding *Pogonolycus*, sphenotic and parietal in contact.

Although pigment patterns vary individually in *Iluocoetes* and in several other zoarcids (Anderson 1982), the colour pattern of the juvenile holotype of *Iluocoetes facali* Lloris and Rucabado (1987) is similar to other examined juvenile specimens of *Iluocoetes fimbriatus* Jenyns, including a darker band on head between the anteroventral edge of the eye and the upper jaw. Juvenile *I. facali* differs from

juvenile *Patagolycus melastomus* not only in general head and body colour but also in body squamation: sparse on *I. facali* vs. dense in *P. melastomus*, and head squamation: absent in *I. facali* vs. present on nape and opercle in *P. melastomus.*

Patagolycus gen. nov. is similar to *Iluocoetes* mainly in having submental cartilaginous crests, frontal corner squared, frontal ramus long, five branchiostegal rays, posttemporal ventral ramus well developed, posterior hyomandibular ramus elongate, and palatopterygoid series well developed. However the two genera differ in many characters, several easily observed (table 5).

The similarities found between *Patagolycus melastomus* sp. nov. and *Iluocoetes fimbriatus* in body colour, as well as in many meristic and morphometric characters, represent a remarkable example of how challenging zoarcid taxonomy can be. Are they cryptic species?. Bickford *et al.*, (2007) consider two or more species to be cryptic if they are, or have been, classified as a single nominal species because they are at least superficially morphologically indistinguishable. *Patagolycus melastomus* is not described yet, it's being described herein. But are *Patagolycus melastomus* sp. nov. and *Iluocoetes fimbriatus* truly cryptic?. After detailed comparisons of specimens of the two species, we found some key morphological characters that are species-specific and distisguished *P. melastomus* from *I. fimbriatus* (table 5). Thus, we can refer to both species as pseudo-cryptic or pseudo-sibling species (Sáez and Lozano, 2005).

Our phylogenetic tree was constructed using only 78 morphological characters. Morphological characters used to diagnose genera of zoarcids reveal a great degree of homoplastic evolution (Anderson, 1994); for this reason, the phylogenetic results of this chapter are indicative.

Table 5. Salient diagnostic characters of late juvenile and adult *Iluocoetes* and *Patagolycus*

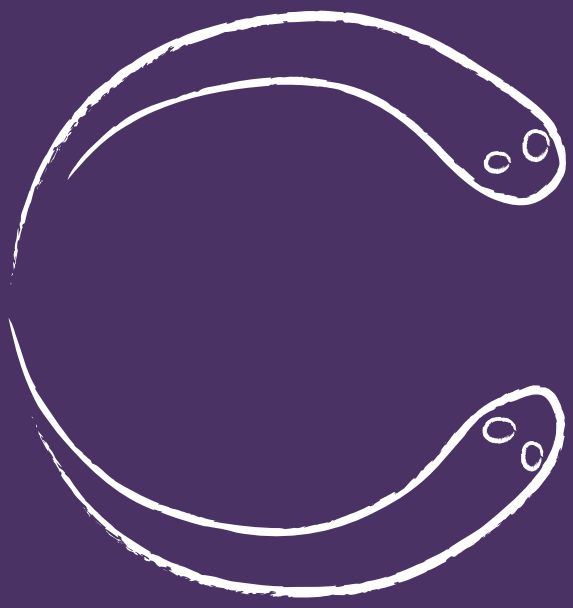
Character	*ILUOCOETES*	*PATAGOLYCUS*
Color of oral cavity	pale	black
Dark snout band	anteroventral eye to upper jaw	anterior edge eye to nasal tube
Squamation of head, pectoral base and axil	scaleless	scaled
Palatine teeth	9-23	3-7
Posterior nasal pores	1	2
Frontal fusion	frontal bones fused completely	fused anteriorly
Parietal-Parietal articulation	contacting	separated from mid-line
Frontal-Parasphenoid articulation	contacting	separated by pterosphenoid
Sphenotic-Parietal articulation	separated by frontals	contacting
Ceratohyal-Epihyal articulation	smooth*	interdigitating dorsally

*Slightly serrated dorsally in ZMH104782, 302 mm SL. Gosztonyi (1977:214) says "serrated on its most dorsal portion".

2.6 ACKNOWLEDGEMENTS

We thank Rafael del Río, Julio Martínez Portela, and Matusa Amoedo (Centro Oceanográfico de Vigo, Instituto Español de Oceanografía) for the donation of specimens of the new species captured by them in SW Atlantic Ocean (Atlantis-09 and Atlantis-10 campaigns), and Dr. Atila E. Gosztonyi for the donation of two specimens of *Argentinolycus elongatus* (as *Iluocoetes elongatus*). We thank Dr. Ralf Thiel and Irina Eidus (ZMH) for the loan of specimens; to James Maclaine and Oliver Crimmen (NHM) for his kindness to the first author during his visit to the museum, as well as for the loan of specimens. Specials thanks to Oliver Crimmen for the excellent radiographs of the holotype of *Iluocoetes fimbriatus*; to Tracy Heath (NHM) for the loan of specimens. Gabriela Piacentino and Gustavo Chiaramonte (MACN) provide us information on specimens in their care. We are also grateful to Carmen Benito (Universidad de Barcelona, Spain) for the X-rays, Jordi Corbera for the illustrations, and to Muriel, daughter of the first author, for the English revision of the manuscript. This manuscript also benefited from the constructive criticism by anonymous

reviewers, and in particular from the extensive and thorough review by Dr. M. E. Anderson. Authors received financial support from the Ministerio de Ciencia e Innovación, Spain (Acción Complementaria CTM2009-07583-E/ANT).



CHAPTER 2

Description of two new species of *Santelmoa* (Teleostei: Zoarcidae) from the Southern Ocean

3 Description of two new species of *Santelmoa*, ***Santelmoa fusca*** sp. nov. and ***Santelmoa antarctica*** sp. nov. (Teleostei: Zoarcidae) from the Southern Ocean.

3.1 ABSTRACT

Detailed examination of eelpouts in collected material from the Gerlache Strait and the Bellingshausen Sea, during the Spanish Antarctic Expeditions Bentart 03 and Bentart 06, and from the Bransfield Strait, during the Danish Galathea 3 Expedition, at depths between 1056 and 1837 m, revealed two undescribed species of *Santelmoa* Matallanas, 2010. Herein, *Santelmoa fusca* sp. nov. and *Santelmoa antarctica* sp. nov. are described on the basis of twelve specimens. *Santelmoa fusca* can be separated from all other *Santelmoa* species by the following characters: mouth terminal; two posterior nasal pores; lateral line double; two irregular rows of palatine teeth; dorsal fin rays 109-113; anal fin rays 88-94; vertebrae 27-29 + 87-91 = 114-118; two pyloric caeca well developed; scales reduced to tail; pelvic fins and vomerine teeth present. *Santelmoa antarctica* can be separated from all other *Santelmoa* species by the following characters: mouth subterminal; two posterior nasal pores; suborbital pores seven (6 + 1); lateral line double; single row of palatine teeth; supraoccipital dividing the posterior end of frontals; central radials notched; dorsal fin rays 109-112; anal fin rays 89-93; vertebrae 27 + 89-92 = 116-119; two pyloric caeca well developed; scales, ventral fins and vomerine teeth present. *Santelmoa fusca* and *S. antarctica* can readily be separated from each other by squamation (reduced to tail vs. on the tail and on the posterior part of body); suborbital pore pattern (6 + 0 vs. 6 + 1), as well as several morphometric characters. The relationships of the two new species with congeners are discussed.

3.2 INTRODUCTION

The benthic fish fauna of the Southern Ocean is dominated by notothenioids (Clarke and Johnston, 1996; Eastman, 2005). However, in the Bellingshausen Sea, zoarcids predominate both in number and biomass (Matallanas and Olaso, 2007). The zoarcids possibly radiated out from boreal seas following the coasts of America throughout the Southern Ocean (Regan, 1914; Andriashev, 1965; Anderson, 1994). With 36 known Antarctic species in 15 genera, according to recent revisions and descriptions (Anderson, 1990, 2006; Møller and Stewart, 2006; Matallanas, 2009a, b, c, 2010, 2011a, b; Iglésias *et al*., 2012), the family Zoarcidae is one of the most speciose benthic fish families in Antarctic waters.

In the present chapter, two new species, *Santelmoa fusca* and *Santelmoa antarctica*, are described on the basis of twelve specimens collected from the Gerlache Strait, Bransfield Strait, and Bellingshausen Sea, Southern Ocean, at depths of 1056-1837 m. The relationships of the two new species with congeners are discussed.

3.3 MATERIALS AND METHODS

The type specimens of *Santelmoa fusca* were caught in the Gerlache Strait during the Spanish Antarctic expedition Bentart 03 on board of the R/V Hespérides, collected by Jesús Matallanas and Ignacio Olaso, 26 February 2003, and in the Bransfield Strait during the Danish Galathea 3 Expedition, R/V Vædderen, collected by Peter Rask Møller and Steen Knudsen, 27 January 2007. The type specimens of *S. antarctica* were caught in the Bellingshausen Sea during the Spanish Antarctic Expedition Bentart 06 on board of the R/V Hespérides, collected by Jesús Matallanas and Ignacio Olaso, 28 February 2006. All type specimens of *S. antarctica* as well as the holotype and three paratypes of *S. fusca* have been deposited at the UAB fish collection (Zoología, Universidad Autónoma de Barcelona); four paratypes of *S. fusca* belong to the ZMUC (Zoological Museum, University of Copenhagen).

Counts, measurements, and general terminology follow Gosztonyi (1977, 1988), Anderson (1982, 1988a, 1994), Voskoboinikova and Laius (2003), Voskoboinikova *et al*., (2010). Head pore terminology follows Gosztonyi (1977), Anderson (1982) (see annex 1 and 2). Measurements were made with ocular

micrometre 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 Alizarin Red stained specimens.

Following abbreviations are used: SL, standard length; HL, head length; A, anal fin; D, dorsal fin; P, pectoral fin; r1, uppermost radial; r2 and r3, central radials; r4, lowermost radial.

Comparative material examined

Santelmoa carmenae Holotype:UAB:B03GSZ51, 264 mm SL, Gerlache Strait, 64.3205800S 61.89703800W, 1056 m depth, 26 February 2003; paratypes: UAB:B03GSZ33, 234 mm SL; UAB:B03GSZ42, 277 mm SL; UAB:B03 GSZ52, 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; UAB:B03GSZ34, 248 mm SL, used for anatomical analysis: suspensorium and pectoral girdle; all specimens captured with the holotype.

Santelmoa elvirae Holotype: UAB:B06MBZ39, 305 mm SL, Bellingshausen Sea, 68.480S 86.380W, 1,837 m depth, 28 January 2006; paratypes: UAB:B06MBZ36, 351 mm SL; UAB:B06MBZ38, 349 mm SL; UAB:B06MBZ37, 345 mm SL, used for anatomical analysis: cranium, palatal series and pectoral girdle; all specimens captured with the holotype (fig.22).

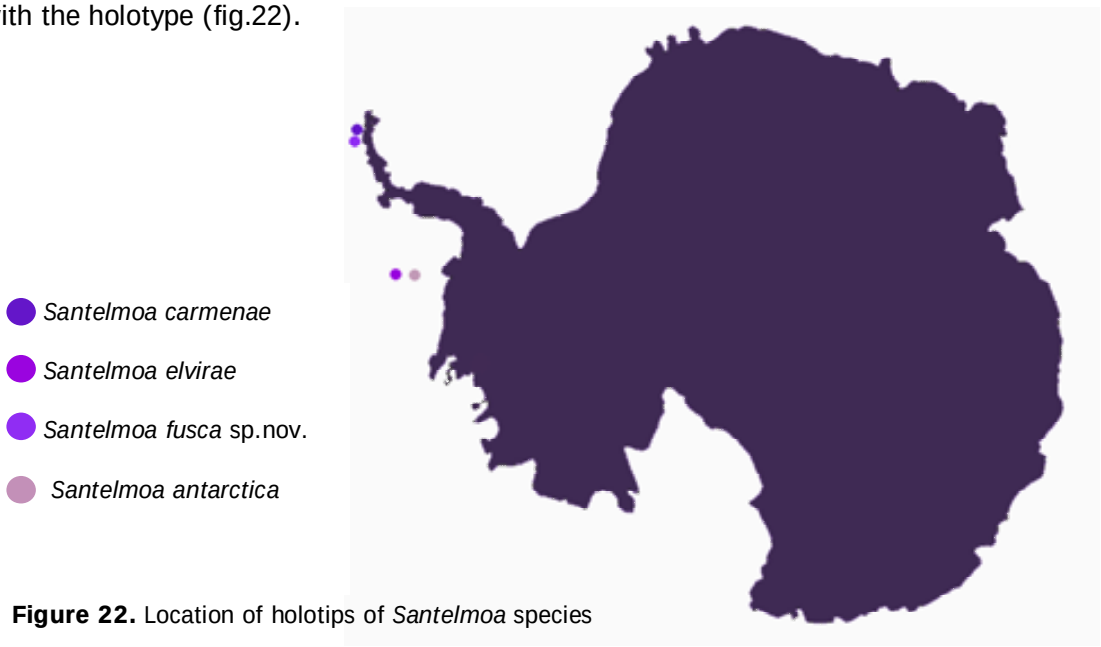


Figure 22. Location of holotips of *Santelmoa* species

3.4 RESULTS

3.4.1 *Santelmoa fusca* sp. nov.

(Figs. 23, 24 and 25; Table 6)

Material examined. Holotype UAB:B03GSZ48, 330 mm SL female, Gerlache Strait, Station 24 N, 64.320S 61.970W, 1056 m depth, baited traps, 26 February 2003.

Paratypes UAB:B03GSZ31, 301 mm SL female; UAB:B03GSZ49, 242 mm SL male; UAB:B03GSZ50, 206 mm SL male, captured with the holotype; ZMUC P766589, 244 mm SL female; ZMUC P766593, 220 mm SL male; ZMUCP766784, 301 mm SL female, and ZMUC P766788, 277 mm SL, Bransfield Strait, haul 36, 63.570S, 61.410W, 1118-1157 m depth, shrimp trawl, 27 January 2007; UAB:B03GSZ10, 266 mm SL female (used for anatomical analysis: cranium, palatal series, hyoid arch and pectoral girdle), captured with the holotype.

Etymology. The specific name, *fusca*, is after the Latin word *fuscus* (dark) and refers to the body colour of type specimens.

Diagnosis. A species of *Santelmoa* as defined by Matallanas (2010) with the following characters: mouth terminal; oral valve overlapping the anterior edge of vomer; two posterior nasal pores of similar size; lateral line double with ventral and medio-lateral branches; two irregular rows of palatine teeth; vomerine teeth present; dorsal fin rays 109-113; anal fin rays 88-94; pectoral fin rays 15-17; vertebrae asymmetrical, 27-29 + 87-91 = 114-118; two pyloric caeca well developed; pseudobranch filaments 3-6, elongated. Scales reduced to tail, absent on head and body.

Description. Counts and proportional measurements presented in table 6. Body nearly round in cross section; tail elongated and laterally compressed. Head ovoid; snout well developed and rounded, mouth terminal; end of maxilla extending to the posterior margin of pupil; lower lip with a small posterior lobe; nasal tube well developed, reaching the upper lip when depressed forward.

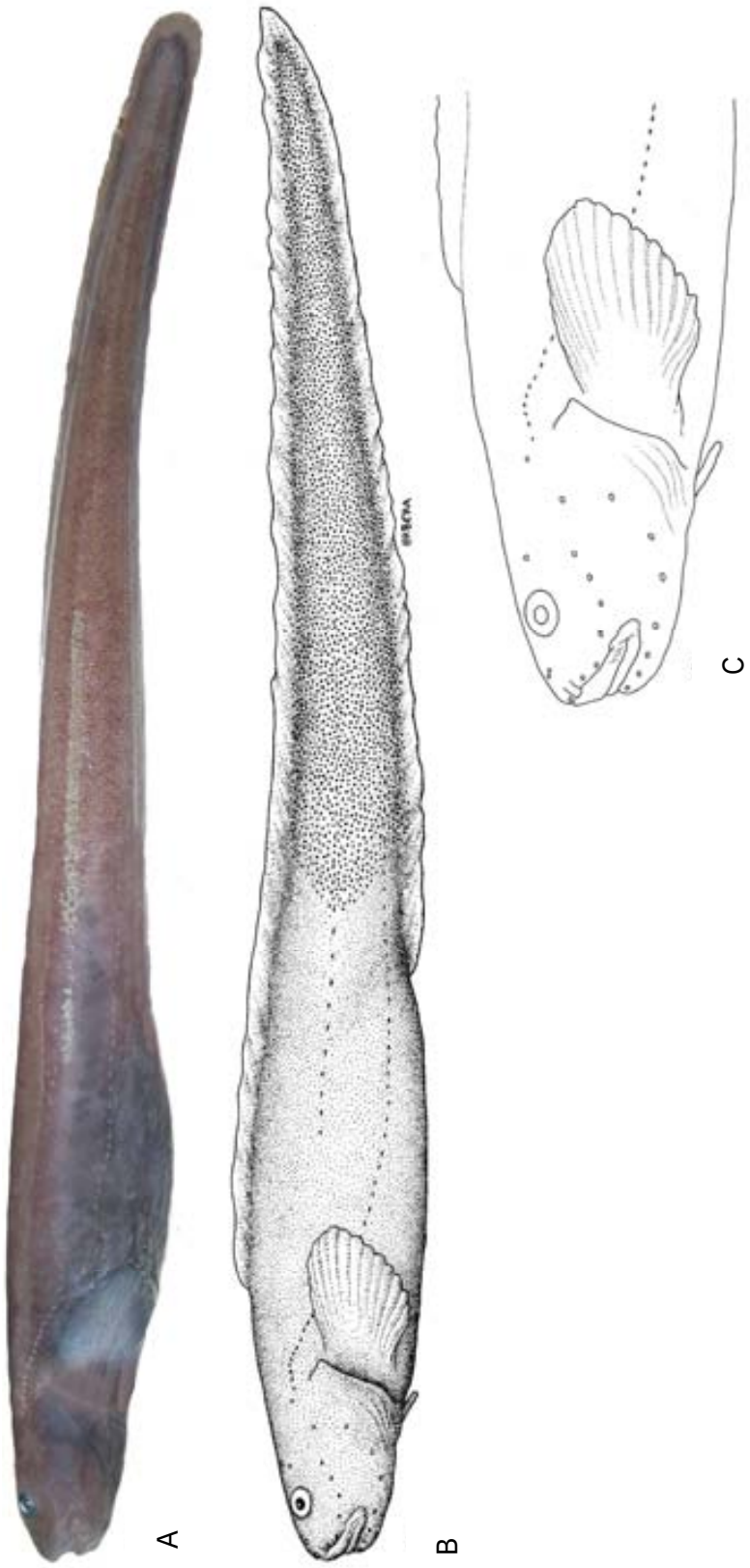


Figure 23. *Santelmoa fusca* sp. nov., UAB:B03GSZ48 (holotype), 330 mm SL female, from Gerlache Strait. Left lateral view (photograph in fresh condition just after capture) **(A)**, Left lateral view **(B)**, Left lateral view of head showing pore pattern **(C)**.

Oral valve well developed, overlapping the anterior edge of vomer and well separated from the palate laterally. Eye round, not entering dorsal profile of head. Gill slit extending ventrally to just ventral edge of pectoral fin base; opercular lobe triangular. Pectoral fin with exerted lower rays. Upper end of the pectoral fin base at body midline, its lower end above ventral profile of body. Pelvic fin rays joined, ensheathed by the dermis (fig. 23b,c).

All teeth conical. Premaxilla with two rows anteriorly and single row posteriorly; dentary with 3-4 irregular rows anteriorly merging onto single row posteriorly; a patch of 4-7 teeth on vomer; palatine teeth 7-15, in two irregular rows anteriorly and single row posteriorly. Two welldeveloped pyloric caeca. Gill rakers 13-16 (3-4 + 10-12), forked. Pseudobranch filaments 3-6, elongated.

Cephalic lateralis pore system with pores small and rounded. Nasal pores 3, one anterior and two posterior nasal; first nasal pore located anteromesial to nostril tube; the two posterior nasal pores located dorsoposterior to it, and both of similar size. Postorbital pores two (positions one and four). Six suborbital pores all on the ventral ramus. Eight preoperculomandibular pores (fig. 23c). Interorbital and occipital pores absent. Lateral line configuration double: ventral branch with numerous closely set neuromasts, beginning just behind the fourth postorbital pore, and extending ventrolaterally to the end of the tail; mediolateral branch originating well before anal fin origin and coursing just above mid-body to tail tip. Flesh and skin firm; scales extend completely across tail to a vertical behind anal fin origin; vertical fins naked anteriorly but scaled posteriorly to about a third its length; head, body, abdomen, and pectoral fin base and axil, scaleless (fig. 23b).

Neurocranium narrowed (fig. 24a). Anterior portion of frontals fused with no trace of a suture, posterior portion separate showing a complete suture; frontal ramus long, with an anterior foramen in the interorbital space; frontal corner squared. Sphenotic protruding beyond the margin of frontal. Parasphenoid wing reaching above mid-height of the trigeminofacialis foramen. Frontal and parasphenoid not separated by pterosphenoid. Intercalar very elongated, protruding into prootic, and excluding exoccipital and pterotic articulation. Sphenotic and parietal separated by frontal and pterotic. Anterior portion of supraoccipital narrow and protruding slightly between the posterior end of frontals; posterior portion with a well-developed median crest;

supraoccipital excluded from exoccipital by epioccipital. Parietals separated from mid-line.

Palatopterygoid series well developed. Ectopterygoid overlapping both anterior and dorsal surface of quadrate (fig. 24b); lower margin of mesopterygoid not in contact with quadrate. Anterior surface of quadrate strongly serrated. Capitulum of palatine with a noticeable lateral prominence. Metapterygoid large, elongated. Posterior ramus of hyomandibula short. Symplectic with a small posterior strut. Hyoid bar with ceratohyal–epihyal joint serrated. Six branchiostegal rays.

Pectoral girdle (fig. 25) with a strong post-temporal bearing a well-developed ventral ramus. A cartilaginous oval lamina attached to the supracleithrum; another cartilaginous lamina attached to the postero-dorsal end of cleithrum. Scapular foramen is open anteriorly; there is a prominent postero-dorsal scapular strut. The posterior margin of scapula covers 1.5 radials. Coracoid with a posterior strut. Radials 4, unnotched, the uppermost smaller. Cartilaginous basal plate without foramina. Postcleithrum is present.

Vertebrae asymmetrical, 27-29 + 87-91 = 114-118. Last precaudal vertebrae associated with dorsal fin rays 22-23; Dorsal fin origin associated with vertebrae 5-6, with 0-1 free pterygiophores. Terminal dorsal fin ray associated with second preural vertebrae. Two or three anal fin pterygiophores, with 2-3 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. Caudal fin rays 10-12, with two epural, four or five upper hypural, and four or five lower hypural rays.

Colour of holotype in fresh. Medium to dark brown, with dark vertical fins; pectoral fin bluish, with darker margins; opercular region and abdomen dark violet; lateral lines and scales white. Colour of preserved specimens. Dark brown uniform; abdomen dark grey; pectoral fin light brown, with darker margins; nasal tube unpigmented; lining of mouth light; oral cavity, dark grey; peritoneum black.

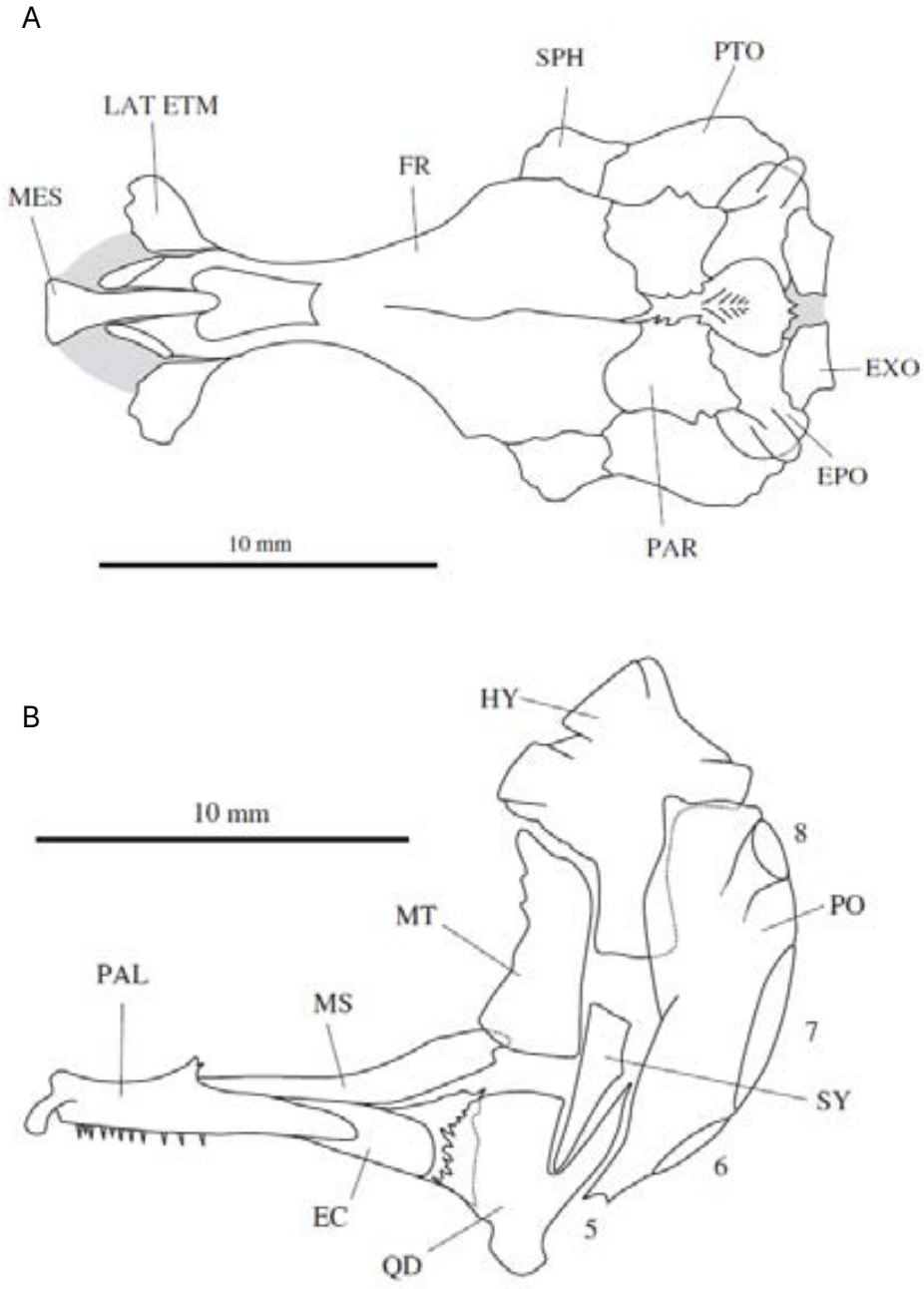


Figure 24. *Santelmoa fusca* sp. nov. Cranium, dorsal view **(A)** and left suspensorium and preopercle **(B)**. EC, ectopterygoid; EPO, epioccipital; EXO, exoccipital; FR, frontal; HY, hyomandibula; LAT ETM, lateral ethmoid; MES, mesethmoid; MS, mesopterygoid; MT, metapterygoid; PAL, palatine; PAR, parietal; PO, 5 , 6, 7 and 8 preopercular pores; PTO, pterotic; QD, quadrate; SPH, sphenotic; SY, symplectic.

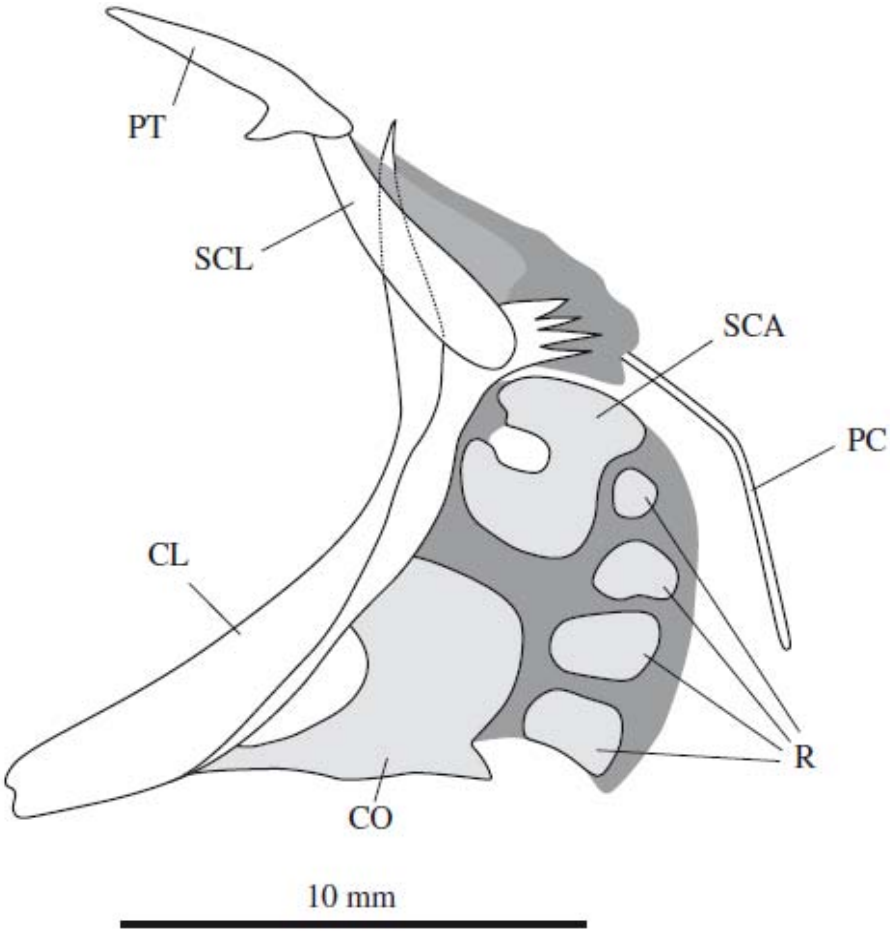


Figure 25. Left lateral view of pectoral girdle of *S. fusca* sp. nov. CL, cleithrum; CO, coracoids; PC, postcleithrum; PT, post-temporal; R, radials; SCA, scapula; SCL, supracleithrum.

Table 6. Counts and Measurements of *Santelmoa fusca* sp.nov. (see annex 1)

Santelmoa fusca	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB: B3GSZ48	UAB: B3GSZ10	UAB: B3GSZ31	UAB: B03GSZ49	UAB: B03GSZ50	ZMUC P766589	ZMUC P766593	ZMUC P766784	ZMUC P766788	
Standard length SL (mm)	330	266	301	242	206	244	220	301	277	206-330
Sex	Female	Female	Female	Male	Male	Female	Male	Female	-	
Meristic characters										
Dorsal fin rays	110	112	110	109	110	113	111	110	110	109-113
Anal fin rays	91	89	91	88	88	94	92	90	89	88-94
Caudal fin rays	12	11	10	10	11	11	11	12	11	10-12
Pectoral fin rays	15	15	15	16	16	17	17	16	15	15-17
Precaudal vertebrae	27	27	27	27	27	27	29	27	28	27-29
Caudal vertebrae	89	91	89	87	87	91	89	87	88	87-91
Total vertebrae	116	118	116	114	114	118	118	114	116	114-118
First D fin pteryg. with Vert.	5	6	5	6	6	6	6	5	6	5-6
Gill rakers	4+12	-	3+10	-	3+12	-	-	-	-	13-16
Pseudobranchial filaments	3	-	6	-	3	-	-	-	-	3-6
Posterior nasal pores	2	2	2	2	2	2	2	2	2	2
Suborbital pores	6+0	6+0	6+0	6+0	6+0	6+0	6+0	6+0	6+0	6+0
Morphometric characters (% SL)										
Head length	12.3	11.9	12.9	13.2	14.0	12.8	12.7	13.2	12.7	11.9-14.0
Head width	7.7	6.7	7.3	6.7	7.4	7.1	7.1	8.4	7.5	6.7- 8.4
Head height	7.3	7.2	7.0	7.3	7.8	7.6	7.0	7.6	7.8	7.0-7.8
Snout length	2.9	2.2	2.9	2.6	3.1	3.6	3.0	2.6	2.8	2.2-3.6
Nostril tube length	0.8	0.6	0.8	0.7	0.8	0.5	0.8	0.7	0.5	0.5-0.8

Table 6. Continued

Santelmoa fusca	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB: B3GSZ48	UAB: B3GSZ10	UAB: B3GSZ31	UAB: B03GSZ49	UAB: B03GSZ50	ZMUC P766589	ZMUC P766593	ZMUC P766784	ZMUC P766788	
Standard length SL (mm)	330	266	301	242	206	244	220	301	277	206-342
Sex	Female	Female	Female	Male	Male	Female	Male	Female	-	
Eye diameter	1.8	1.0	1.2	1.4	1.2	1.2	1.3	1.2	1.5	1.0-1.5
Interorbital width (hard)	1.1	1.0	1.2	1.4	1.2	1.2	1.3	1.2	1.5	1.0-1.5
Upper jaw length	5.2	4.4	4.9	5.0	5.0	4.2	3.9	4.7	4.1	3.9-5.2
Lower jaw length	6.0	5.6	6.4	6.1	5.9	6.3	5.9	5.7	5.7	5.6-6.4
Predorsal length	15.4	15.4	15.9	16.1	16.0	14.3	13.6	16.9	16.2	13.6-16.9
Preanal length	35.9	35.7	33.8	33.8	35.4	33.6	31.8	38.2	40.0	31.8- 40.0
Tail length	64.8	64.2	69.1	68.5	67.9	69.6	71.3	63.9	63.0	63.0-71.3
D fin height at A fin origin	1.7	1.9	2.4	2.6	3.0	1.6	1.6	1.7	1.8	1.6-3.0
Body height at A fin origin	8.7	7.1	8.9	8.3	7.3	6.9	6.5	6.6	7.6	6.5-8.9
Pectoral fin length	8.5	7.4	8.0	7.7	8.5	8.9	8.1	8.4	8.6	7.4-8.9
Pectoral fin base height	4.1	3.2	3.8	3.8	3.7	3.4	2.6	3.6	2.6	2.6-4.1
Pelvic fin length	1.3	1.5	1.5	1.5	1.7	1.5	1.5	1.2	1.8	1.2-1.8
Caudal fin length	2.4	2.2	2.9	2.5	3.3	3.6	2.7	2.3	1.4	1.4-3.6
Gill slit length	4.5	4.4	4.7	5.1	5.4	4.3	4.0	4.8	4.8	4.0-5.4
Opercular lobe length	0.9	0.9	1.1	0.9	1.0	0.6	0.6	0.8	0.7	0.6-1.1
Isthmus width	4.1	3.8	3.8	3.8	4.5	5.4	4.3	5.6	5.1	3.8-5.6
Snout to anterior scales	39.4	42.1	39.8	42.1	45.1	42.1	40.2	44.5	42.9	39.4-45.1

Table 6. Continued.

Santelmoa fusca	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	UAB: B3GSZ48	UAB: B3GSZ10	UAB: B3GSZ31	UAB: B03GSZ49	UAB: B03GSZ50	ZMUC P766589	ZMUC P766593	ZMUC P766784	ZMUC P766788	
Standard length SL (mm)	330	266	301	242	206	244	220	301	277	206-342
Sex	Female	Female	Female	Male	Male	Female	Male	Female	-	
Morphometric character (%HL)										
Head width	63.0	56.3	56.4	50.6	52.7	55.3	56.3	63.6	59.4	50.6-63.6
Head height	60.0	60.7	54.6	55.9	55.5	59.3	55.1	57.1	61.1	54.6-61.1
Upper jaw length	42.8	37.4	38.2	37.8	35.5	33.2	30.9	35.5	32.5	30.9-42.1
Pectoral fin length	69.2	62.2	61.8	60.0	60.6	69.7	63.7	63.6	68.0	60.0-69.7
Snout length	23.9	18.3	22.8	20.3	22.0	27.9	23.8	20.2	22.7	18.3-27.9
Eye diameter	16.0	18.2	15.3	18.1	18.2	18.3	19.6	16.8	13.7	13.7-19.6
Interorbital (hard)	8.8	8.5	9.4	10.6	8.6	9.5	10.3	9.0	11.6	8.5-11.6
Pelvic fin length	11.0	10.7	11.8	11.5	12.7	11.7	11.7	9.27	14.1	10.7-14.1

A anal fin; D dorsal fin; HL head length; pteryg pterygiophore; SL standard length; Vert. vertebrae

3.4.2 *Santelmoa antarctica* sp. nov.

(Figs. 26 and 27; Table 7)

Material examined. Holotype UAB:B06MB32Z27, 330 mm SL female, Bellingshausen Sea, Station MB32A, 69.470S 86.270W, 1,837 m depth, Agassiz trawl, 28 January 2006.

Paratypes UAB:B06MB32Z28, 301 mm SL female; UAB:B06 MB32Z8, 281 mm SL female (used for anatomical analysis: cranium, palatal series, hyoid arch and pectoral girdle). Both specimens captured with the holotype.

Etymology. The specific name *antarctica* is after the type locality.

Diagnosis. A species of *Santelmoa* as defined by Matallanas (2010) with the following characters: mouth subterminal; oral valve reaching the anterior edge of vomer; two posterior nasal pores, posterior one smaller; suborbital pores seven (6 + 1); lateral line double with ventral and medio-lateral branches; supraoccipital dividing the posterior end of frontals; basal pectoral plate with one foramen between scapular strut and r1; r2 and r3 notched; single row of palatine teeth; dorsal fin rays 109-112; anal fin rays 89-93; pectoral fin rays 17; vertebrae asymmetrical, 27 + 89-92 = 116–119; gill slit extending ventrally to just lower end of pectoral fin base; two pyloric caeca well developed; pseudobranch filaments 3, elongated. Scales, ventral fins and vomerine teeth present.

Description. Counts and proportional measurements presented in table 7. Body ovoid in cross section; tail elongated and laterally compressed. Head ovoid; snout well developed and rounded, mouth subterminal; end of maxilla reaching to a vertical through the posterior margin of pupil; lower lip with a reduced posterior lobe; nasal tube pigmented reaching the upper lip when depressed forward. Oral valve nearly reaching the anterior edge of vomer, and well separated from the palate laterally. Eye ellipsoid, not entering dorsal profile of head. Small prickles on lips and anterior part of snout. Gill slit extending ventrally to ventral edge of pectoral fin base; opercular lobe triangular. Upper end of the pectoral fin base at body midline, its lower end above ventral profile of body. Pelvic fin rays joined, ensheathed by the dermis (fig. 26b, c).

All teeth conical. Premaxilla with two rows anteriorly and single row posteriorly; dentary with three irregular rows anteriorly merging suddenly onto two posteriorly; 5-6 teeth on vomer. Nine to ten teeth in an irregular row on each palatine. Pyloric caeca well developed. Gill rakers 14-16 (3 + 11-13), forked. Pseudobranch filaments 3, elongated.

Cephalic lateralis pore system with pores small and rounded. Nasal pores 3, one anterior and two posterior nasal; first nasal pore located anteromesial to nostril tube; the two posterior nasal pores located dorsoposterior to it, the posterior one smaller and both coalescent. Postorbital pores two (positions one and four). Suborbital pores seven (6 + 1), six of them on the ventral ramus and one on the ascending ramus. Eight preoperculomandibular pores (fig. 26c). Interorbital and occipital pores absent. Lateral line configuration double: ventral branch with numerous closely set neuromasts, beginning just behind the fourth postorbital pore, and extending ventrolaterally to the end of the tail; mediolateral branch originating before anal fin origin and coursing just above mid-body to tail tip. Flesh and skin firm; scales extend completely across body to before anal fin origin; vertical fins nearly scaleless; head and anterior part of body, abdomen, and pectoral fin base and axil, scaleless (fig. 26b).

Neurocranium narrowed. Anterior portion of frontals fused with no trace of a suture, posterior portion separate showing a complete suture; frontal ramus long, with an anterior foramen in the interorbital space; frontal corner squared. Sphenotic protruding beyond the margin of frontal. Parasphenoid wing reaching above mid-height of the trigeminofacialis foramen, with a long articulation with the pterosphenoid and a well-developed ramus extending onto the prootic. Frontal and parasphenoid not separated by pterosphenoid. Intercalar well developed, excluding exoccipital and pterotic articulation, but not reaching the prootic. Prootic and pterotic juncture interdigitating. Sphenotic and parietal separated by frontal and pterotic. Supraoccipital well developed: anterior portion slender, extending between the posterior portion of frontals; posterior portion broad, with a well-developed median crest. Supraoccipital excluded from exoccipital by epioccipital. Parietals separated from mid-line.

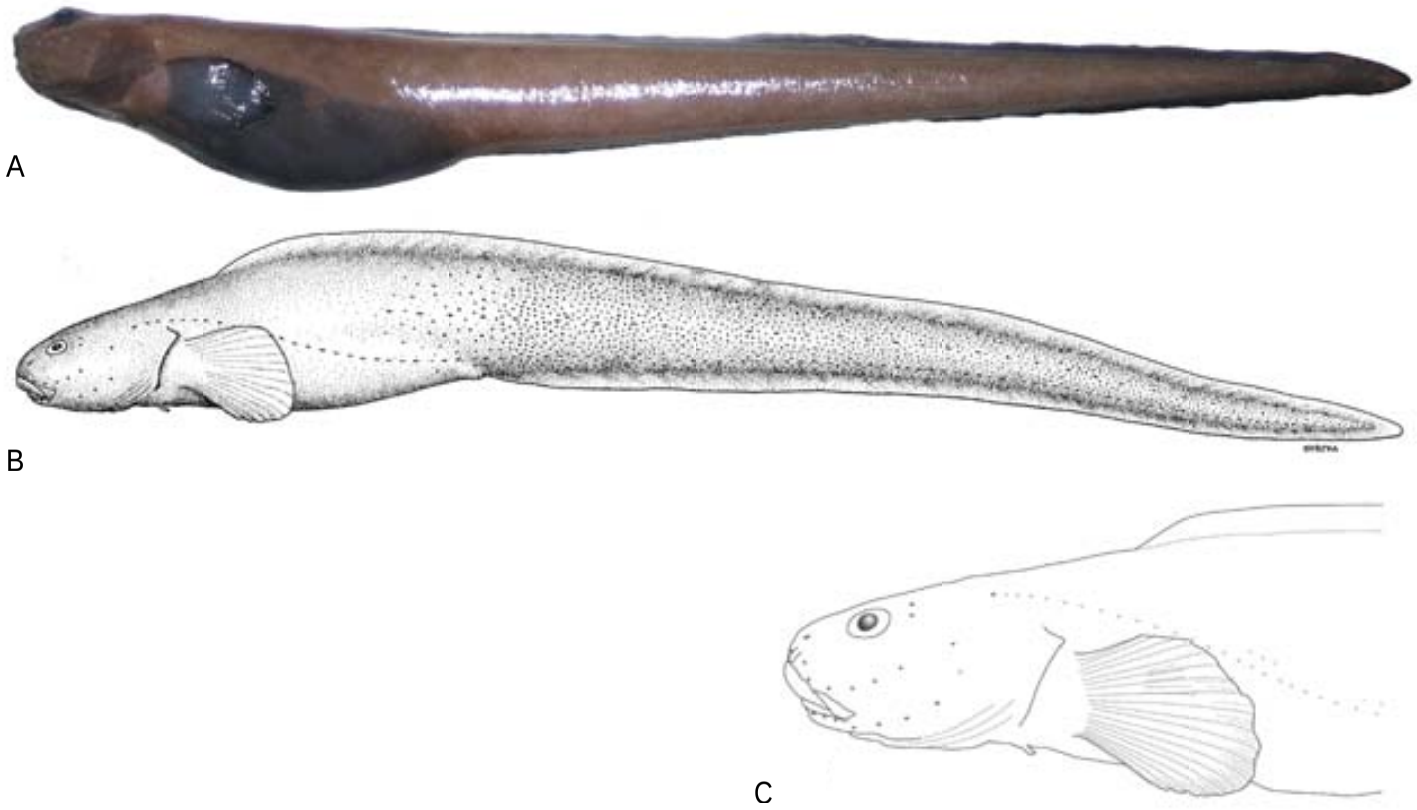


Figure 26. *Santelmoa antarctica* sp. nov. UAB:B06MB32Z27 (holotype), 330 mm SL female, from Bellingshausen Sea Left. Lateral view (photograph in fresh condition just after capture) **(A)**. Left lateral view **(B)**. Left lateral view of head showing pore pattern **(C)**.

Palatopterygoid series well developed. Ectopterygoid overlapping both anterior and dorsal surface of quadrate; lower margin of mesopterygoid not in contact with quadrate. Anterior surface of quadrate serrated. Metapterygoid large. Capitulum of palatine with a noticeable lateral prominence. Posterior ramus of hyomandibula short. Symplectic with no posterior strut. Hyoid bar with ceratohyal–epihyal joint serrated dorsally only. Six branchiostegal rays.

Pectoral girdle (fig. 27) with a strong post-temporal bearing a well-developed ventral ramus. Supracleithrum with a posterior lamina. Cleithrum with a posteriorly directed oval lamina. Scapular foramen open anteriorly; prominent postero-dorsal scapular strut. The posterior margin of scapula covers 1.5 radials. Coracoid with a posterior strut and a small foramen. Radials 4: uppermost (r1) and lowermost (r4) rounded; r2 with a notch on its ventral margin, and r3 with a notch on its dorsal margin. Cartilaginous basal plate with one foramen, smaller than the width of the radial, between scapular strut and r1. Postcleithrum is present.

Vertebrae asymmetrical, 27 + 89-92 = 116-119. Last precaudal vertebrae associated with dorsal fin ray 22; dorsal fin origin associated with vertebrae 5–6, with one free pterygiophore. Terminal dorsal fin ray associated with second preural vertebrae. Three anal fin pterygiophores, with three 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. Caudal fin rays 11-12, with two epural, four upper hypural and five lower hypural rays.

Colour of holotype in fresh. Medium brown, with dark vertical fins; pectoral fin and abdomen blackish; lateral lines and scales white. Colour of preserved specimens. Mid brown uniform; abdomen, pectoral fin, and vertical fins, darker; lining of mouth and oral cavity light; palate grayish; peritoneum black.

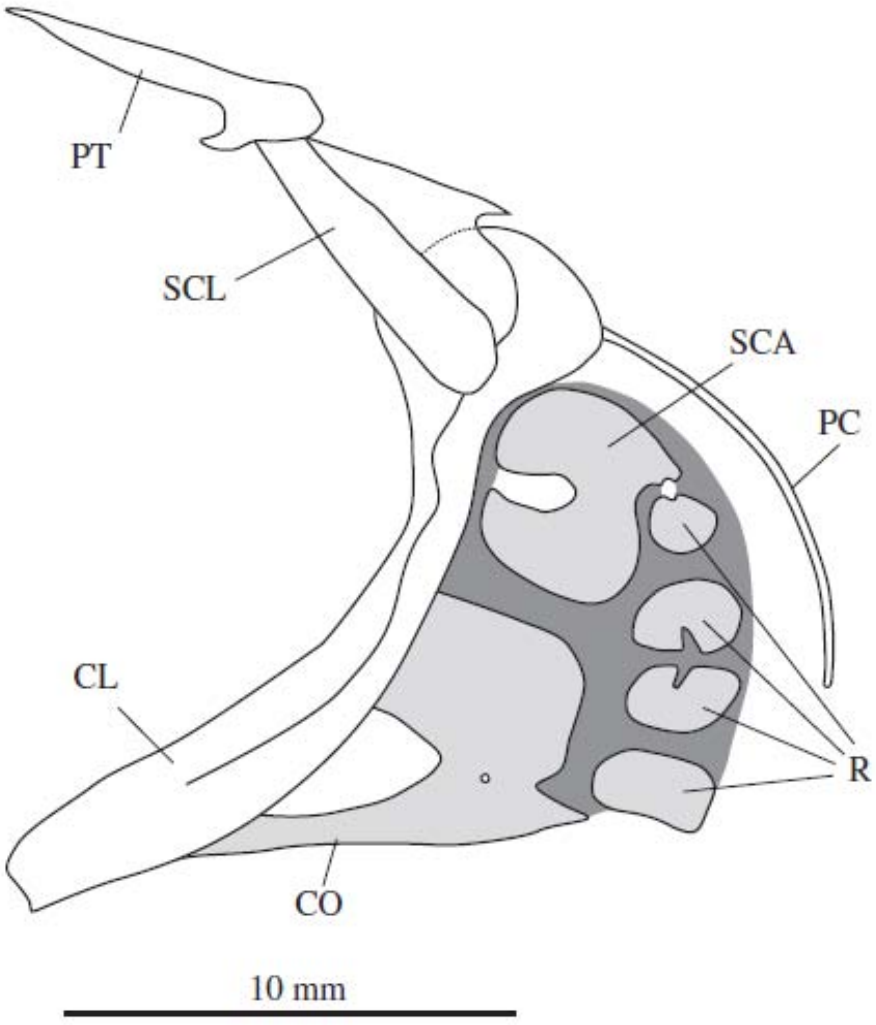


Figure 27. Left lateral view of pectoral girdle of *S. antarctica* sp. nov. CL, cleithrum; CO, coracoids; PC, postcleithrum; PT, post-temporal; R, radials; SCA, scapula; SCL, supracleithrum.

Table 7. Counts and Measurements of *Santelmoa antarctica* sp.nov. (see annex 1)

Santelmoa antarctica	Holotype	Paratype	Paratype	Range
	UAB:B06-MB32Z27	UAB:B06-MB32Z28	UAB:B06-MB32Z8	
Standard length SL (mm)	277	302	281	277-281
Sex	Female	Female	Female	
Meristic characters				
Dorsal fin rays	112	112	109	109-112
Anal fin rays	90	93	89	89-93
Caudal fin rays	11	11	12	11-12
Pectoral fin rays	17	17	17	17
Precaudal vertebrae	27	27	27	27
Caudal vertebrae	92	92	89	89-92
Total vertebrae	119	119	116	116-119
First D fin pteryg. With Vert.	5	6	6	5-6
Gill rakers	3+11	3+13	3+11	14-16
Pseudobranchial filaments	3	3	-	3
Posterior nasal pores	2	2	2	2
Suborbital pores	6+1	6+1	6+1	6+1
Morphometric characters (% SL)				
Head length	11.6	11.6	12.4	11.6-12.4
Head width	6.1	6.5	6.2	6.1-6.5
Head height	7.1	6.7	6.9	6.7-7.1
Snout length	2.6	2.7	2.6	2.6-2.7
Nostril tube length	0.6	0.6	0.5	0.5-0.6
Eye diameter	1.8	1.7	1.6	1.6-1.8
Interorbital width (hard)	0.9	0.9	0.9	0.9
Upper jaw length	4.2	4.2	4.1	4.1-4.2
Lower jaw length	5.5	5.2	5.5	5.2-5.5
Predorsal length	15.1	15.2	16.3	15.1-16.3
Preanal length	33.2	32.4	35.1	32.4-35.1
Tail length	69.6	70.2	67.6	67.6-70.2
D fin height at A fin origin	1.7	1.9	2.0	1.7-2.0
Body height at A fin origin	7.9	7.9	7.3	7.3-7.9
Pectoral fin length	8.0	7.8	8.4	8.0-8.4
Pectoral fin base height	3.3	3.6	3.7	3.3-3.7

Table 7. Continued

Santelmoa antarctica	Holotype	Paratype	Paratype	Range
	UAB:B06-MB32Z27	UAB:B06-MB32Z28	UAB:B06-MB32Z8	
Standard length SL (mm)	277	302	281	277-281
Sex	Female	Female	Female	
Pelvic fin length	1.0	0.9	1.0	0.9-1.0
Caudal fin length	2.8	2.6	2.7	2.6-2.8
Gill slit length	4.6	4.1	4.3	4.1-4.6
Opercular lobe length	0.6	0.6	0.6	0.6
Isthmus width	3.6	3.9	3.7	3.6-3.9
Snout to anterior scales	29.1	31.4	27.1	27.1-31.4
Morphometric character (% HL)				
Head width	52.1	56.4	50.1	50.1-56.4
Head height	60.8	57.8	56.6	56.6-60.8
Upper jaw length	36.7	36.7	33.5	33.5-36.7
Pectoral fin length	68.8	67.1	67.9	67.1-68.8
Snout length	22.2	23.3	21.4	21.4-23.3
Eye diameter	15.7	14.8	12.8	12.8-15.7
Interorbital (hard)	8.0	7.7	7.7	7.7-8-0
Pelvic fin length	9.2	7.9	8.6	7.9-9.2

A anal fin; D dorsal fin; HL head length; pteryg pterygiophore; SL standard length; Vert. vertebrae

3.5 DISCUSSION

The two new species are placed in *Santelmoa* by having the following characters: anterior portion of left and right frontals fused; scapular foramen open; ceratohyal-epihyal articulation interdigitating; cranium narrowed; supratemporal commissure and occipital pores absent; intercalary reaching the prootic and/or excluding exoccipital and pterotic articulation; ascending rami of the parasphenoid wing high; 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.

Santelmoa fusca sp. nov. differs from *S. carmenae*, type species of the genus, in meristic counts (table 8; *S. fusca* first): dorsal fin rays (109-113 vs. 91-95); anal fin rays (88-94 vs. 75-79); precaudal vertebrae (27-29 vs. 24-25); caudal vertebrae (87-91 vs. 75-79), and total vertebrae (114-118 vs. 99-104). Some morphometric characters are also different in the two species (*S. fusca* first): tail

length (63.0-71.3 % SL vs. 58.3-59.8); snout to anterior scales (39.4-45.1 % SL vs. 11.5-18.5); pelvic fin length (10.7-14.1 % HL vs. 4.1-8.7). Finally, some additional characters to distinguish *S. fusca* sp. nov. from *S. carmenae* are the following (*S. fusca* first): posterior nasal pores (2 vs. 1); squamation (scales reduced to tail vs. extended across the body, abdomen, and pectoral fin base and axil); lateral line configuration (two branches vs. three branches); pyloric caeca development (well developed vs. small nubbs); coracoid (with no foramina vs. with a small foramen), and foramina in the cartilaginous basal plate of the pectoral girdle (with no foramina vs. with a small foramen between the two central radials).

Santelmoa fusca sp. nov. agrees with *S. elvirae* in many meristic and in most morphometric characters (table 8). The two species differ in the following characters (*S. fusca* first): pectoral fin rays (15-17 vs. 18-19); snout to anterior scales (39.4-45.1 % SL vs. 11.6-12.3); head height (54.6-61.1 % HL vs. 46.1-49.6), and pelvic fin length (10.7-14.1 % HL vs. 4.0-6.2). Both species differ also in the following anatomical characters (*S. fusca* first): mouth position (terminal vs. inferior); squamation (reduced to tail vs. extended across the body, abdomen, and pectoral fin base and axil); palatine teeth (2 rows vs. 1 row); pyloric caeca development (well developed vs. barely produced);intercalar (reaching prootic vs. protruding into prootic); coracoid (with no foramen vs. with a small foramen), and foramina in the cartilaginous basal plate of the pectoral girdle (with no foramina vs. with 3 foramina: one between each two radials).

Santelmoa antarctica sp. nov. differs from *S. carmenae*, type species of the genus, in meristic counts (Table 8. *S. antarctica* first): dorsal fin rays (109-112 vs. 91-95); anal fin rays (89-93 vs. 75-79); precaudal vertebrae (27 vs. 24-25); caudal vertebrae (89-92 vs. 75-79), and total vertebrae (116-119 vs. 99-104). Some morphometric characters are also different in the two species (*S. antarctica* first): head length (6.1-6.5 % SL vs. 7.7-10.6); head width (6.1-6.5 % SL vs. 7.7-10.6); preanal length (32.4-35.1 % SL vs. 40.1-41.6); tail length (67.6-70.2 %SL vs. 58.3-59.8); snout to anterior scales (27.1-31.4 % SL vs. 11.5-18.5). Finally, some additional characters to distinguish *S. antarctica* sp. nov. from *S. carmenae* are the following (*S. antarctica* first): posterior nasal pores (2 vs. 1); squamation (dense on the tail,scattered on the posterior part of body vs. extended across the body, abdomen, and pectoral fin base and axil); lateral line configuration (two branches vs. three

branches); suborbital pore pattern (6 + 1 vs. 6 + 0); pyloric caeca development (well developed vs. barely produced); intercalar (no reaching prootic vs. reaching prootic); posterior strut on symplectic (absent vs. present); coracoid (with no foramen vs. with a small foramen), and foramina in the cartilaginous basal plate of the pectoral girdle (one foramen between scapular strut and r1 vs. one foramen between r2 and r3).

Santelmoa antarctica sp. nov. agrees with *S. elvirae* in meristic characters (Table 8). However, the two species differ in the following morphometric characters (*S. antarctica* first): snout to anterior scales (27.1-31.4 % SL vs. 11.6-12.3); upper jaw length (4.1- 4.2 % SL vs. 4.9-6.2); lower jaw length (5.2-5.5 % SL vs. 6.3-7.2); head height (56.6-60.8 % HL vs. 46.1-49.6); pectoral fin length (67.1-68.8 % HL vs. 48.3-59.5), and pelvic fin length (7.9-9.2 % HL vs. 4.0-6.2). Both species differ also in the following anatomical characters (*S. antarctica* first): mouth position (subterminal vs. inferior); suborbital pore pattern (6+1 vs. 6+0); squamation (extensive on tail, scattered on the posterior part of body vs. dense on tail and across the body, abdomen, and pectoral fin base and axil); suborbital pore pattern (6+1 vs. 6+0); pyloric caeca development (well developed vs. barely produced); intercalary (no reaching prootic vs. protruding into prootic), and foramina in the cartilaginous basal plate of the pectoral girdle (one between scapular strut and r1 vs. three: one between each two radials).

Santelmoa antarctica sp. nov. agrees with *S. fusca* sp. nov. in meristics and in most morphometric characters (Tables 6, 7, 8). The two new species differ in the following morphometric characters (*S. antarctica* first): snout to anterior scales (27.1-31.4 % SL vs. 39.4-45.1); interorbital width (7.7-8.0 % HL vs. 8.5-11.6), and pelvic fin length (7.9-9.2 % HL vs. 10.7-14.1). Additionally, both species differ in the following anatomical characters (*S. antarctica* first): suborbital pore pattern (6 + 1 vs. 6 + 0); squamation (on the tail and scattered on the posterior part of body vs. reduced to tail); palatine teeth rows (1 vs. 2); intercalary (no reaching prootic vs. protruding into prootic); supraoccipital (dividing the posterior end of frontals vs. no dividing the posterior end of frontals); pectoral radial shape (r2 and r3 notched vs. all unnotched), and foramina in the cartilaginous basal plate of pectoral girdle (one foramen between scapular strut and r1 vs. with no foramina).

Table 8. Counts and measurements of the four species of *Santelmoa* (see annex 1).

	S. carmenae	*S.elvirae*	*S.fusca*	*S.antarctica*
SL (mm)	234-277	305-349	206-330	277-281
Meristic characters				
Dorsal fin rays	91-95	108-111	109-112	109-112
Anal fin rays	75-79	93-94	88-91	89-93
Caudal fin rays	10-11	11	10-12	11-12
Pectoral fin rays	16	18-19	15-16	17
Precaudal vertebrae	24-25	26-27	27	27
Caudal vertebrae	75-79	90-93	87-91	89-92
Total vertebrae	99-104	116-119	114-118	116-119
First D fin pteryg. with Vert.	6-8	6	5-6	5-6
Gill rakers	2-3+10-12	3+13	4+12	3+11
Pseudobranchiae	3-5	3-5	3	
Morphometric characters (% SL)				
Head length	13.9-18.5	12.9-14.1	11.9-14.0	11.6-12.4
Head width	7.7-10.6	5.7-6.7	6.7-7.7	6.1-6.5
Head height	8.2-8.9	6.3-6.9	7.0-7.8	6.7-7.1
Snout length	3.5-5.6	2.9-4.3	2.2-3.1	2.6-2.7
Nostril tube length	0.6-0.8	0.4-0.7	0.6-0.8	0.5-0.6
Eye diameter	2.3-2.8	2.0-2.2	1.9-2.5	1.6-1.8
Interorbital width (hard)	1.0-1.2	0.8-1.1	1.0-1.4	0.9
Upper jaw length	5.5-9.8	4.9-6.2	4.4-5.4	4.1-4.2
Lower jaw length	6.8-10.5	6.3-7.2	5.6-6.4	5.2-5.5
Predorsal length	17.6-23.4	16.4-17.6	15.4-16.1	15.1-16.3
Preanal length	40.1-41.6	33.9-36.5	33.8-35.9	32.4-35.1
Tail length	58.3-59.8	65.5-68.1	64.2-69.1	67.6-70.2
D fin height above A fin origin	2.4-2.5	1.6-1.8	1.7-3.0	1.7-2.0
Body height at A fin origin	8.2-9.7	6.6-7.8	7.1-8.9	7.3-7.9
Pectoral fin length	7.2-9.1	6.8-7.7	7.4-8.5	8.0-8.4
Pectoral fin base height	3.9-4.2	3.0-3.3	3.2-4.1	3.3-3.7
Pelvic fin length	0.7-1.2	0.5-0.8	1.3-1.7	0.9-1.0
Caudal fin length	2.1-2.9	2.0-2.3	2.2-3.3	2.6-2.8
Gill slit length	5.2-5.9	3.5-4.5	4.4-5.4	4.1-4.6
Opercular lobe length	0.6-0.9	0.7-0.9	0.9-1.1	0.6
Isthmus width	4.4-5.5	3.2-3.9	3.8-4.5	3.6-3.9
Snout to anterior scales	11.5-18.5	11.6-12.3	39.4-45.1	27.1-31.4
Morphometric characters (% HL)				
Head width	50.7-59.2	41.3-49.3	50.6-63.0	50.1-56.4
Head height	48.0-59.5	46.1-49.6	54.6-60.7	56.6-60.8
Upper jaw length	36.8-54.5	38.4-44.0	35.5-43.8	33.5-36.7
Pectoral fin length	40.8-62.2	48.3-59.5	60.0-69.2	67.1-68.8
Snout length	23.5-30.5	23.0-30.9	18.3-23.9	21.4-23.3
Eye diameter	14.5-18.6	15.0-17.4	15.3-18.2	12.8-15.7
Interorbital (hard)	6.2-8.1	6.5-8.0	8.6-10.6	7.7-8.0
Pelvic fin length	4.1-8.7	4.0-6.2	10.7-12.7	7.9-8.6

A anal fin; *D* dorsal fin; *HL* head length*; pteryg*. pterygiophore; *SL* standard length**;** *Vert*. vertebrae.

3.6 ACKNOWLEDGMENTS

We thank the scientific team, the captain, crew and UTM technicians of the R/V Hespérides for their help during the Bentart 03 and Bentart 06 cruises, on which many specimens were captured. Special thanks to José Castro ‘‘Córdoba’’ for his expertise in fishing with the traps and to Dr. Ignacio Olaso for helping onboard with the collection of type specimens. We are also grateful to Carmen Benito for the X-rays, Jordi Corbera for the illustrations, and Muriel, daughter of the first author, for the English correction of the draft manuscript. This manuscript also benefited from the constructive criticism by reviewers (Gento Shinohara and Mario la Mesa). The Bentart cruises were supported by the Spanish Antarctic Programme (CICYT), and the Galathea 3 Expedition was conducted under the auspices of the Danish Expedition Foundation. This study was supported by a grant from the Ministerio de Ciencia e Innovación, Spain: ‘‘Culminación del estudio taxonómico integrado de Zoárcidos (Teleostei, Perciformes) antárticos (CTM2011-1585-E)’’, and a grant from the Danish National Research Foundation, ‘‘Evolution of Polar fishes’’.

CHAPTER 3

A new species of *Pachycara* from Solomon Sea (Western South Pacific Ocean)

4 Description of ***Pachycara matallanasi*** sp.nov. from Solomon Sea (Western South Pacific Ocean)

4.1 ABSTRACT

A new species of zoarcid fish, *Pachycara matallanasi* sp.nov., is described. Specimens were collected in the Solomon Sea during the Danish expedition Galathea 3. The new species is the second member of the genus in the Western South Pacific Ocean. *P.matallanasi* sp.nov. can be distinguished from its congers by the following combination of characters: body without scales, pelvic fin absent, mediolateral line, dorsal fin ray associated with vertebra 5-6, total vertebrae 103-108. Smooth ceratohyal-epihyal articulation, posttemporal with well-developed ventral ramus and coracoid with a posterior strut and a small foramen.

4.2 INTRODUCTION

The genus *Pachycara* is placed within subfamily Lycodinae that according to recent revisions and descriptions includes 38 genera (table 9) and around 190 species (Anderson, 1994; Anderson and Fedorov, 2004; Matallanas, 2009a, 2009b, 2009c, 2010, 2011a, 2011b; Mincarone and Anderson, 2008; Matallanas and Corbella, 2012).

Genus *Pachycara* was described for the first time by Zugmayer (1911a). *Pachycara obesa* was the type species which was initially described from a single specimen taken in the abyssal North Atlantic by the expeditions of Prince Albert I of Monaco (Zugmayer, 1911a, b). A second specimen of the type specie was collected off Virginia by Markle and Sedberry (1978). The type species was renamed *Pachycara bulbiceps* (Garman, 1899) as a result of synonomy between *Maynea bulbiceps* Garman, 1899 and *Pachycara obesa* Zugmayer, 1911a. Markle and Sedberry (1978) redescribed the type species and they concluded that the species differed from all other zoarcids in the following combination of characters: no pelvic fin, no lateral line, 18 to 19 pectoral rays, large gill opening extending below lower edge of pectoral base, dorsal origin above middle of pectoral fin, small scales, and habitat below 2400m.

Considerable systematic confusion exists in *Pachycara* and several revisions of the genus have attempted to established diagnostic characters for all species including osteological observations and keys to species (fig. 28) (Anderson, 1989, 1990, 1991, 1994; Anderson and Peden, 1988; Anderson and Bluhm, 1997; Møller and Anderson, 2000). *Austrolycichthys* Regan, 1913 was synonymized with *Pachycara* by Anderson (1988c), and Whitley (1931) proposed to replace the name *Pachycara* by *Pachycarichthys* for existing two homonyms names. In the course of time, many species have been included in the genus *Pachycara* after several revisions: *Maynea bulbiceps* Garman 1899, *Phucocoetes suspectus* Garman 1899; *Lycodes microcephalus* Jensen, 1902; *Lycodes brachycephalus*, Pappenheim, 1912; *Lycenchelys crassiceps* Roule, 1916 and *Lycodes brachycephalus* (Pappenheim, 1912) (Anderson and Fedorov, 2004).

After many reviews, the genus is defined by the following combination of characters: Body robust, tail short, mental crest absent, suborbital bones 6-8; canal with 5-7 pores; parasphenoid wing below mid-height of trigeminofacialis foramen; palatopterygoid series well developed; scales present; pyloric caeca present; lateral

line(s) present; vomerine and palatine teeth present; pseudobranch and pelvic find present or absent; total vertebrae 92-125 (Anderson, 1988c, 1989, 1994; Møller and Anderson, 2000).

Many species of *Pachycara* have been described. Currently it is a specious genus of the *Lycodinae* with 25 known species, according to the last revisions and descriptions (Anderson and Fedorov, 2004; Anderson and Mincarone, 2006; Møller and King, 2007; Shinohara, 2012) (table 9), and several undescribed species are known (Møller pers. comm.).

Genus *Pachycara* are found in most of the world's oceans, except the Arctic and the Mediterranean Sea (Anderson, 1994; Anderson and Fedorov, 2004) and is poorly represented in the Western Pacific (Anderson, 1989). Only *P. garricki* Anderson, 1990 has been reported from western South Pacific and recently *P. moelleri* has been described from western North Pacific (Shinohara, 2012) (fig. 29).

The purpose of this chapter is to describe a new species from the Solomon Sea a relatively unknown area for the subfamily Lycodinae.

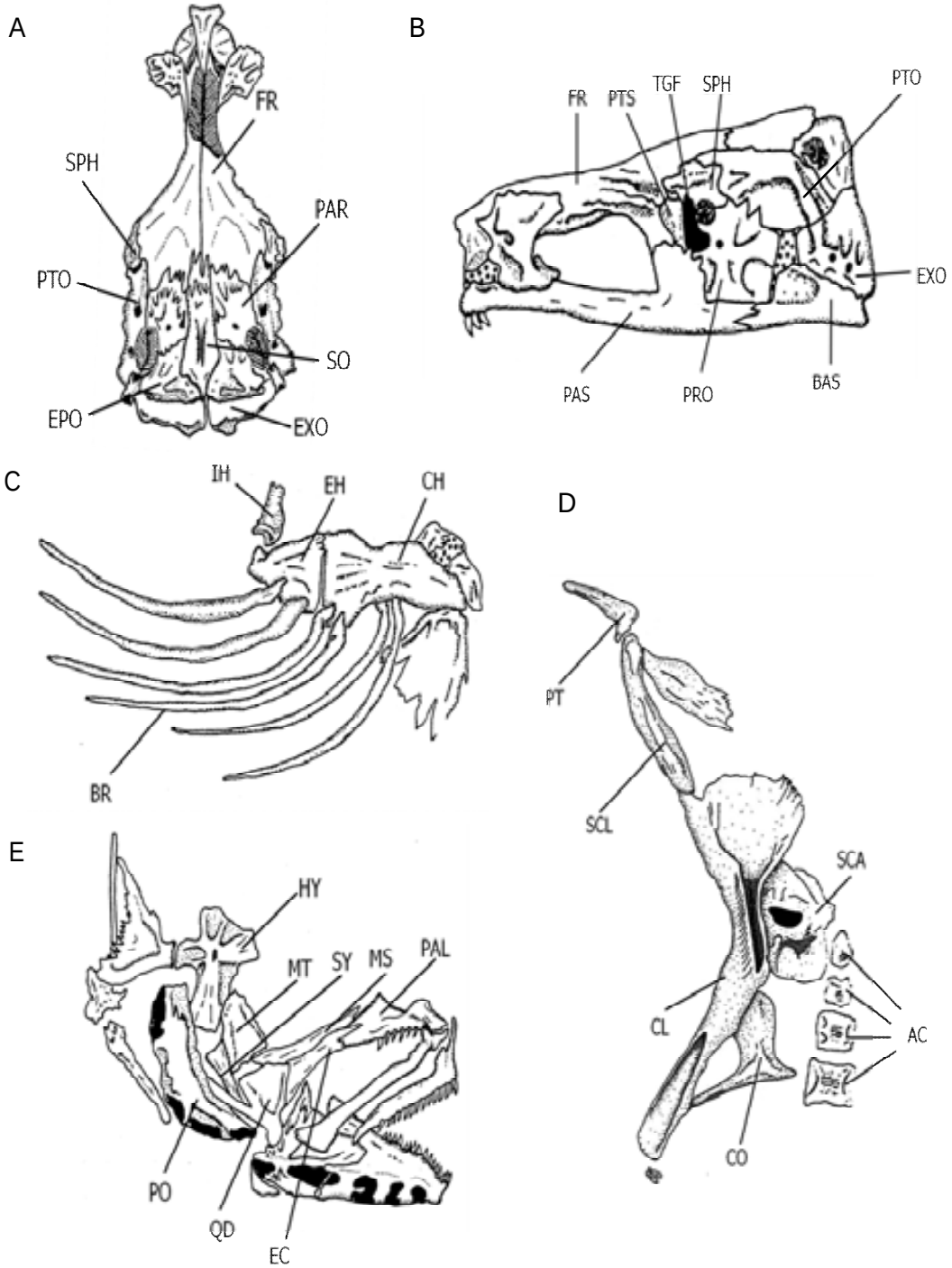


Figure 28. *Pachycara gymninium,* BCPM 980-100, 281mm.), Neurocranium, dorsal view **(A)**, Neurocranium, left lateral view **(B)**, Hyoid bar **(C)**, Pectoral girdle (*Pachycara bulbiceps*) **(D)** and Jaws, suspensorium and opercular bones **(E)** (Anderson, 1989). AC, actinost; BAS, basioccipital; BR, branchiostegal rays; CH, ceratohyal; CL, cleithrum; CO, coracoid; EC, ectopterygoid; EH, epihyal; EPO, epioccipital; EXO, exoccipital; FR, frontal; HY, hyomandibula; IH, interhyal; MS, mesopterygoid; MT, metapterygoid; PAL, palatine; PAR, parietal; PAS, parasphenoid; PO, preopercle; PRO, prootic; PT, posttemporal; PTO, pterotic; PTS, pterosphenoid; QD, quadrate; SCA, scapula; SCL, supracleithrum; SO, supraoccipital; SPH, sphenotic; SY, symplectic; TGF, trigeminofacialis foramen.

Table 9. Species of *Pachycara* and distribution.

Species	Author(s)	Year	
P. bulbiceps	(Garman)	1899	Eastern Pacific and North Atlantic
P. suspectum	(Garman)	1899	Eastern Pacific
P. crassiceps	(Roule)	1916	Eastern Atlantic
p. gymninium	Anderson and Peden	1988	Eastern North Pacific
P. lepinium	Anderson and Peden	1988	Eastern North Pacific
P. mesoporum	Anderson	1989	Eastern South Pacific
P. crossacanthum	Anderson	1989	Eastern Atlantic
P. rimae	Anderson	1989	Eastern Pacific
P. pammelas	Anderson	1989	Eastern South Pacific
P. sulaki	Anderson	1989	Western Atlantic
P. shcherbachevi	Anderson	1989	Northern Indian Ocean
P. microcephalum	(Jensen)	1902	Eastern North Atlantic
P. brachycephalum	(Pappenheim)	1912	Antarctica
P. garricki	Anderson	1990	Western South Pacific
P. goni	Anderson	1991	Antarctic Ocean
P. thermophilum	Geistdoerfer	1994	Atlantic Ocean
P. nazca	Anderson and Bluhm	1997	Eastern Pacific
P. arabica	Møller	2003	Western Indian Ocean
P. andersoni	Møller	2003	Western Indian Ocean
P. saldanhai	Biscoito and Almeida	2004	Atlantic
P. alepidotum	Anderson and Micarone	2006	South Western Atlantic
P. dolichaulus	Anderson	2006	South East Pacific Ocean
P. priedei	Møller and King	2007	Southern Indian Ocean
P. cousinsi	Møller and king	2007	Southern Indian Ocean
P. moelleri	Shinohara	2012	Western North Pacific

Colour points indicate position on the map (fig. 29)

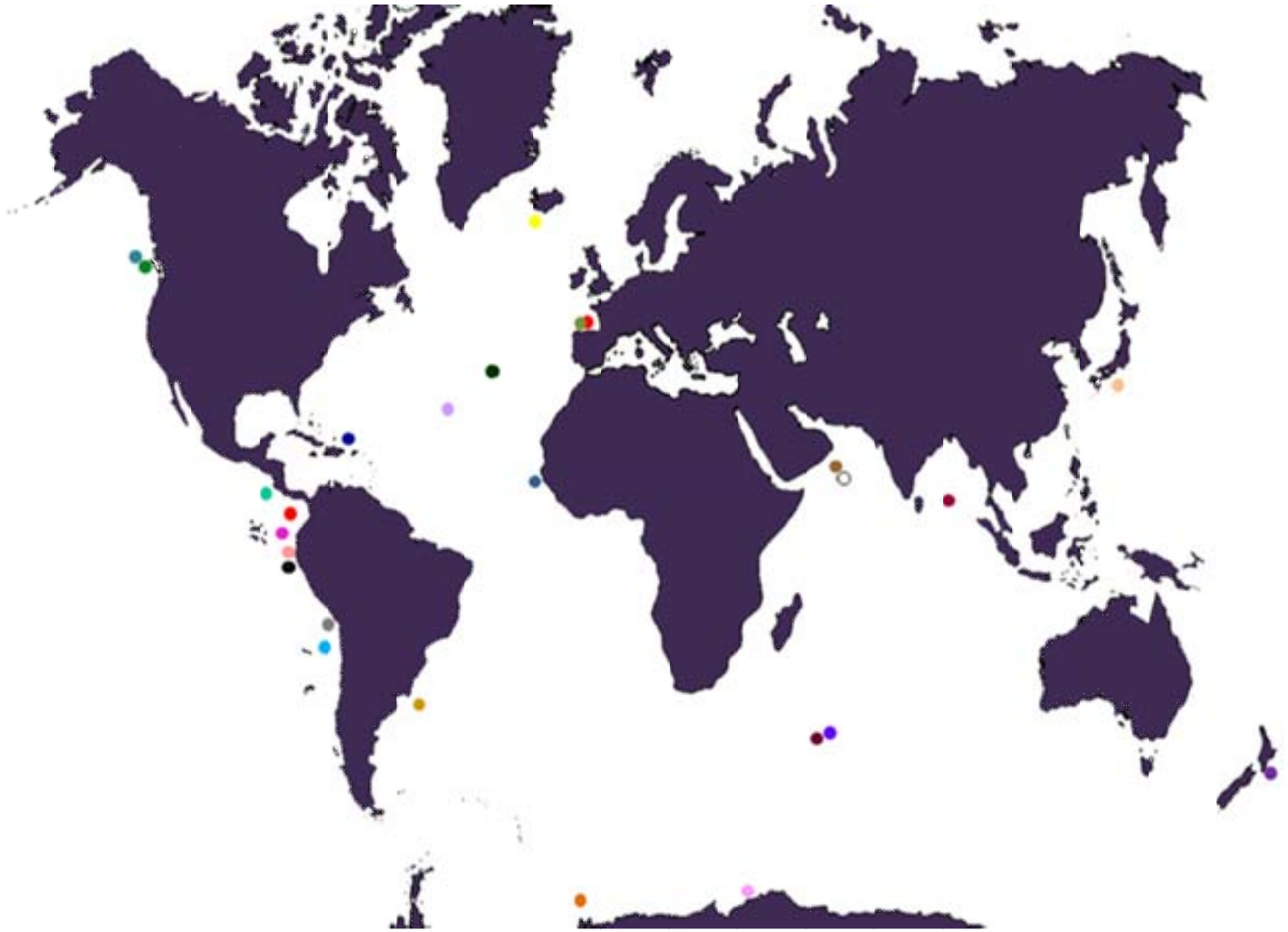


Figure 29. Approximate locations where holotypes of *Pachycara* species were collected (Anderson and Fedorov, 2004; Biscoito and Almeida, 2004; Anderson and Micarone, 2006; Anderson, 2006; Møller and King, 2007, Shinohara, 2012). Colour points indicate the name of the species (table 9).

4.3 MATERIALS AND METHODS

Specimens were collected in the Solomon Sea (Western South Pacific Ocean) 7°49'4''S, 156°02'8'' during the Danish expedition Galathea 3, R/V VÆDDEREN, st. 061228-01, 28 Dec. 2006 (fig. 30). Specimens were caught by a 1.2 m Agassiz trawl, depth 4350-4450 m. All material was deposited at the Ichthyological collection of Natural History Museum of Denmark. Muscle tissue samples were stored in absolute ethanol for a molecular analysis.

Counts, measurements and general terminology follow Gosztonyi (1977, 1988) and Anderson (1982) (see annex 1 and 2). Measurements were made with ocular micrometer or dial caliper to nearest 0.1 mm and all specimens were radiographed. Staining method used was a solution containing 75% ETOH and 25% water in which enough alizarin dye crystals are dissolved to give the liquid a urine-yellow color (Springer and Johnson, 2000).

DNA were extracted from muscle tissue using QIAmp Tissue Kit from Qiagen. PCR conditions were for the Cytochrome oxidase subunit I (COI): one initial cycle of denaturation (94ºC, 10min), followed by 30 cycles (94ºC for 1 min, 55ºC for 1min, 72ºC for 1min) and finally one cycle (72ºC for 5min) using primers FishF1-TCAACCAACCACAAAGACATTGGCAC30 and FishR1-TAGACTTCTGGGTGGCCAA AGAATCA30 (Ward *et al*., 2005). For the amplification of the Control Region (CR) following conditions were applied: one initial cycle of denaturation (94ºC, 2min) followed by 30 cycles (96ºC for 15sec, 55ºC for 15sec, 72ºC for 1min and 30sec) and finally one cycle (72ºC for 10min). Primers for CR: L15927-Thr_(M59)AGAGCGTCGGTCTTGTAAKCCG and H885-12S_(M70)TAACCGCGGYG GCTGGCACGA (Miya *et al*., 2001).

Sequences were obtained in both directions and were aligned using ClustalX 2.0.11 (Thompson *et al*., 1997). The genetic distances were calculated with Kimura 2-parameter model (Kimura, 1980) using MEGA 5.03 (Tamura *et al*., 2007). Sequences belonging to some genera of subfamily Lycodinae were collected in Bellingshausen Sea during the Spanish Antarctic expedition Bentart-2006; In SW Atlantic Ocean, Falkland (Malvinas) Island, during Atlantis-2010 campaign of the "Centro Oceanográfico de Vigo (Instituto Español de Oceanografía)" and during Galathea-3 expedition of the Natural History Museum of Denmark.

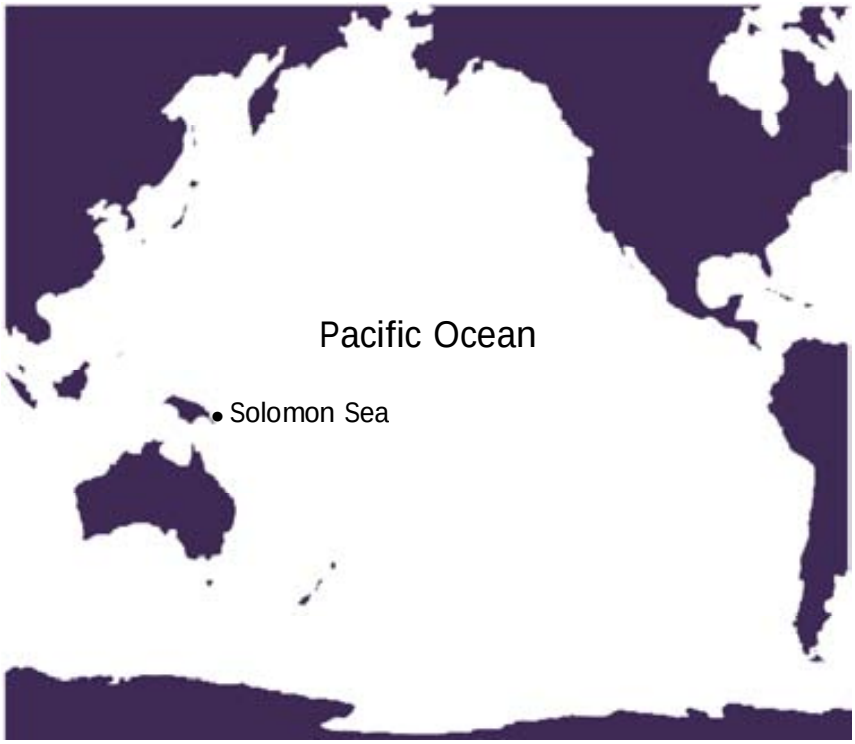


Figure 30. Map of Solomon Sea

4.4 RESULTS

Pachycara matallanasi sp.nov.

(Figs. 31-34; Table 10)

4.4.1 Material examined

HOLOTYPE: Natural History Museum of Denmark (ZMUC 766564), 140 mm SL, Solomon Sea (Western South Pacific Ocean), 7°49'4"S, 156°02'8"E, Galathea 3 exp., R/V VÆDDEREN, st. 061228-01, 28 Dec. 2006, 1.2m Agassiz trawl, depth 4350-4450m.

PARATYPES: ZMUC P766566, male, 124mm SL; ZMUC P766569, 102mm SL; ZMUC P766567,female, 138mm SL; ZMUC P766568; ZMUC P766563, female, 148mm SL and ZMUC P766565 female, 141mm SL and ZMUC P766562 (used for anatomical analysis: cranium, palatal series, hyoid arch and branchiostegals, pectoral girdl). All specimens were captured with the holotype.

Etymology. In honour of Dr. Jesús Matallanas (Universitat Autònoma de Barcelona) for his many contributions to the taxonomy of the family Zoarcidae.

Diagnosis. A species of *Pachycara* distinguished from congeners by the body without scales, pelvic fin absent, mediolateral line, dorsal fin ray associated with vertebra 5-6, total vertebrae 103-108, smooth ceratohyal-epihyal articulation, posttemporal with well-developed, ventral ramus and coracoid with a posterior strut and a small foramen.

Description. (Counts and measurements are in table 10). Body robust, head ovoid; body elongated and tail compressed laterally along its entire length; eyes elliptical, mouth inferior, flesh and skin firm. Body naked, without scales. Gill slit extending ventrally to just below ventral edge of pectoral fin base; nasal tub short, unpigmented, not reaching upper lip when depressed forward. Gill slit extending below edge of pectoral fin base, opercular lobe small. Lower lip without a lateral lobe (fig.31).

Teeth in jaws, vomer and palatine conical. 6-12 premaxilla teeth in 1-2 rows, 5-8 teeth on vomer; palatine teeth 4-8, in 1-2 rows. Dentary teeth 17-18 in 2-3 irregular rows. Pyloric caeca 2. Gill rakers 2+11-2+15, like leaf. Pseudobranch filaments 5-6.

Cephalic lateralis pore system with pores moderately large (except the eigth preoperculomandibular pore). Nasal pores 2, first nasal pore located anteromesial to nasal tube, the other posteromesially. Suborbital pore 7, all in the ventral ramus (7+0), preoperculomandibular pores 8-9, 6 arising from dentary, 1 anguloarticular and 1-2 from preopercle; postorbital pores 2, located at position 1 and 4 (position 2 and 3 in one holotype: ZMUC 766564) (fig.32). Interorbital pore absent (present in one

paratype: ZMUC 7665649). Supratemporal commisure and occipital pores absent. A regular serie of neuromasts between suborbital and preoperculomandibular pores.

Lateral line configuration with a single mediolateral branch beginning just behind the fourth postorbital pore and extending laterally to the end of the tail. Some neuromast as a short row on dorsal area (fig. 31).

Neurocranium wide (its width about 50 % of total cranium length). Parasphenoid wing reaching mid-height of the trigeminofacialis foramen, and broadly articulated with the pterosphenoid. Frontal and parasphenoid not separated by pterosphenoid (fig. 33c).

A wide cartilaginous area between parasphenoid, prootic and exoccipital. Frontal bones separate, showing a complete suture; frontal ramus long; frontal corner squared. Sphenotic and parietal separated by frontal. Parietals squarish and separated from the cranial mid-line. Supraoccipital excluded from exoccipital by epiotic; no supratemporal commissure across parietals.

Palatopterygoid series well developed, with mesopterygoid overlapping half of the dorsal surface of quadrate and ectopterygoid overlapping the entire anterior surface of quadrate. Metapterygoid large. Posterior ramus of hyomandibula short. Symplectic with no posterior strut (fig. 33a).

Hyoid bar with ceratohyal-epihyal joint smooth along whole length. Six branchiostegal rays; anteriormost two attached on the inner surface of ceratohyal; remainder four inserted on the outer side of the hyoid bar: 2 on ceratohyal and 2 on epihyal (fig. 34).

Pectoral girdle with a posttemporal bearing a well-developed ventral ramus. Supracleithrum with a posteriorly-directed lamina weakly ossified. Scapular foramen closed; prominent postero-dorsal scapular strut. Coracoid with a posterior strut and a small foramen. Radials 4, the uppermost smaller. Cartilaginous basal plate with no foramina. Postcleithrum present. Pelvic fin absent (fig. 33b).

Vertebrae simetrical, total vertebrae 103-108 (29- 31 + 73-78). Dorsal fin origin associated with vertebrae 5-6 with 0-1 free predorsal pterygiophores.

Colour in alcohol uniform brown, abdomen dark bluish. Oral cavity, light and peritoneum black.

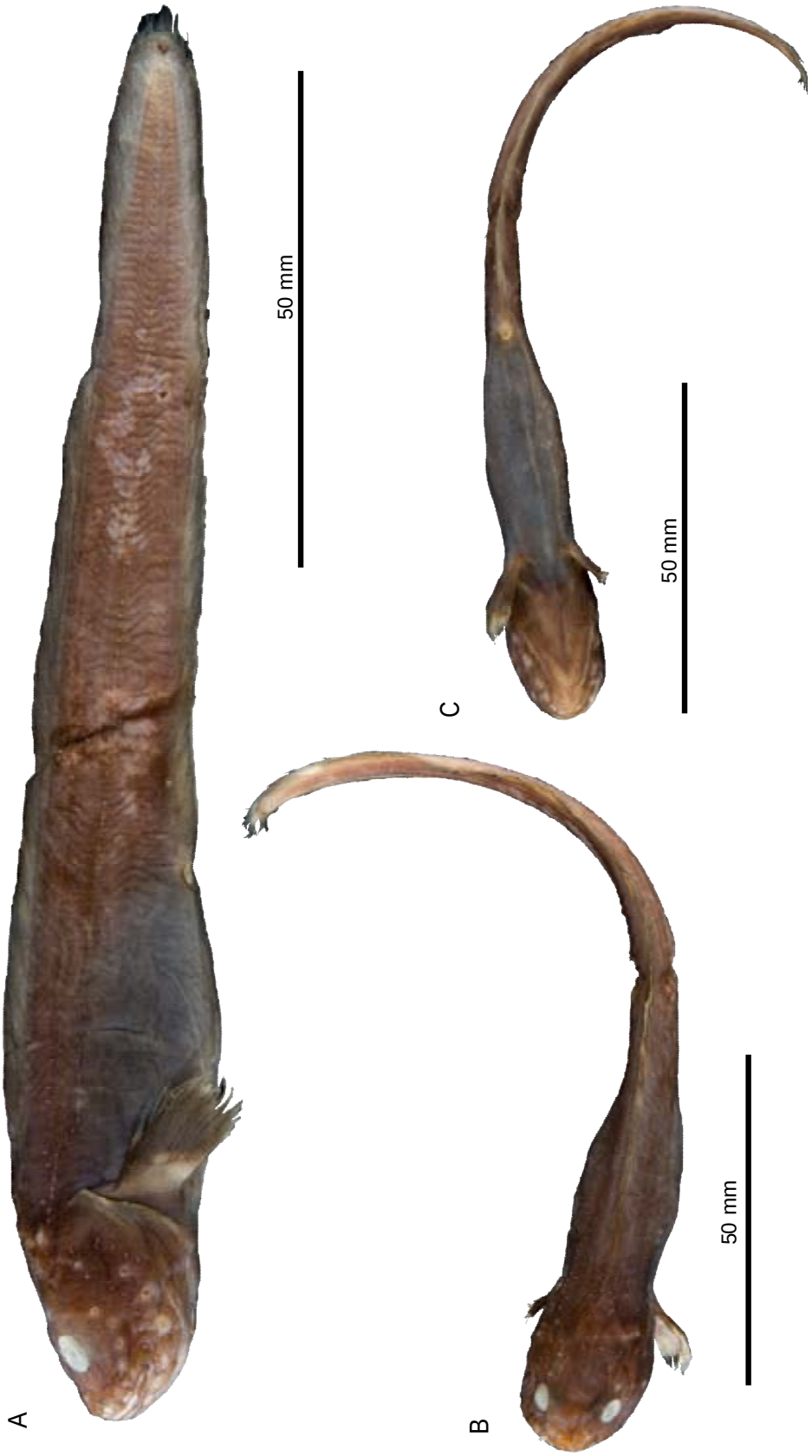


Figure 31. *Pachycara matallanasi* sp.nov. Holotype (ZMUC P766564), 140 mm SL (Photo: Natural History Museum of Denmark). Left lateral view **(A)**, Dorsal view **(B)** and Ventral view **(C)**.

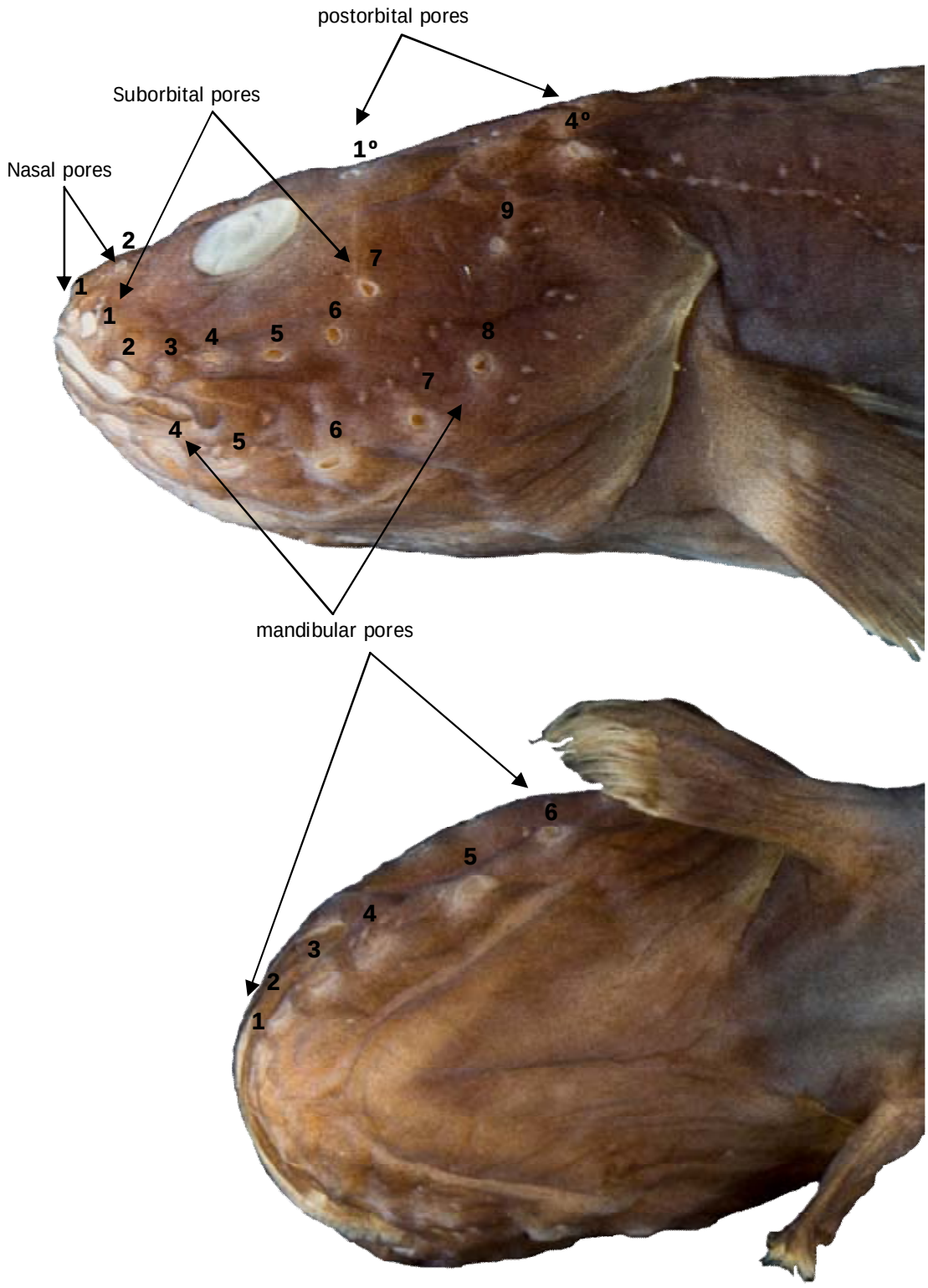


Figure 32. Head pores of *Pachycara matallanasi* sp. nov. Holotype (ZMUC P766564)

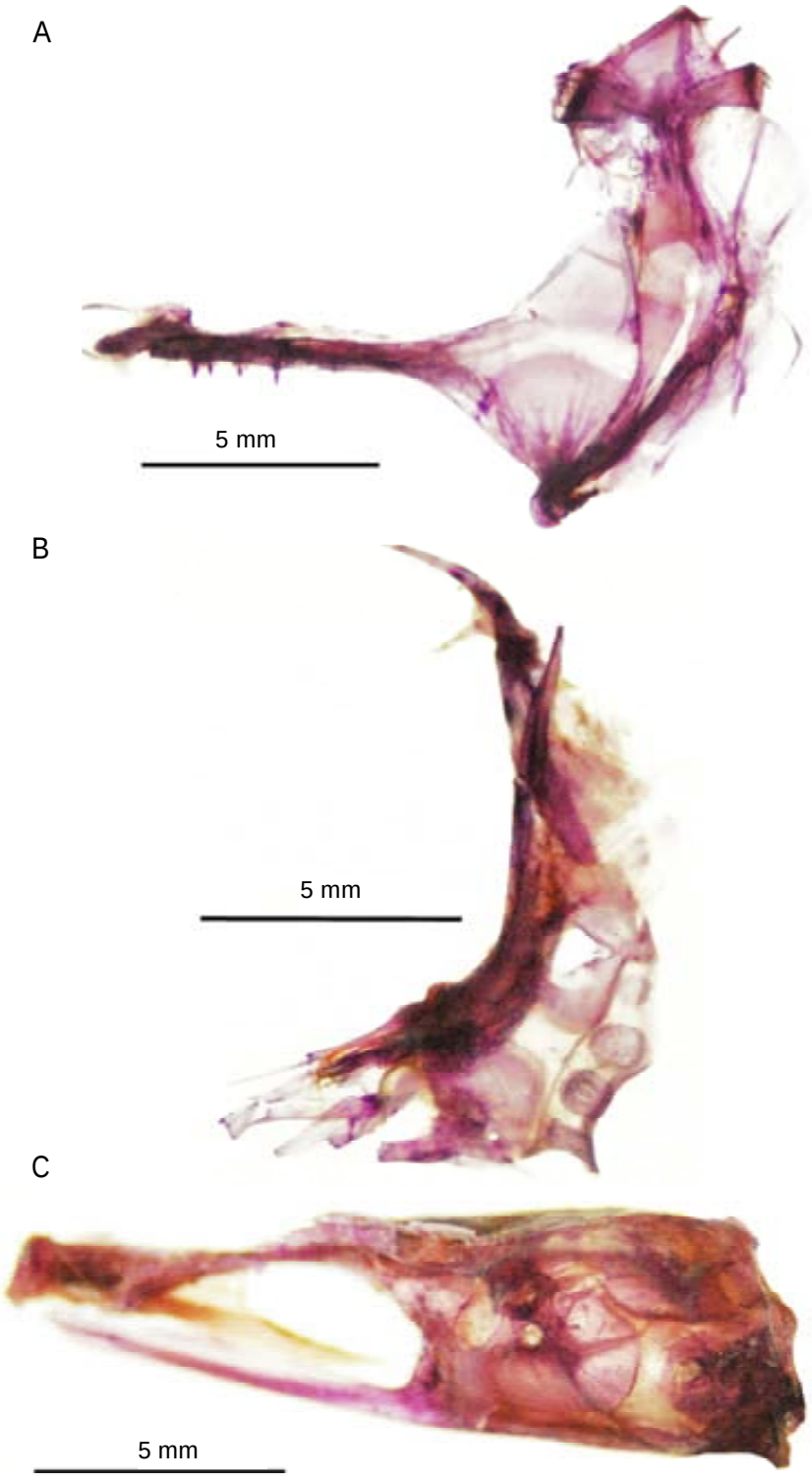


Figure 33. Left suspensorium and preopercle **(A)**, Left lateral view of pectoral girdle **(B)** and Lateral view of cranium **(C)** of *Pachycara matallanasi* sp.nov.

DNA barcode Cytochrome oxidase subunit I (COI) of *Pachycara matallanasi* sp.nov. (Holotype: ZMUC P766564):

GTACAGCTCTAAGCCTCCTCATTCGAGCGGAGCTAAGCCAACCCGGCGCCCTCCTGGGGGAC
GACCAAATTTACAATGTCCTTGTTACAGCGCATGCGTTCGTAATAATTTTCTTTATAGTAATA
CCAATTATGATCGGGGGGTTTGGAAACTGACTTGTGCCCTTGATAATCGGGGCCCCGGACAT
AGCATTTCCCCGAATAAACAACATGAGCTTTTGACTCCTTCCCCCATCTCTTCTTCTCCTCCTC
GCTTCTTCGGGGGTAGAGGCGGGGGCTGGGACAGGGTGAACAGTCTACCCCCCTCTCTCTG
GTAACTTGGCCCACGCAGGGGCCTCCGTTGATTTAACAATCTTCTCCCTTCACCTAGCAGGG
ATCTCTTCGATCCTCGGGGCAATTAATTTCATTACAACCATCATTAACATGAAGCCCCCCGCG
ATCTCCCAGTACCAGACACCCCTCTTCGTCTGATCAGTGCTTATCACGGCGGTCCTACTCCTC
CTCTCTCTCCCCGTCCTCGCAGCTGGTATCACCATGCTCCTGACAGATCGTAACCTTAACACC
ACCTTCTTCGACCCCGCCGGGGGAGGAGACCCAATCCTTTACCAACA (610bp)

DNA barcode Control Region (CR) of *Pachycara matallanasi* sp.nov. (Holotype: ZMUC P766564):

TTTCACTTATGGCTTAATGTTTATCACTGCTGAGTTCCCTTGAGGGTGTGGCTAAGCAAGGC
GTCATGGGCTCAACTAGAGATGTGCCTGATACCTGCTCCTTGTTCCCGGGCGGGGAACTGTG
GGGCATTCTCACAGGAGTGCGGATACTTGCATGTGTAAGTTTGGCTAAAGTTGATAGTAAAG
TCAGGACCAAGCCTTTGTGCTTGCGGGGCTTTCTAGGGCCCATCTTAACATCTTCAGTGTTA
TGCTTTGCTTAAGCTACGTTAGCAACTGCATTGTTGCAATAATGTAAATTAGCAAAAAGAAAG
CATAATTTTCGCCCACTATAACTACTAGGGGTTGTCCTGTTTCCGGGGGGTTTTCAGGAGTC
TTAGTGATCTCTCGAGTTATAGGGGGGTAGGGGGGTTTTACGCGCGAGAAAACCGGGGTAC
TAATAGATATCATTCGAGTGAACAAGCACTACTTATGCTCTTGATATTAACATATGCAATTCT
TCTGTAAAGTCTTTCCAACACTCATTCATATTACGTGTTTTCATTCGCTAAACGCTCACGCTT
ATTAGTTAATACCGTGTGCGCTCTGTTATGTCAGGTGAAAGGAAAAAGAAAAAAGGAACCAG
ATGCGCCTGTGGAGTGAACGCCCGGCATGCTGAGTCATCTCGCTTATGCTCTCCACCATTAA
TCTATGTAAGTGTCGATGAAAGTGCAGTGAGTCAAGCGGGCTTATGGCCCTGACAGAGGAAC
CAAATGCCAGGAATAGTGCACTCTGTGAAACCCCCACGAATACTTGTCCCTCACCCTCAATAA
CCGTTAGCCTTAAGAAATCAACTGTTGGTCGGTTCTTACTACATCGCATACTGCGATTTGACG
GGTTGTGGAAAAACGTATATCTTAACCGGTGGTTAAAATGTGTTCGGTCTTAAATTTCGCCT
ATCCTTGAATTCGTATAGATGTTACCTACATTACTAACTGCTTTATATATACCTTAGGTATAT
GATGATATATGAGGGGGTTACTACTATATATGTTGATTATACATATATATGTCCTAGATAACC
ATTGAAATGGTTAAAATAAATGTGTGGGGATTATACATATATGTACTAGGTACATACATGATA

TAAGTACATACGCGCAAAGAATAGTTTAGTTTAGAATTCTAGCTTTGGGAGCTAGGGGTGGG
A (1190bp)

Nucleotide sequence of *Pachycara matallanasi* sp. nov. diverged from *Pachycara priedei* from Southern Pacific Ocean: COI (614pb) in 2 % and CR (1276bp) in 2.72 %.

New species differs from the most similar genera of the genus *Pachycara* (*Lycodes* and *Lycenchelys*). Genetic divergence (COI, 614pb) with genus *Lycenchelys* is 4.19 % (*L. wilkesi*), 4.96 % (*L. bachmanni*), 5.46 % (*L. antarctica*) and 5.46 % (*L. platyrhina*). Genetic divergence with genus *Lycodes* is 8% (*L. frigidus)* and 7 % (*L. vahli*).

The most divergence are found in some endemic Magellan species: *Plesienchelys stehmanni* (7.01%); *Patagolycus melastomus* (7.30%); *Iluocoetes fimbriatus* (7.61%); *Austrolycus depressiceps* (9.17%) and with *Lycodapus pachysoma* from Eastern Pacific and Southern Ocean (7.21%) and *Lycodonus mirabilis* from Western North Atlantic (8.63%).

Figure 34. Left hyoid bar and branchiostegal rays of *Pachycara matallanasi* sp.nov.

Table 10. Counts and Measurements of *Pachycara matallanasi* sp.nov. (see annex 1)

P. matallanasi	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Range
	ZMUC 766564	ZMUC 766563	ZMUC 766565	ZMUC 766566	ZMUC 766567	ZMUC 766569	
Standard length SL (mm)	140	148	141	124	138	102	102-148
Sex	-	Female	Female	Male	Female	-	
Meristic characters							
Dorsal-fin rays	100	97	101	98	-	-	97-101
Anal-fin rays	83	77	81	79	81	79	77-83
Caudal-fin rays	3+6+3	2+6+4	2+5+5	2+5+5	2+6+4	2+5+5	12
Pectoral-fin rays	17	-	18	19	18	18	17-19
Precaudal vertebrae	29	30	31	30	31	29	29-31
Caudal vertebrae	78	73	77	76	76	77	73-78
Total vertebrae	107	103	108	106	107	106	106-108
1st dorsal-fin pterygiophore with vertebrae	5	5	5	6	5	5	5-6
Gill rakers	2+15	2+11	2+12	2+11	-	-	13-17
Pseudobranchial filaments	-	6	-	5	-	-	5-6
Morphometric characters (% SL)							
Head length (HL)	16.6	17.1	17.8	15.4	16.7	16.4	15.4-17.8
Head width	9.3	9.7	9.4	8.4	7.1	7.7	7.1-9.7
Head height	9.8	10.4	9.1	9.5	9.5	7.2	7.2-10.4
Snout length	5.0	5.0	5.0	4.3	4.2	4.0	4.0-5
Nostril tube length	0.5	0.6	0.5	0.5	0.5	-	0.5-0.6
Interorbital width (bony margin)	1.5	1.5	1.5	1.2	1.0	1.6	1.0-1.6
Upper jaw length	6.21	5.7	6.8	5.2	6.1	5.7	5.2-6.8
Lower jaw length	8.57	8.9	9.2	9.9	8.3	8.8	8.3-9.9
Predorsal length	18.9	19.8	20.8	15.5	14.7	19.1	14.7-20.8

Table 10. continued

P. matallanasi	Holotype ZMUC 766564	Paratype ZMUC 766563	Paratype ZMUC 766565	Paratype ZMUC 766566	Paratype ZMUC 766567	Paratype ZMUC 766569	Range
Preanal length	39.2	42.5	40.3	31.4	31.1	39.8	31.1-42.5
Pectoral-fin length	9.4	9.8	9.9	-	-	-	9.4-9.9
Pectoral-fin base height	4.8	3.6	4.2	4.2	3.1	4.6	3.1-4.8
Gill slit length	6.8	6.5	7.5	6.2	-	-	6.2-7.5
Isthmus width	4.8	4.9	4.7	4.3	4.2	-	4.2-4.9
Morphometric characters (% HL)							
Head width	78.7	84.7	74.7	68.3	58.9	48.1	48.1-84.7
Head height	83.0	90.0	72.4	76.6	79.2	45.1	45.1-90.0
Upper jaw length	52.4	49.7	53.9	42.5	51.1	35.9	35.9-52.4
Pectoral-fin length	79.4	84.8	79.0	-	-	-	79.0-84.8
Snout length	42.7	43.2	39.8	34.4	34.7	24.3	24.3-43.2
Interorbital (bony margin)	14.15	13.4	12.3	10.3	9.0	10.7	9.0-14.15

HL head length; *SL* standard length

4.5 DISCUSSION

Pachycara is a difficult genus to identify because it doesn't provide autapomorphic character states and is defined by a combination of characters (Anderson, 1989; Møller and Anderson, 2000). Furthermore, except for the absence of pelvic fins, *Pachycara* is very similar to other genera of Lycodinae (*Lycodes* and *Lycenchelys*) (Markle and Sedberry, 1978) and very few characters allow separation of the three genera (Møller and Anderson, 2000) (table 11). The new species is included in *Pachycara* on the basis of the combination of characters defined by Anderson (Anderson, 1988, 1989, 1994) and following the few characters that allow separation of *Pachycara, Lycodes* and *Lycenchelys* (Møller and Anderson, 2000).

COI and CR sequences also supports that this new species belongs to the genus *Pachycara* because sequences of *Pachycara matallanasi* sp. nov. diverges from sequences belonging to genus *Lycodes* and genus *Lycenchelys* and less divergence is found with *Pachycara priedei* from Southern Indian Ocean.

Table 11. Informative characters for separation of *Pachycara*, *Lycodes* and *Lycenchelys* (Møller and Anderson, 2000).

Character	*Pachycara*	*Lycodes*	*Lycenchelys*
Submental crest	Absent	Present	Absent
Suborbital head pores	5-7	6-11	6-10
Pectoral fin rays	14-19	16-24	13-21
Parasphenoid wing	Reduced	Unreduced	Reduced
Palatopterygoid bone series	Well developed	Well developed	Week

With this new species, there are 26 species within the genus *Pachycara* (table 9). *Pachycara matallanasi* sp. nov. is the first record of the genus in the Solomon Sea and the third species from Western Pacific Ocean, the other two species are *P. garricki* Anderson, 1990 and *P. moelleri* Shinohara, 2012 (fig.29). Furthermore *P. matallanasi* sp.nov. has a particular feature: the lack of scales. Until now, this character has been described only in two species of *Pachycara*, (*P. shcherbachevi* Anderson, 1989 (Møller,

2003) from Northern Pacific Ocean and *P. alepidotum* Anderson and Micarone, 2006 from South Western Atlantic).

The new species differs from *P. shcherbachevi* and *P. alepidotum* in several characters (*Pachycara matallanasi* sp.nov., first): Pelvic fins (absent vs. present); lateral line (mediolateral branch completed vs. four rows in P. *shcherbachevi*); suborbital pores (seven vs. six); vertebrae (103-108 vs. 120-122 in *P. shcherbachevi* and 92-94 in *P. alepidotum*). Some morphometric characters are also different, (*Pachycara matallanasi* sp.nov. first; values in percent SL): Head length (15.4-17.8 vs. 11.4-12.0 in *P. alepidotum*); head width (7.1-9.7 vs. 9.6-11.1 in *P. alepidotum*); preanal length (31.1-42.5 vs. 44.8-47.5 in *P. alepidotum*); upper jaw length (5.2-6.8 vs. 4.6-4.8 in *P. shcherbachevi*); lower jaw length (8.3-9.9 vs. 4.0-4.8 in *P. shcherbachevi*); gill slit length (6.2-7.5 vs. 5.4-6.1 in *P. alepidotum* and 4.6 in *P. shcherbachevi*); dorsal fin origin associated with vertebrae (5-6 vs. 4 in *P. alepidotum* and 7-8 in *P. shcherbachevi*). Osteologic characters are not included in *P. shcherbachevi* and *P. alepidotum* description.

Species without scales inhabit in separated areas and were caught in a bit different depth: *P. matallanasi* sp. nov. southwestern Pacific Ocean (4350-4450 m); *P. alepidotum* southwestern Atlantic Ocean (788-807 m) (Anderson and Micarone, 2006) and *P. shcherbachevi* Indian Ocean (2600-3190 m) Anderson, 1989; Møller, 2003).

Only *P. garricki* Anderson, 1990 have been reported from Western South Pacific (fig. 29). The two species differs in several features (*Pachycara matallanasi* sp.nov. first): squamation (absent vs. present); pelvic fins (absent vs. present); postorbital pores (2, positions 1 and 4 vs. 3 positions 1, 3 and 4).

One curious point is that few species of *Pachycara* have been described in the western Pacific Ocean (fig. 29). It is otherwise an area where many species of Zoarcidae have been described and the western north Pacific is probably the origin of Zoarcids with a wealth of species. This point was raised by Anderson (1989) who noted that the genus *Pachycara* is poorly represented in the Western Pacific, but perhaps the cause of this could be an inadequate sampling, like Møller (2003) commented, in the Indian Ocean. Although, in the last years expeditions are increased especially in the Japan Sea, since *P. garricki* (Anderson, 1990) was described no more species of *Pachycara* have been described in this area.

I208 0482 0084

CHAPTER 4

Molecular and morphological phylogenies of some genera of subfamily Lycodinae (Teleostei: Zoarcidae)

5 Molecular and Morphological Phylogenies of some genera of Subfamily Lycodinae (Teleostei: Zoarcidae)

5.1 ABSTRACT

Molecular and morphological phylogenetic analyses of some genera of the subfamily Lycodinae were carried out. The analysis combined sequences of the mitochondrial genes Cytochrome Oxidasa I (COI) and Control Region (CR). Resulting trees, with concatenation of two genes and including morphologic data, display the same topology. The genetic differences between genus *Lycodapus* and the other genera studied were very high and the last genus described *Patagolycus* Matallanas and Corbella, 2012 and *Iluocoetes* Jenyns, 1842 appear as two separated groups. A complete review of some genera of the subfamily Lycodinae is required.

5.2 INTRODUCTION

The family Zoarcidae is one of the best represented in number of genera and species in the marine fish faunas of the southern South America and Antarctic waters (Gosztonyi, 1977; Anderson, 1994; Anderson and Fedorov, 2004; Shinohara *et al*., 2004; Shinohara and Sakurai, 2006; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2009c, 2010, 2011a, 2011b; Matallanas and Corbella, 2012; Matallanas *et al*., 2012).

The subfamily Lycodinae is represented by 26 genera in Antarctic waters and in the Magellan Province, according to the last revisions and descriptions (Anderson and Fedorov, 2004; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2010; Matallanas and Corbella, 2012). Only two of these genera (*Lycenchelys* and *Oidiphorus*) are common in both areas. Five genera (*Lycodichthys*, *Gosztonyia*, *Bellingshausenia*, *Bentartia* and *Santelmoa*) are endemic to the Antarctic region (Anderson, 1990, 1991, 2006; Anderson and Gosztonyi, 1991; Matallanas, 2009a, 2009b, 2010). The Magellan Province contains sixteen genera (Norman, 1937; Gosztonyi, 1977, 1981; Anderson, 1988a, b; Matallanas and Corbella, 2012), with fourteen endemic genera (Anderson and Gosztonyi, 1991; Matallanas and Corbella, 2012).

A comprehensive revision of the family Zoarcidae was carried out by Anderson (1994) who established a morphological grounding and provided a phylogenetic hypothesis of the relationship between most of the endemic Magellan Province genera. Matallanas (2010) provided cladograms showing a hypothesis of the interrelationships among the Antarctic and Magallanic Lycodine genera, including four Antarctic genera recently described (Matallanas, 2009a, 2009b, 2010).

Studies with molecular genetics methods have begun recently in the family Zoarcidae (Møller and Gravlund, 2003; Radchenko *et al*., 2008a, 2008b, 2008c, 2009; Smith *et al*., 2012). For this reason, relationships among genera of subfamily Lycodinae are still poorly known. Radchenko *et al*., (2009) carried out a molecular and morphologic studies of some genera of subfamily Lycodinae (*Lycodes, Bothrocarina, Allolepis, Bothrocara, Lycogrammoides* and *Petroschmidtia*) for the elucidation of their relationships since the status of these taxa has been questioned in the past (Schmidt, 1938; Jordan and Hubbs, 1925; Masuda *et al*., 1984; Toyoshima, 1985; Amaoka *et al*., 1995; Fedorov and Parin, 1998; Sheiko and Fedorov, 2000; Nakabo, 2002; Fedorov *et*

al., 2003; Fedorov, 2004). Møller and Gravlund (2003), studied the relationships of the species of *Lycodes* employing two mitochondrial genes, cytochrome b and 12S, and discussing both, the evolution of morphologic characters and the biogeography of the genus. However, the systematic status of some genera and species of the subfamily Lycodinae as well as the relationships among them are not still resolved.

5.3 MATERIALS AND METHODS

Genetic studies were carried out using samples of the following species of the subfamily Lycodinae: *Lycodapus pachysoma* Peden and Anderson, 1978; *Pachycara priedei* Møller and King, 2007; *Pachycara matallanasi* Corbella and Møller (chapter 3); *Plesienchelys stehmanni* (Gosztonyi, 1977); *Lycenchelys wilkesi* Anderson, 1988a; *Piedrabuenia ringueleti* Gosztonyi, 1977; *Lycenchelys bachmanni* Gosztonyi, 1977; *Austrolycus depressiceps* Regan, 1913; *Iluocoetes fimbriatus* Jenyns, 1842; *Patagolycus melastomus* Matallanas and Corbella, 2012; *Ophthalmolycus amberensis* (Tomo, Marschoff and Torno, 1977); *Santelmoa fusca* Matallanas, Corbella and Møller, 2012; *Pachycara brachycephalum* (Pappenheim, 1912), *Oidiphorus brevis* (Norman, 1937)(fig.12).

Specimens were collected in the Bellingshausen Sea during the Spanish Antarctic expedition, Bentart-2003 and 2006 on board the RV “Hespérides”, as well as in the SW Atlantic Ocean, Falkland (Malvinas) Island, during the Atlantis-2009 and 2010 campaign of the “Centro Oceanográfico de Vigo (Instituto Español de Oceanografía)” and during the Danish Galathea-3 expedition around the world in 2006-2007. Muscle samples were fixed in absolute ethanol for molecular analysis except in some samples that it were fixed during few days in formalin and then seven years in ethanol at room temperature.

5.3.1 Morphological data

Most of the specimens were easily identified but for the identification of some of them an anatomical analysis was required. Cranium, palatal series, hyoid arch, branchiostegal rays and pectoral girdle had to be studied. Counts, measurements and

general terminology follow Gosztonyi (1977, 1988) and Anderson (1982, 1994). Pore terminology follows Gosztonyi (1977) and Anderson (1982) (see annex 1 and 2). Measurements were made with ocular micrometer or dial calipers to the nearest 0.1 mm.

Morphological data are based on 78 transformation series (TS). The definitions of the character states in this paper follow those of Anderson (1994) with some additions and modifications (Matallanas, 2010). TS numbers used here are those assigned to each character by Anderson (1994), with the following modifications and additions: Frontal fusion (TS23) could be considered as multi-state (0, 1, 2) (Matallanas, 2010); TS77, basioccipital-exoccipital fusion (Matallanas, 2010) and TS78, intercalar development are added (Matallanas and Corbella, 2012) (table 13).

The TS series used are as follows. TS1, adult body form: body robust (0), body slender (1); TS2, tail length: relatively short (0), elongate (1); TS3, squamation: present (0), absent (1); TS4, condition of flesh: firm (0), gelatinous (1); TS5, lateral line: present (0), absent (1); TS6, lower jaw: not deep (0), deep (1); TS7, lip development: present (0), absent (1); TS8, upper lip attachment: free (0), adnate (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); TS13, oral valve enlargement: free edge extends to or before vomer (0), free edge greatly overlaps vomer (1); TS14, chin pad: absent (0), present (1); TS15, submental crests: 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); TS19, eye lens: normal (0), with opaque matter (1); TS20, parasphenoid wing height: ascending rami of parasphenoid wing reaches above the mid-height of the trigeminofacialis foramen (TGF) (0), parasphenoid wing broad, but without dorsal ramus projecting above ventral base of TGF (1); TS21, frontal corner: squared off (0), tapering (1); TS22, frontal ramus: long (0), shortened (1); TS23, frontal fusion: frontal bones 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 mid-line (0), in

contact (1); TS28, supraoccipital blade: present (0), absent (1); TS29, supraoccipital–exoccipital articulation: narrowly contacting or excluded by epioccipitals (0), broadly contacting (1); TS30, anterior section of pterotic: narrower than posterior section (0), wider than posterior section (1); TS31, head pores: present (0), absent (1); TS32, interorbital pores: present (0), absent (1); TS33, suborbital bone configuration: circular pattern (0), L-shaped pattern (1); TS34, dorsalmost preopercular foramina: foramen 7 at mid-height of preopercle, foramen 8 below dorsal edge (0), foramen 7 above mid-height of preopercle, foramen 8 at dorsal edge (1); TS35, preopercular and mandibular canals: continuous (0), separated (1); TS36, number of lateral extrascapulars: 2 (0), 0-1 (1); TS37, supratemporal commissure and occipital pores: present (0), absent (1); TS38, postorbital pores, present (0), absent (1); TS39, posterior nasal pores: present (0), absent (1); TS40, posterior nasal pore development: single (0), double (1); TS41, dentary foramina: foramina for preoperculomandibular pores 1-4 present (0), anterior foramina absent (1); TS42, pore from ventralmost preopercular foramen: absent (0), present (1); TS43, male caniniform dentition: absent (0), present (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 ventral edge of 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); TS53, lower pharyngeal teeth: present (0), absent (1); TS54, upper pharyngeals: 3 (0), 2 (1); TS55, shape of first epibranchial: rod-like (0), fan-shaped (1); TS56, postorbital canal passage: through lateral extrascapulars, posttemporal and supracleithrum (0), through lateral extrascapulars only (1); TS57, posttemporal ventral ramus: well developed (0), weak or absent (1); TS58, cleithrum ventral ramus: absent (0), present (1); TS59, scapular foramen: enclosed by bone (0), open (1); TS60, scapular strut: present (0), absent (1); TS61, postcleithrum: present (0), absent (1); TS62, number of pectoral actinosts (=radials): 4 (0), 2-3 (1), absent (2); 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); TS66, pelvic bone: present (0), absent (1); TS67, number of vertebrae: 58–71 (0); 72–105 (1), 109–134 (2), 134–150 (3); TS68, retrograde dorsal fin origin: first pterygiophore associated with vertebrae 1-2 (0), associate with vertebrae 3-17 (1); TS69, advanced dorsal fin origin: first pterygiophore associated with vertebrae 1 or greater (0), first pterygiophore anterior to first vertebrae (1); TS70, posterior dorsal-fin pungent spines: absent (0), present (1); TS71, middle-dorsal-fin elements: absent (0), present (1); TS72, free dorsal-fin pterygiophores: 0-2 (0), 3-14 (1); TS73, unpaired fin scutes: absent (0), present (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); TS78, intercalar development: reaching prootic and excluding exoccipital–pterotic articulation (0); not reaching prootic and more or less reduced (1).

Table 12. Genera and species used in this study

Genera		Code	Location	Expedition
Austrolycus	*depressiceps*	ZMUC 7877	Magellan Province	Galathea-3
	depressiceps	ZMUC 8339	Magellan Province	Galathea-3
Iluocoetes	*fimbriatus*	UAB.ZP24a	Magellan Province	Atlantis-2009-2010
	fimbriatus	UAB.ZP26a	Magellan Province	Atlantis-2009-2010
	fimbriatus	UAB.ZP23	Magellan Province	Atlantis-2009-2010
	fimbriatus	UAB.ZP44	Magellan Province	Atlantis-2009-2010
Lycenchelys	*wilkesi*	ZMUC 7827	Antarctica	Galathea-3
	wilkesi	ZMUC 7852	Antarctica	Galathea-3
	bachmanni	UAB.ZP11	Magellan Province	Atlantis-2009-2010
Lycodapus	*pachysoma*	ZMUC 7760	Antarctica	Galathea-3
	pachysoma	ZMUC 7840	Antarctica	Galathea-3
	pachysoma	UAB.ZLP38A	Antarctica	Bentart-2003-2006
Oidiphorus	*brevis*	UAB.ZP40	Magellan Province	Atlantis-2009-2010
Ophthalmolycus	*amberensis*	ZMUC 7681	Antarctica	Galathea-3
Pachycara	*brachycephalum*	ZMUC 7738	Antarctica	Galathea-3
	brachycephalum	ZMUC 7740	Antarctica	Galathea-3
	brachycephalum	ZMUC 7683	Antarctica	Galathea-3
	brachycephalum	ZMUC 7684	Antarctica	Galathea-3
	matallanasi	ZMUC 7359	Solomon Sea	Galathea-3
	matallanasi	ZMUC 7366	Solomon Sea	Galathea-3
	matallanasi	ZMUC 7365	Solomon Sea	Galathea-3
	matallanasi	ZMUC 7362	Solomon Sea	Galathea-3
	matallanasi	ZMUC 7361	Solomon Sea	Galathea-3
	matallanasi	ZMUC 113	Solomon Sea	Galathea-3
	matallanasi	ZMUC 7360	Solomon Sea	Galathea-3
	priedei	ZMUC 73	Southern Indian Ocean	Galathea-3
Patagolycus	*melastomus*	UAB.ZM23	Magellan Province	Atlantis-2009-2010
	melastomus	UAB.ZM18	Magellan Province	Atlantis-2009-2010
	melastomus	UAB.ZM2	Magellan Province	Atlantis-2009-2010
	melastomus	UAB.ZM1	Magellan Province	Atlantis-2009-2010
Piedrabuenia	*ringueleti*	UAB.ZP2	Magellan Province	Atlantis-2009-2010
Plesienchelys	*stehmanni*	UAB.ZP39	Magellan Province	Atlantis-2009-2010
Santelmoa	*fusca*	ZMUC 7658	Antarctica	Galathea-3
	fusca	ZMUC 7659	Antarctica	Galathea-3
	fusca	ZMUC 7826	Antarctica	Galathea-3
	fusca	ZMUC 7857	Antarctica	Galathea-3
	fusca	ZMUC 7858	Antarctica	Galathea-3
	fusca	ZMUC 8301	Antarctica	Galathea-3
	fusca	ZMUC 7655	Antarctica	Galathea-3

Table 13. Character matrix for estimation the phylogenetic relationships between species studied.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Austrolycus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Lycenchelys	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Lycodapus	0	0	1	1	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Lycodes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0
Ophthalmolycus	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0
Pachycara	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Piedrabuenia	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Plesienchelys	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	1	0	0	0
Iluocoetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	1	1	0	0	-	1	0	0	0
Patagolycus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0	-	1	0	0	1
Santelmoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0
Gymnelus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Austrolycus	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	-	1	0	0	0	0	1	1	1	0	0
Lycenchelys	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	0	1
Lycodapus	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	2	1	-	0	1	1	0	0	0	0	0	1	1	1	0	1
Lycodes	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Ophthalmolycus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Pachycara	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	0	1
Piedrabuenia	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	1	1	1	0	1
Plesienchelys	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1*
Iluocoetes	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Patagolycus	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1
Santelmoa	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	1
Gymnelus	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	-	0	1	0	0	0	0	0	0	1	1	1	0	1

*Inadvertently not reported in Anderson, 1994 (Anderson,pers.comm.)

5.3.2 Molecular data

Total genomic DNA was extracted from muscle tissue using both, the QIAmp Tissue Kit (Qiagen) following the supplier's protocol and the FENOSALT method (Pérez and Presa, 2011). This method is a combination of the salting-out method (Miller, 1988) and the standard phenol:chloroform method (Sambrook, 1998).

In some genera (*Patagolycus*, *Iluocoetes*, *Oidiphorus*, *Lycodapus*, *Santelmoa*, *Plesienchelys*, *Lycenchelys* and *Piedrabuenia*) a cytochrome b fragment was amplified using primers: GLU-5(L)'-TGA and CB2-5(H') (table 14). Amplifications were carried out in a Mastercycler thermocycler (Eppendorf) as follows: initial denaturation at 95°C for 2 min; 30 cycles of 94°C for 1 min, 52°C for 1 min, 72°C for 1 min; and 1 cycle at 94ºC for 30s, 52ºC for 30s and the final extension step at 72°C for 5 min.

Cytochrome Oxidase I (COI) and Control Region (CR) were amplified for all samples. The COI was amplified using primers FishF1 and FishR1 (Ward et *al*., 2005) as well as CO1 and CO2 (Radchenko *et al*., 2009) (table 14). Two different pairs of primers were used because DNA extraction was carried out in two different laboratories (Universidad de Vigo and Natural History Museum of Denmark). The PCR program for the COI consisted of one initial cycle of denaturation at 94ºC for 10 min, following by 35 cycles of 94ºC for 1min, 55ºC for 1min, 72ºC for 1min; and finally one cycle at 72ºC for 5min.

For the amplification of the CR the following primers were used: L15927-Thr_ (M59) and H885-12S_(M70) (Miya *et al*., 2001) (table 14). With the exception of *Piedrabuenia ringueleti*, *Lycenchelys bachmanni* and *Iluocoetes fimbriatus* since it was impossible to obtain Control Region sequences. For this reason, the following internal primers were designed: CR126 and CR372; CR368 and CR720; CR835 and CR1069. For CR, the following conditions were used: one initial cycle of denaturation at 94ºC for 2 min, following by 30 cycles of 96ºC for 15 sec, 55ºC for 15sec, 72ºC for 1 min and 30 seconds; and finally one cycle at 72ºC for 10 min. The PCR products were cleaned using QuiaAmp columns and silica membrane binding. Sequencing of amplified fragments of DNA was made on both directions with the same primer pair used for PCR amplification. Sequencing was performed using the ABI Prism DNA Sequencing Kit (Terminator Cycle sequencing Ready Reactions) in an ABI Prism 310.

5.3.3 Phylogenetic analyses

Sequences were edited using the computer program Bioedit v7.0.5.2 (Hall, 1999). The alignment was obtained using ClustaX (Thompson *et al*., 1997). Gaps were recoded as separate presence/absence character with the aid of the program SeqState version 1.4.1 (Müller, 2005). Genetic distances between genera were estimated with Kimura 2-parameter model (Kimura, 1980) using MEGA 5.0.3 (Tamura *et al*., 2007).

Phylogenetic relationships were estimated by Maximum Likelihood (ML) with RAxML 7.0.0 (Stamatakis, 2006). Nodal support was checked in 1000 cycles of bootstrap analysis and model of nucleotide substitution (GTR++Γ+I) were specified for each gene partition. Bayesian inference (BI) analyses were conducted with MrBayes v.3.2.1 (Ronquist and Huelsenbeck, 2003). One million generations were run using Markov Chain Monte Carlo (MCMC) in two independent runs.

The resulting trees were visualized and edit with FigTree v.1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/). A sequence of *Gymnelus viridis* was designed as outgroup taxa because of Gymnelinae is considered a sister group of the *Lycodinae*.

Table 14. Primers used in this study

	Primer	Sequence	Source
COI	GLU-5(L)	TGACTTGAAGAACCAC/TCGTTG	Palumbi,1996
	CB2-5(H')	AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA	Kocher *et al*., 1989
	FishF1	TCAACCAACCACAAAGACA TTGGCAC	Ward et *al*., 2005
	FishR1	TAGACTTCTGGGTGGCCAAAGAATCA	Ward et *al*., 2005
	CO1	CCAATCACAAAGACATTGG	Radchenko *et al*., 2009
	CO2	AGGAGGTGTTGGGGGAAGAA	Radchenko *et al*., 2009
CR	L15927-Thr_(M59)	AGAGCGTCGGTCTTGTAAKCCG	Miya *et al*., 2001
	H885-12S_(M70)	TAACCGCGGYGGCTGG CACGA	Miya *et al*., 2001
	CR126	AGGAGTGCGGATACTTGCAT	This study
	CR372	TCGAGAGATCACTAAGACTCCTGA	This study
	CR368	TTCAGGAGTCTTAGTGATCTCTCG	This study
	CR720	TGCACTTTCATCGACACTTACA	This study
	CR835	TCAACTGTTGGTCGGTTCTT	This study
	CR1069	TCAACATATATAGTAGTAACCCCCTCA	This study

5.4 RESULTS AND DISCUSSION

The alignment of the combined COI and CR gene fragments was 1920 bp long (627 and 1293 bp respectively) with 564 variables sites. The percentage of variable sites is higher in CR (33.2%) than in COI (26.8%), as expected for its supposedly rapid rate of evolution (Brown, 1985; Hoelzel *et al*., 1991; Lee *et al*., 1995).

Among the species studied, the degree of divergence in COI and CR varies from 1.12% to 12.63% excluding the outgroup (*Gymnelus viridis*). The divergence of 1.12% is between *Patagolycus melastomus and Iluocoetes fimbriatus* but this value was calculated based on a COI fragment of 627 bp and a CR fragment of 127 bp. The reason for this is because in *Iluocoetes fimbriatus* was not possible obtains a large fragment of CR and although internal primers were designed only a short sequence was obtained. The next lowest value is 1.90% observed between *Piedrabuenia ringueleti* and *Lycenchelys bachmanni*. The greatest divergence was observed between *Austrolycus depressiceps* and *Lycodapus pachysoma*. Table 16 shows the genetic distances among all the genera studied calculated with Kimura 2-parameter model (Kimura, 1980).

Cytochrome b was amplified from some genera from Magellan Province and species of *Santelmoa* from the Southern Ocean. Genetic distance is shown in Table 15. The lowest value is 1.0 % between *Patagolycus melastomus* and *Iluocoetes fimbriatus* and the great divergence is 15.55% between *Iluocoetes fimbriatus* and *Lycodapus pachysoma*.

Table 15. Genetic distances between the species studied calculated based on a 376 bp Cytb fragment (in %)

	1	2	3	4	5	6	7	8
1. *Iluocoetes fimbriatus*								
2. *Lycenchelys bachmanni*	6.73							
3. *Lycodapus pachysoma*	15.55	12.98						
4. *Oidiphorus brevis*	14.18	9.97	11.40					
5. *Patagolycus melastomus*	1.0	6.37	15.33	13.18				
6. *Piedrabuenia ringueleti*	10.39	3.61	12.23	8.42	9.74			
7. *Plesienchelys stehmanni*	10.53	6.65	11.91	9.46	10.33	5.11		
8. *Santelmoa elvirae*	12.36	7.47	9.46	9.0	11.17	5.86	5.52	
9. *Santelmoa fusca*	11.86	6.95	10.42	9.46	11.17	5.11	5.52	2.43

Table 16. Genetic distances among species studied combining COI and CR (in %), COI 627 bp; CR 1234 bp.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *Austrolycus depressiceps*													
2. *Iluocoetes fimbriatus*	8.44												
3. *Lycenchelys bachmanni*	8.91	8.11											
4. *Lycenchelys wilkesi*	10.29	9.19	6.23										
5. *Lycodapus pachysoma*	12.63	11.11	9.30	7.94									
6. *Ophthalmolycus amberensis*	10.28	8.31	5.85	4.25	8.03								
7. *Pachycara matallanasi*	9.93	8.06	5.92	4.67	8.66	5.03							
8. *Pachycara priedei*	10.14	8.21	6.45	4.28	8.66	4.27	2.76						
9. *Patagolycus melastomus*	8.29	1.12	8.02	9.62	10.90	8.57	8.03	8.02					
10. *Piedrabuenia ringueleti*	9.55	8.73	1.90	6.80	10.00	6.79	6.49	7.03	8.63				
11. *Plesienchelys stehmanni*	11.44	10.46	6.06	5.91	10.40	6.10	6.93	7.28	10.97	6.82			
12. *Santelmoa fusca*	10.09	9.00	6.88	4.08	9.03	4.61	4.10	4.10	9.21	6.26	6.88		
13. *Pachycara brachycephalum*	10.09	8.73	6.02	3.86	8.64	3.53	5.00	3.22	9.21	6.98	5.87	3.19	
14. *Gymnelus viridis*	17.06	16.87	13.62	13.49	12.79	12.95	13.34	12.17	16.89	13.86	15.78	12.69	12.75

Some genera studied in this study have never been sequenced but genetic differences of genes COI, cytochrome b and 16S rRNA have been studied in some genera of subfamily Lycodinae (*Lycodes*, *Petroschmidtia* (included by Anderson (1994) in the synonymy of the genus *Lycodes*), *Lycogrammoides*, *Bothrocara* and *Allolepis* (included by Anderson (1994) in the synonymy of the genus *Bothrocara*) (Radchenko *et al*., 2009). The closest sequences were found between *Bothrocara* and *Allolepis* (4.20%) (Radchenko *et al*., 2009) the divergence is higher than that found between *Piedrabuenia ringueleti* and *Lycenchelys bachmanni* (1.90%). The highest level of genetic differences was found between *Petroschmidtia* and *Bothrocarina* (8.81%) (Radchenko *et al*., 2009) a low value compared with the divergence found between *Austrolycus depressiceps* and *Lycodapus pachysoma* (12.63%). The mean genetic distances between subfamily *Lycodinae* and *Gymnelinae* (*Gymnelus viridis*) is 14.17% (12.17-17.06, *Pachycara priedei* and *Austrolycus depressiceps* respectively). A similar value (13.87%) was obtained based on cytochrome b sequences between genus Lycodinae (*Lycodes* and *Lycogrammoides*) and Gymnelinae (*Hadropareia* and *Magadania*) (Radchenko *et al*., 2008b).

Molecular phylogenetic analyses were carried out by different methods (Maximum Likelihood and Bayesian inference) and resulted in well resolved trees (fig. 35 and 36). Molecular phylogeny was analyzed concatenating Cytocrome Oxidase subunit I (COI) and Control Region (CR). The Maximum Likelihood and Bayesian trees inferred from the COI and CR gene data are shown in figures 35 and 36.

Bayesian inference of all datasets (COI, CR and morphology characters) is shown in figure 37. All resulting trees display the same topology but with different statistical support (figs. 35, 36 and 37). The topology of the strict consensus tree of the 9 most parsimony trees of morphologic data is resolved without support nodes above 50%.

The topology of the tree shows that *Lycodapus pachysoma* is separated from the other genera studied with a high branch support (figure 35, 36 and 37). Within the big group there are 4 clades. One clade groups species of *Pachycara* (*P. priedei and P. matallanasi*). The second group brings together the endemic species from the Magellan Province (*Piedrabuenia ringueleti*, *Lycenchelys bachmanni*, *Austrolycus depressiceps*, *Iluocoetes fimbriatus* and *Patagolycus melastomus*). Other clade consist of species from Antarctic waters (*Santelmoa fusca*, *Pachycara brachycephalum* and

Ophthalmolycus amberensis) and in the last group, there are *Plesienchelys stehmani*, endemic from Magellan Province and *Lycenchelys wilkesi* from the Southern Ocean.

Patagolycus, the last genus described by Matallanas and Corbella, 2012 and *Iluocoetes* Jenyns 1842, redescribed in the chapter 1, appear as two separated groups with high statistical support in Bayesian inference. Although in the Maximum Likelihood tree it is not so clear for *Patagolycus melanostomus* (fig 36). Genetic distances between these two genera are 1.35 % in COI and 1% in Cytochrome b. In order to obtain sequences for the CR in *Iluocoetes* internal primers were designed, but only 127 nucleotides were obtained because samples were not in optimal conditions. The divergence between these genera in Cytb and COI is low but the morphological differences between them are evident (see chapter 1 and figure 37). More molecular studies would be desirable.

Pachycara brachycephalum is clearly separated from the other species of *Pachycara* (*P. priedei and P. matallanasi*) (fig. 35, 36 and 37) and is closely related with *Ophthalmolycus amberensis* with a well supported node. *Pachycara* is a widely distributed genus with a large number of species. The systematic status of this genus has been revised by many authors (Anderson, 1989, 1990, 1991, 1994; Anderson and Peden, 1988; Anderson and Bluhm, 1997; Møller and Anderson, 2000) but it is still unclear. As the present results suggest it is most likely that *Pachycara* may be polyphyletic and it is also expected that *Pachycara brachycephalum* would be a mix of several species. The last new genera described of the subfamily Lycodinae (*Gosztonyia*, *Bellingshausenia*, *Santelmoa* and *Bentartia*) (Matallanas, 2009a, 2009b, 2010), expose that a detailed osteologic study is needed for descriptions of new genera and new species because most often measurements are not a specific character. The same case is shown in species of *Lycenchelys* (*L. wilkesi and L. bachmani*) which appear in two separated clusters with a 6.23% of divergence between them. A complete review of these genera is required with anatomic and molecular data.

Phylogenetic trees inferred from COI, CR and morphologic characters are shown in Figure 37. In general, there are few common synapomorphic characters to support the clades. *Lycodapus pachysoma* is separated from all other genera of subfamily Lycodinae studied including species from Southern Ocean. *Lycodapus pachysoma* presents 12 synapomorphic characters (gelatinous flesh, lateral line

absent, oral valve absent; frontal ramus shortened; preopercular and mandibular canals separated; anterior foramina absent; pore from ventralmost preopercular foramen present; male caniniform dentition present; branchiostegal membrane free of isthmus; scapula strut absent; actinost 2-3; pectoral fin minute and nub-like) while all other genera share the following characters: squamation present; interorbital pore absent; pectoral fin well developed and number of pelvic fin rays 2-3 (fig. 37).

The degree of divergence in COI and CR between *Lycodapus pachysoma* and all other species varies from 7.94% (*Lycenchelys wilkesi*) to 12.63% (*Austrolycus depressiceps*), and almost the same divergence (12.79%) with the outgroup *Gymnelus viridis* (Subfamily *Gymnelinae*). It is an important divergence compared with the other genera of Lycodinae. The systematic status of this genus is unclear; *Lycodapus* was placed as a monotypic subfamily Lycodapinae (Schmidt, 1950). Anderson (1994) defined it as “a bizarre genus” but it was placed within subfamily Lycodinae and within “Bothrocara group” joining with genus *Bothrocara, Bothrocarina and Lycogrammoides* on the basis of one synapomorphy character, the loss of the oral valve (Anderson, 1994). Detaï *et al.,* (2011) performing a widely molecular phylogeny of actinopterygian diversity, within Zoarcidae clade *Lycodapus* is separated from all other genera (*Ophtalmolycus*, *Lycodichthys*, *Lycenchelys*, *Pachycara* and *Oidiphorus*). This study shows a clear divergence between *Lycodapus* and other genera studied (*Pachycara, Plesienchelys, Lycenchelys, Piedrabuenia, Austrolycus, Iluocoetes, Patagolycus, Ophthalmolycus* and *Santelmoa*). However, Radchenko *et al.,* (2009) have remarked that, it is necessary to perform a complete molecular study including all genera of Lycodinae to make a decision about its systematic.

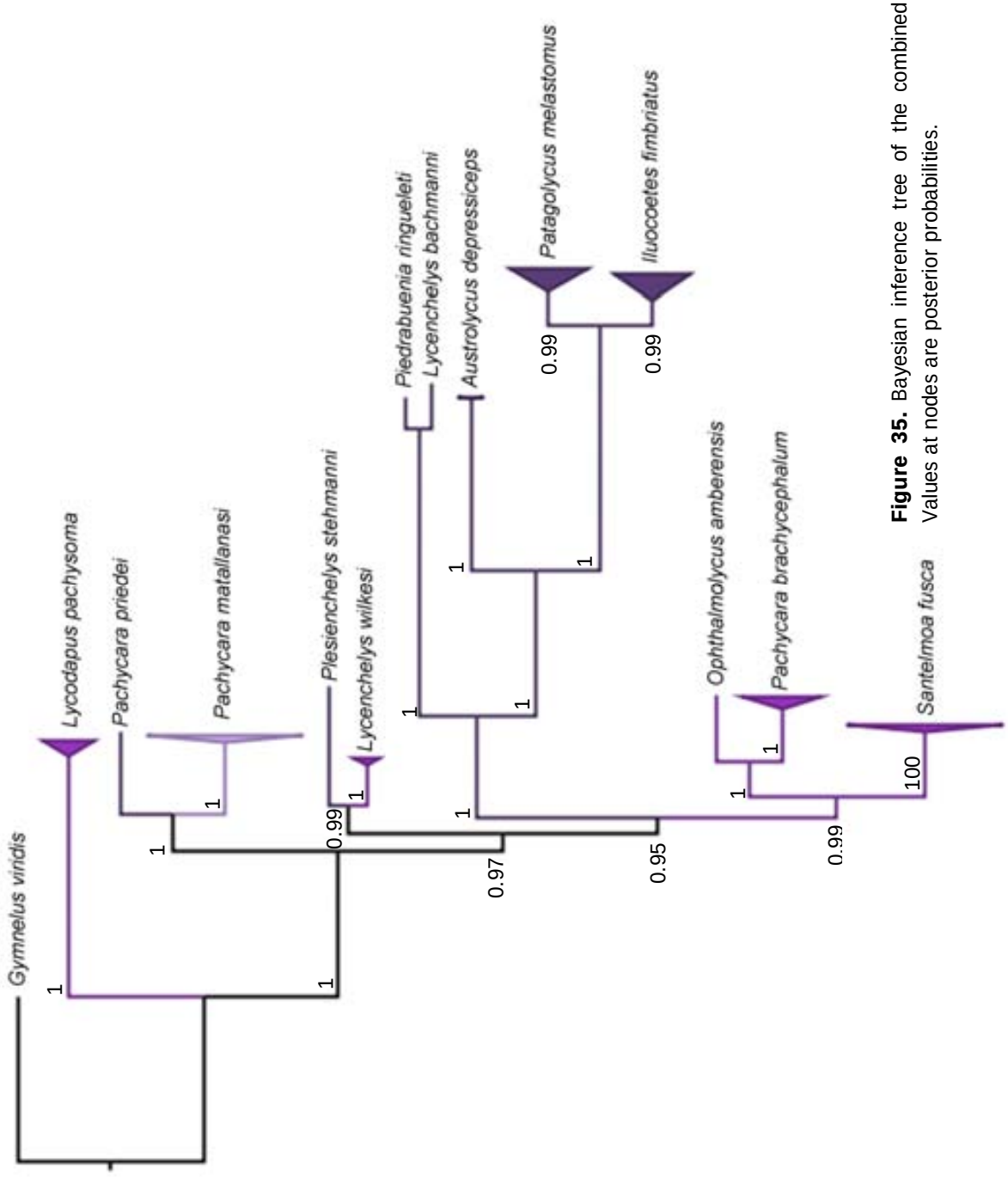


Figure 35. Bayesian inference tree of the combined COI and CR dataset. Values at nodes are posterior probabilities.

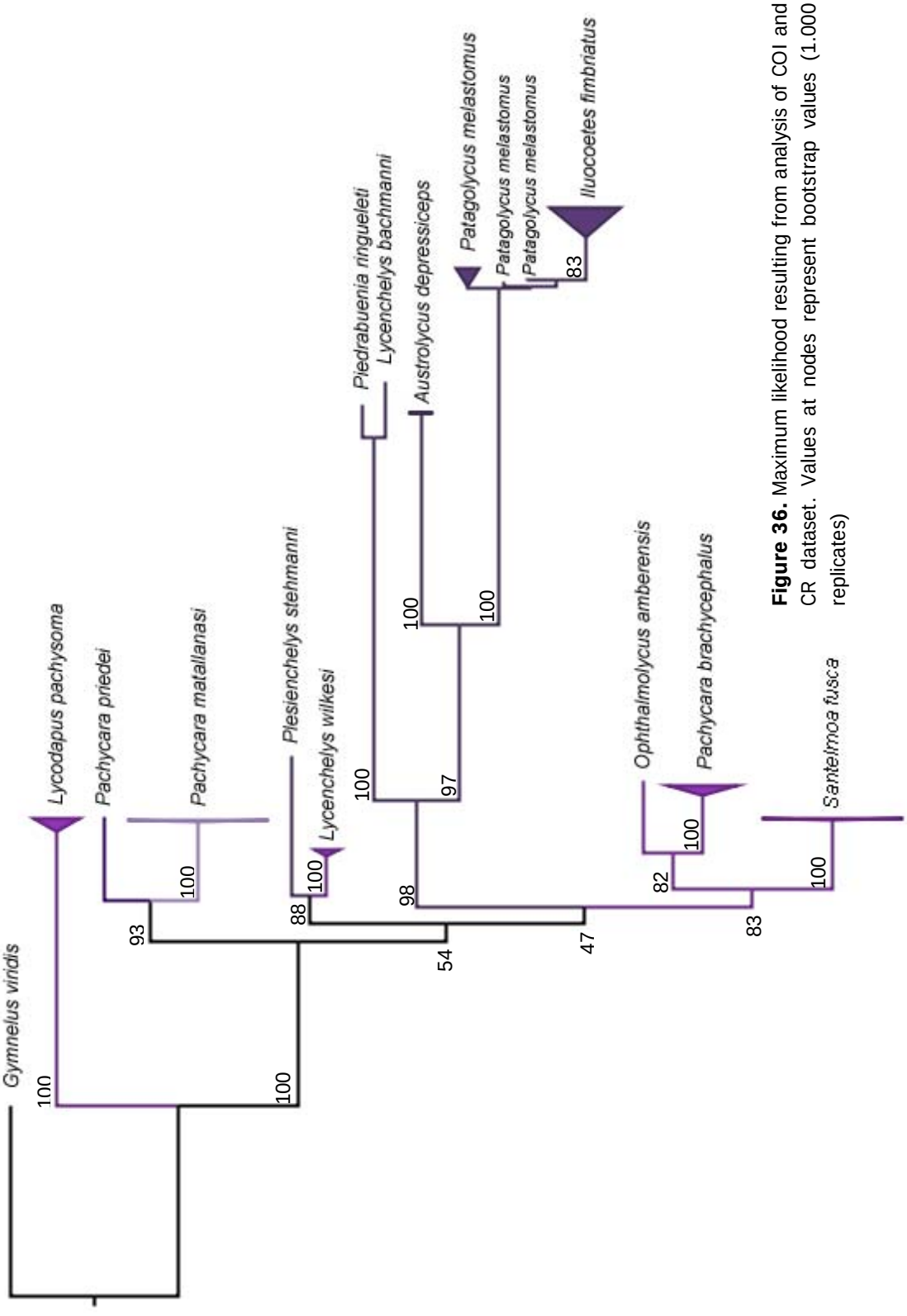


Figure 36. Maximum likelihood resulting from analysis of COI and CR dataset. Values at nodes represent bootstrap values (1.000 replicates)

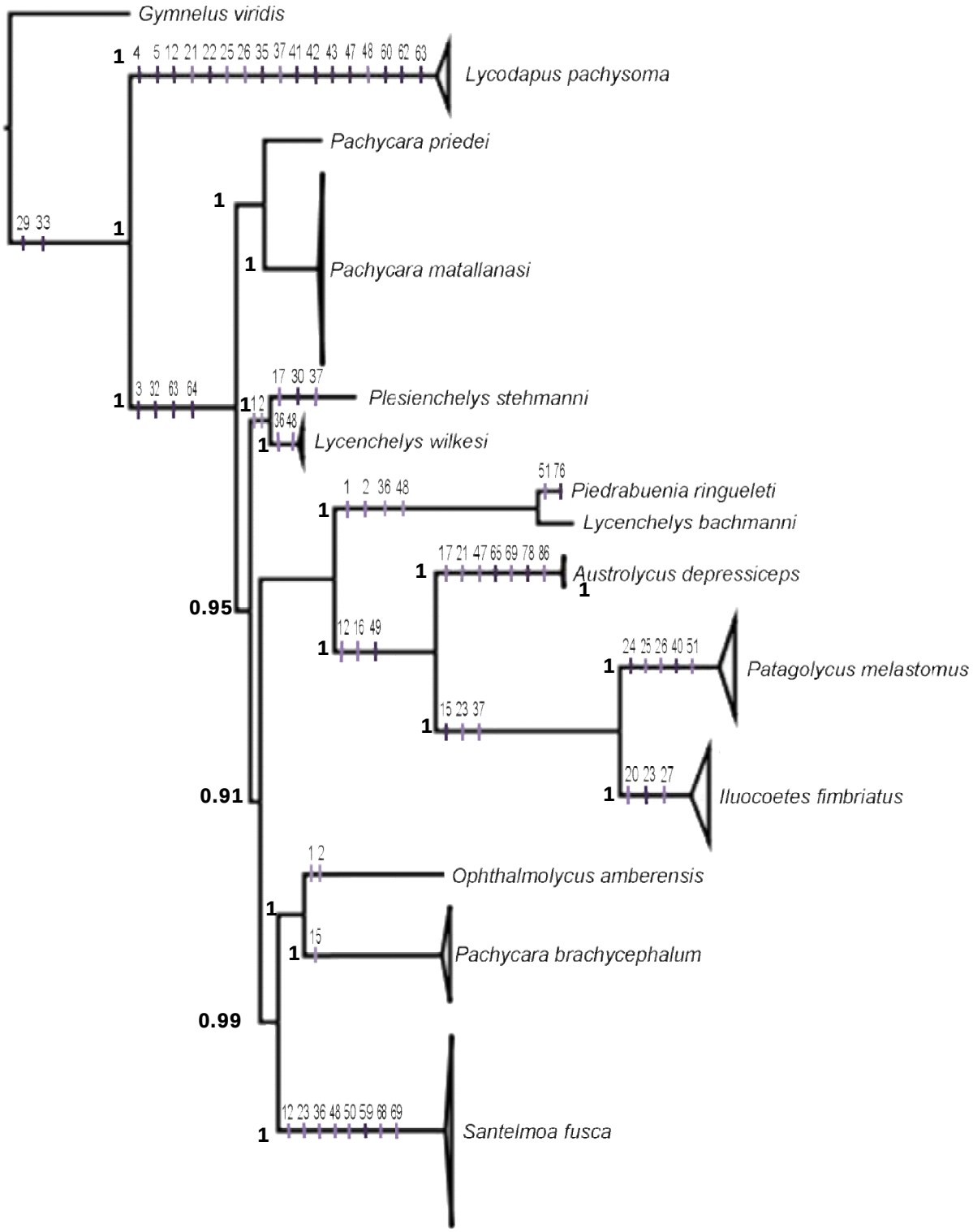


Figure 37. Bayesian inference tree of combined COI, CR and morphologic data. Bold values represent posterior probabilities. Lilac boxes are homoplastic apomorphies and black boxes: synapomorphies.

For the first time, several genes from new species have been sequenced in this study including COI sequence of *Santelmoa elvirae* which has not been added in the analysis because CR sequences were problematic. Probably, the DNA was degraded because the sample was not immediately fixed after the fish died.

DNA barcode COI of *Santelmoa elvirae* (UAB.1MB32) (627bp) (genetic distances are shown in table 17):

GTACAGCTCTAAGCCTCCTCATTCGAGCGGAGCTAAGCCAACCCGGCGCCCTCCTGGGAGAC
GACCAAATTTATAATGTCCTTGTTACAGCGCATGCGTTCGTAATAATTTTCTTTATAGTAATA
CCAATTATGATCGGGGGTTTTGGAAACTGGCTTGTGCCCTTGATAATCGGGGCCCCGGACAT
AGCATTTCCCCGAATAAACAACATGAGCTTTTGACTCCTTCCCCCATCTTTTCTCCTCCTCCTT
GCTTCTTCGGGGGTGGAGGCGGGTGCTGGAACAGGATGAACAGTCTACCCCCCTCTTTCTG
GAAACTTAGCCCACGCAGGGGCCTCCGTTGATTTAACAATCTTCTCCCTTCACTTAGCAGGGA
TTTCTTCGATCCTCGGGGCAATTAACTTCATTACAACCATCATTAACATGAAGCCCCCTGCGA
TCTCCCAGTACCAGACACCCCTCTTCGTCTGATCAGTACTTATCACGGCGGTCCTGCTCCTCC
TTTCTCTCCCCGTCCTCGCAGCTGGTATCACCATGCTCCTGACAGATCGTAACCTCAACACCA
CCTTCTTCGACCCCGCCGGGGGAGGAGACCCAATCCTTTACCAACACCTATTCTGATTCTTTG

Table 17. Genetic distances between *Santelmoa elvirae* and other species studied of COI (627 bp)

Santelmoa elvirae	
Austrolycus depressiceps	8.02
Iluocoetes fimbriatus	7.18
Lycenchelys bachmanni	5.31
Lycenchelys wilkesi	2,86
Lycodapus pachysoma	6,89
Ophthalmolycus amberensis	2.43
Pachycara matallanasi	4.13
Pachycara priedei	2.67
Patagolycus melastomus	7.21
Piedrabuenia ringueleti	5.31
Plesienchelys stehmanni	5.63
Santelmoa fusca	3.84
Pachycara brachycephalum	2.56
Gymnelus viridis	11.74

DNA barcode COI of *Santelmoa fusca* (ZMUC.7656) (627bp): (Described in chapter 2):

GCACAGCTCTAAGCCTCCTCATTCGAGCGGAGCTAAGCCAACCCGGCGCCCTCCTGGGGGAC
GACCAAATTTATAATGTCCTTGTTACAGCGCATGCGTTCGTAATAATTTTCTTTATAGTAATA
CCAATTATGATCGGGGGCTTTGGAAACTGACTTGTGCCCTTGATAATCGGGGCCCCGGACAT
AGCATTTCCCCGAATAAACAACATGAGCTTTTGGCTCCTTCCCCCATCTTTTCTCCTCCTCCT
TGCTTCTTCGGGAGTAGAGGCGGGTGCTGGGACCGGGTGAACCGTTTACCCCCCTCTTTCTG
GTAACTTAGCCCACGCAGGGGCCTCCGTGGATTTAACAATCTTCTCCCTTCACTTAGCAGGG
ATCTCTTCGATCCTCGGGGCAATTAATTTCATTACAACCATCATTAACATGAAGCCCCCTGCG
ATCTCTCAGTACCAGACACCCCTCTTCGTCTGATCCGTACTTATCACGGCGGTCCTGCTCCTC
CTTTCTCTCCCCGTCCTCGCAGCTGGTATCACCATGCTCCTGACAGATCGTAACCTTAACACC
ACCTTCTTCGACCCCGCCGGGGGAGGAGACCCAATCCTTTACCAACACCTATTCTGATTCTTT
G

DNA barcode COI of *Santelmoa priedei* (ZMUC.31) (Møller and King, 2007) (546bp):

CTCTAAGCCTCCTCATTCGAGCGGAGCTAAGCCAACCCGGCGCCCTCCTGGGGGACGACCAA
ATTTACAATGTCCTTGTTACAGCGCATGCGTTCGTAATAATTTTCTTTATAGTAATACCAATT
ATGATCGGGGGGTTTGGAAACTGGCTTGTGCCCTTGATAATCGGGGCCCCGGACATAGCATT
TCCCCGAATAAACAACATGAGCTTTTGACTCCTCCCCCCATCTTTTCTTCTCCTCCTTGCTTCT
TCGGGGGTAGAGGCGGGTGCTGGAACAGGGTGAACAGTCTACCCCCCTCTCTCTGGTAACTT
GGCCCACGCAGGGGCCTCCGTTGATTTAACAATCTTCTCCCTTCACTTAGCAGGGATTTCTTC
GATCCTCGGGGCAATTAATTTCATTACAACCATCATTAACATGAAGCCCCCCGCGATCTCCCA
GTACCAGACACCCCTCTTCGTCTGATCAGTACTTATCACGGCGGTCCTGCTCCTCCTTTCTCT
CCCCGTCCTCGCAGCTGGTATCACCATGCTCCTGACAGATCGTA

DNA barcode COI of *Patagolycus melastomus* (UAB.ZM2, holotype) (627bp): (Described in chapter 1):

GCACAGCTCTAAGCCTCCTCATTCGAGCGGAGCTAAGCCAACCCGGCGCCCTCCTGGGGGAC
GACCAGATTTACAATGTCCTTGTTACAGCGCATGCGTTCGTAATAATTTTCTTTATAGTAATG

CCAATTATGATTGGGGGCTTTGGAAACTGGCTTGTACCCTTAATAATTGGAGCACCGGACAT
GGCATTTCCCCGAATAAACAACATGAGCTTTTGACTCCTTCCCCCCTCTTTTCTCCTCCTCCT
TGCTTCTTCGGGGGTAGAGGCAGGTGCTGGGACAGGGTGAACAGTCTACCCTCCTCTTTCTG
GCAATTTAGCCCACGCAGGGGCCTCCGTTGATTTAACAATCTTCTCACTCCACCTAGCAGGG
ATTTCTTCAATCCTCGGGGCAATTAATTTCATTACAACCATCATTAACATGAAGCCCCCCGCG
ATTTCTCAGTACCAGACGCCCCTCTTCGTCTGATCCGTTCTCGTCACGGCAGTTTTGCTCCTC
CTCTCTCTCCCCGTCCTCGCAGCTGGTATTACCATGCTCCTGACAGATCGTAACCTTAACACC
ACCTTCTTCGACCCCTCCGGGGGAGGAGACCCCATCCTATACCAACATCTGTTCTGATTCTTT
G

Some samples used in this study were not collected for the purpose to do a molecular analysis. Therefore, some samples were not stored in optimal conditions, some of these were old and some were not fixed immediately after the fish died. This is probably the reason why it was difficult to obtain sequences in some genera and why different DNA extraction methods were needed. In addition, a mitochondrial gene rearrangement would be another explanation. In Antarctic notothenioids have been reported that the ND6 gene and $tRNA^{glu}$ had been translocated from their location (between ND5 and cytochromeb gene) to the Control Region (CR) (Zhuang *et al*., 2010). The vertebrate mitochondrial gene order is an ancestral condition and the $ND6_{CR}$ is an adaptative change in Antarctic notothenioids to the protein (Complex 1) of the mitochondrial electron transport chain. A similar case would be found in Antarctic Zoarcidae but more molecular analyses are required.

Short sequences were obtained of *Santelmoa carmenae* that was fixed during few days in formalin and then seven years in ethanol at room temperature. The best results were achieved using QIAmp Tissue Kit from Qiagen.

Background studies show that tissue fixed in formalin and ethanol for a short time (7 days) the DNA is easy to extract for all methods studied but, the extraction from the formalin-fixed specimens that were preserved for 3-4 years is not possible (Chakraborty *et al*., 2006). Although there are some reports of DNA extraction from formalin-fixed (Shiozawa *et al*., 1992; Cano and Poinar, 1993; Shedlock *et al*., 1997; Chase *et al*., 1998) the sequences were small (100-200bp) and they were not useful to determining genetic differences in closer species (Chakraborty *et al*., 2006). In this study, we try to get sequences from several samples fixed as mentioned above but

only one sample has been sequenced. Therefore, as Chakraborty *et al*., (2006) commented the yield is very low in samples fixed in formalin for a long time. However, two short sequences of COI (100pb) and CR (237bp) were obtained (molecular distance with other Lycodinae genera are shown in table 18 and 19).

DNA barcode COI of *Santelmoa carmenae* (100bp):

CCAATTATGATCGGGGGCTTTGGAAACTGACTTGTGCCCTTGATAATCGGGGCCCCGGACAT
AGCATTTCCCCGAATAAACAACATGAGCTTTTGACTCCT

DNA barcode CR of *Santelmoa carmenae* (237bp):

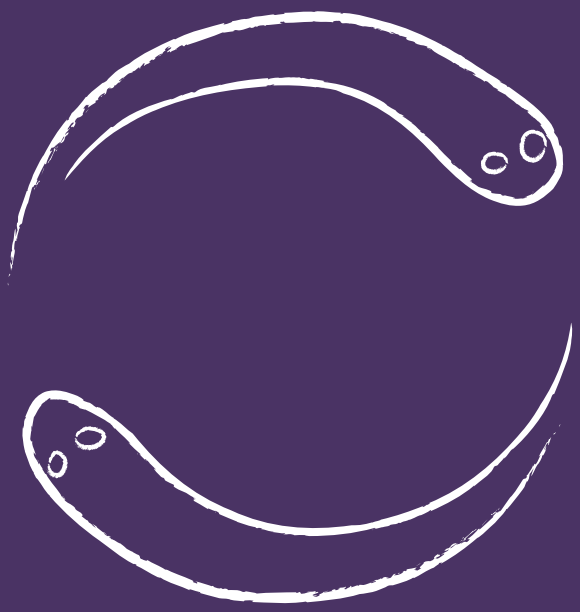
TAAGGAGTGCGGATACTTGCATGTGTAAGTTTAGCTAAAGTTGATAGTAAAGTCAGGACC
AAGCCTTTGTGCTTGCGGAGCTTTCTAGGGCCCATCTTAACATCTTCAGTGTTATGCTTT
GCTTAAGCTACGTTAGCAACTGCATTGTTGCAATAATGTAAATTACCAAAAAAAAAGCAA
AATTTTATCCCATACTAACTACCAGAGGTTTTCCTGTTTTCGGGGGTTTTCAGGAGT

Table 18. Genetic distances between *Santelmoa carmenae* and other species studied of COI (100 bp)

Santelmoa carmenae	
Austrolycus depressiceps	9.4
Iluocoetes fimbriatus	9.2
Lycenchelys bachmanni	5.5
Lycenchelys wilkesi	4.2
Lycodapus pachysoma	7.9
Ophthalmolycus amberensis	3.1
Pachycara matallanasi	1.0
Pachycara priedei	2.0
Patagolycus melastomus	9.2
Piedrabuenia ringueleti	6.7
Plesienchelys stehmanni	4.3
Santelmoa fusca	1.0
Pachycara brachycephalum	0.0
Gymnelus viridis	7.7

Table 19. Genetic distances between *Santelmoa carmenae* and other species studied of CR (237 bp)

Santelmoa carmenae	
Austrolycus depressiceps	4.4
Iluocoetes fimbriatus	5.1
Lycenchelys bachmanni	3.7
Lycenchelys wilkesi	3.1
Lycodapus pachysoma	5.8
Ophthalmolycus amberensis	1.8
Pachycara matallanasi	1.8
Pachycara priedei	3.1
Patagolycus melastomus	5.1
Piedrabuenia ringueleti	4.4
Plesienchelys stehmanni	2.4
Santelmoa fusca	4.4
Pachycara brachycephalum	2.4
Gymnelus viridis	12



DISCUSSION

6 GENERAL DISCUSSION

Maybe one of the most difficult tasks for taxonomists is to delimit species. The question “what is species?” has been widely discussed for many years and at least 26 species concepts exist (Mayden, 1997; Wilkins, 2006). The biological species concept is probably the most accepted and it defines specie as “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr, 1942). Nevertheless, for most taxa it is not possible to know if they are really isolated. For this reason, other methods such as morphological species concept, based in anatomic traits and phylogenetic methods (Dayrat, 2005), have been used to delimit species.

In recent years, the improvement in molecular biology has provided new tools to the taxonomists to classify organisms. But this issue has elicited a great debate about the advantages and disadvantages of this new technology compared to traditional methods.

It is necessary to differentiate between delimiting species and identifying species in order to understand the DNA potential (Prendini, 2005). “DNA barcoding” has appeared to facilitate the identification of species, which uses a short standardized gene region that belongs to a particular species (Hebert *et al*., 2003). But this method requires a complete database providing sequences of all species (Dayrat, 2005; Prendini, 2005) and perhaps it is too optimistic to expect that all species can be classified by a short fragment of one mitochondrial gene (Lipscomb *et al*., 2003; Mallet and Willmott, 2003; Seberg *et al*., 2003; Tautz *et al*., 2003; Moritz and Cicero, 2004). In this way, species identification can be considered the main function of DNA taxonomy (Wheeler, 2004; Scoble, 2004; Wheeler *et al*., 2004) and DNA barcodes should be a support data to species description based on anatomic characters (e.g., see Brown *et al*., 2003). Therefore, it will be convenient to include DNA data in descriptions of new species because it provides more information about the new species and it can help to detect cryptic species (Proudlove and Wood, 2003; Godfray and Knapp, 2004; Hebert *et al*., 2004).

Dayrat (2005) considered the species described on the basis of morphologic characters as a hypothesis that should be tested with other kinds of data. In this sense, the author proposes the “integrative taxonomy” as the best possible future for

taxonomy. This method uses different disciplines such as phylogeography, comparative anatomy, population genetics, ecology and behavioural biology for delimiting species. The author also comments that non-morphologic methods cannot substitute the morphologic methods (Will and Rubinoff, 2004) because all methods may present some problems. However, other authors do not agree with Dayrat (2005) at some points. Valdecasas *et al*., (2008) commented that all disciplines have limits for delimiting species and that the attempts to combine different disciplines can be problematic.

At the beginning, there was an initial euphoria with DNA method possibilities, but nobody has demonstrated that DNA data is better than other method; neither that morphology is less efficient for delimiting species than other disciplines (Valdecasas *et al*., 2008). It is clear that DNA is not the solution for all taxonomy problems (Prendini, 2005); therefore, there are no reasons to think that DNA taxonomy will replace the morphology taxonomy (Wheeler, 2004). In conclusion, molecular data is another tool for taxonomists and it should be incorporated into the description of new species or genus as far as possible. But sometimes this is not possible and a thorough morphologic study is enough to make a valid description.

Two new genera have been described in this thesis to increase the number of genera within subfamily Lycodinae. Therefore, 40 genera are currently within the subfamily studied (Anderson and Fedorov, 2004; Mincarone and Anderson, 2008; Matallanas, 2009a, 2009b, 2010; Matallanas and Corbella, 2012). The new genus *Patagolycus* (Matallanas and Corbella, 2012) was described after a detailed anatomical study of specimens classified first as *Iluocoetes fimbriatus*. *Argentinolycus* (Matallanas and Corbella, 2012) has been proposed for the specie *Iluocoetes elongatus* (Smitt, 1898). As a result of this thesis (chapter 1) *Iluocoetes* has been redefined. With these new genera, the endemic Magellan province genera have increased from 12 to 14. This unusual high number of endemic genera in this area shows a possible speciation center of subfamily Lycodinae. This is the case of the Southern Ocean, where there are 5 endemic genera (Anderson, 1990, 1991, 2006; Anderson and Gosztonyi, 1991; Møller and Stewart, 2006; Matallanas, 2009a, 2009b, 2010) and some authors consider that this is a second speciation center of subfamily Lycodinae (Andriashev, 1965, 1987; Briggs, 2000).

Patagolycus differs from *Iluocoetes* in the following characters (*Patagolycus* first): oral cavity color (black vs. pale); dark snout band (anterior edge eye to nasal tube vs. anteroventral eye to upper jaw); squamation (of head, pectoral base and axil scaled vs. scaleless); palatine teeth (3-7 vs. 9-23); posterior nasal pore (2 vs. 1); frontal bones (fused anteriorly vs. fused completely); parietal-parietal articulation (separated from mid-line vs. contacting); frontal-parasphenoid articulation (separated by pterosphenoid vs. contacting); sphenotic-parietal articulation (contacting vs. separated by frontals); ceratohyal-epihyal articulation (interdigitating dorsally vs. smooth).

Iluocoetes differs from *Argentinolycus* in the following characters (*Iluocoetes* first): submental crest (present vs. absent); pelvic-fin membranes (rays ensheathed vs. rays exerted); postorbital pores (1 and 4 vs. 4); branchiostegal ray (5 vs.6); cranium (wide vs. narrowed); frontal bones (fused vs. separate); frontal corner (squared off vs. tapering); parasphenoid wing high vs. low, broad); pyloric caeca (present vs. absent); posttemporal ventral ramus (well-developed vs. absent); ceratohyal-epihyal articulation (smooth vs. interdigitating along entire length).

Phylogenetic study based on anatomical characters shows a clear separation of *Argentinolycus from* both *Patagolycus* and *Iluocoetes* (fig. 21). Resulting trees from molecular data also show that *Patagolycus* and *Iluocoetes* are close groups, but they are separated with high support branch (fig. 35, 36 and 37).

In this thesis (chapter 2) two new species (*Santelmoa antarctica* and *Santelmoa fusca*) have been described from the Gerlache Strait on the basis of a complete external and osteologic study of an adequate series of specimens. The two new species are placed within *Santelmoa* by the following characters: anterior portion of left and right frontals fused; scapular foramen open; ceratohyal-epihyal articulation interdigitating; cranium narrowed; supratemporal commissure and occipital pores absent; intercalar reaching the prootic and/or excluding exoccipital and pterotic articulation; ascending rami of the parasphenoid wing high; 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.

Currently, genus *Santelmoa* described by Matallanas (2010) includes 4 species (*S. carmenae* Matallanas, 2009, type species; *S. elvirae* Matallanas, 2011; *S. fusca* Matallanas, Corbella and Møller, 2012 and *S. antarctica* Matallanas, Corbella and Møller, 2012).

Santelmoa fusca differs from *S. carmenae* on the following characters (*S. fusca* first): dorsal fin rays (109–113 vs. 91–95); anal fin rays (88–94 vs. 75–79); precaudal vertebrae (27–29 vs. 24–25); caudal vertebrae (87–91 vs. 75–79), and total vertebrae (114–118 vs. 99–104); tail length (63.0–71.3 % SL vs. 58.3–59.8); snout to anterior scales (39.4–45.1 % SL vs. 11.5–18.5); pelvic fin length (10.7–14.1 % HL vs. 4.1–8.7); posterior nasal pores (2 vs. 1); squamation (scales reduced to tail vs. extended across the body, abdomen, and pectoral fin base and axil); lateral line configuration (two branches vs. three branches); pyloric caeca development (well developed vs. small nubbs); coracoid (with no foramina vs. with a small foramen), and foramina in the cartilaginous basal plate of the pectoral girdle (with no foramina vs. with a small foramen between the two central radials).

Santelmoa antarctica differs from *S. carmenae* on the following characters (*S. antarctica* first): dorsal fin rays (109–112 vs. 91–95); anal fin rays (89–93 vs. 75–79); precaudal vertebrae (27 vs. 24–25); caudal vertebrae (89–92 vs. 75–79), and total vertebrae (116–119 vs. 99–104); head length (6.1–6.5 % SL vs. 7.7–10.6); head width (6.1–6.5 % SL vs. 7.7–10.6); preanal length (32.4–35.1 % SL vs. 40.1–41.6); tail length (67.6–70.2 %SL vs. 58.3–59.8); snout to anterior scales (27.1–31.4 % SL vs. 11.5–18.5); posterior nasal pores (2 vs. 1); squamation (dense on the tail, scattered on the posterior part of body vs. extended across the body, abdomen, and pectoral fin base and axil); lateral line configuration (two branches vs. three branches); suborbital pore pattern (6 + 1 vs. 6 + 0); pyloric caeca development (well developed vs. barely produced); intercalar (no reaching prootic vs. reaching prootic); posterior strut on symplectic (absent vs. present); coracoid (with no foramen vs. with a small foramen), and foramina in the cartilaginous basal plate of the pectoral girdle (one foramen between scapular strut and r1 vs. one foramen between r2 and r3).

Finally, an interesting new species from Western South Pacific specifically from the Solomon Sea has been described (chapter 3). *Pachycara matallanasi* sp.nov. has been described in detail and molecular information has been provided (sequences of COI and CR). With this new species, we have contributed to the knowledge of the

diversity of *Pachycara* from the Western South Pacific area. This is the first record of the genus in the Solomon Sea and the third species described of this genus from the Western Pacific Ocean. With this new species, there are 26 species within *Pachycara.*

Pachycara matallanasi is included in genus *Pachycara* because it differs itself from *Lycodes* and *Lycenchelys* by having the following characters: submental crest absent; suborbital pores 7; pectoral fin rays 17-19; parasphenoid wing reaching mid-height of the trigeminofacialis foramen and palatopterygoid series well developed.

P. matallanasi has interesting features that are not usual in this genus: the lack of scales and the pelvic fin absent. Until now, the absence of scales has been described only in two species (*P. shcherbachevi* and *P. alepidotum*) but it is not an isolated case. This character can be found in species of other genera, or at least some of them present a decrease of scales. Møller and Gravlund (2003) noted that in *Lycodes*, the reduced squamation is more frequent in Arctic species and agrees with Andriashev (1954) who commented that this condition might be related to low temperature. Most *Pachycara* are from deep waters and two species are from the Southern Ocean (*P. brachycephalum* and *P.goni*) but almost all species present scales. Therefore, it seems that in this case the reduced squamation is not related to low temperatures. Although this character is very variable, it is important to make a detailed description because it can enable species identification with an external observation.

A similar case is the pelvic fin, that it is a very variable character. Among species of *Pachycara,* 15 species present pelvic fins, 8 species lack it (*P. bulbiceps*, *P. nazca*, *P. arabica*, *P. andersoni*, *P. priedei*, *P. cousini*, *P. moelleri* and *P. matallanasi*) and three species depend on the specimen (*P. mesoporum*, *P. sulaki* and *P. brachycephalum*. The absence of pelvic fins may not be significant for delimited genera (DeWitt, 1962) but it is an important external character to facilitate the determination of the specimens. A phylogenetic study is required to determine if specimens without pelvic fin are closer.

Genetic distances between *P. matallanasi* and the other species studied show that the least divergent sequences belong to *Pachycara priedei* Møller and King, 2007 (2.76 %) from the Southern Indian Ocean and *Santelmoa fusca* Matallanas, Corbella and Møller, 2012 (4.10 %) from the Southern Ocean. The most molecular divergence

is found in some endemic Magellan genera, and among them, *Austrolycus depressiceps* is the most divergent (9.17%).

Phylogenetic study is maybe the major outstanding issue in Lycodinae study. Some authors have carried out specific works with few Lycodinae genera (Radchenko *et al*., 2008a, 2008b, 2008c, 2009; Møller and Gravlund, 2003; Smith *et al*., 2012) but a complete phylogenetic study has never been carried out. This is perhaps due to the difficulty in obtaining samples and the large number of genus and species that contain the subfamily Lycodinae. In this way, we have carried out a phylogenetic analysis with species from the three areas studied (Southern Ocean, Western South Atlantic and Western South Pacific) in chapter 4. The resulting tree shows that *Lycodapus pachysoma* is separated from all other species with a high number of anatomic characters with apomorphous state (squamation, condition of flesh, lateral line, oral valve, frontal corner, frontal ramus, preopercular and mandibular canals, dentary foramina, pore from ventralmost, male caniniform dentition, scapular strut and number of actinost).

Species from Magellan Province (*Piedrabuenia ringueleti*, *Lycenchelys wilkesi*, *Austrolycus depressiceps*, *Patagolycus melastomus* and *Iluocoetes fimbriatus*) form a single cluster with a high support branch, whereas some Antarctic species (*Ophthalmolycus amberensis*, *Pachycara brachycephalum* and *Santelmoa fusca*) form another cluster (fig.38). *Pachycara priedei* and *Pachycara matallanasi*, on the one hand, and *Plesienchelys stehmanni* and *Lycenchelys wilkesi* on the other, are two closer couples with a high support branch (bootstrap values, 93% and 88% respectively). However, on the basis of the available information, it is not possible to conclude whether these pairs of species are closer to Magellan species or to Antarctic species because statistic support is limited.

Species identified as *Pachycara brachycephalum*, appeared in a discrete clade from other *Pachycara* species. Genetic distance between *P. brachycephalum* and *Pachycara priedei* is 3.22% and with *Pachycara matallanasi* is 5.0%. The same problem is found in *Lycenchelys wilkesi* and *Lycenchelys bachmanni* with 6.23% of divergence. It evidences that a complete review of some genera of subfamily Lycodinae is required. *Pachycara* is a large genus that perhaps contains several genera.

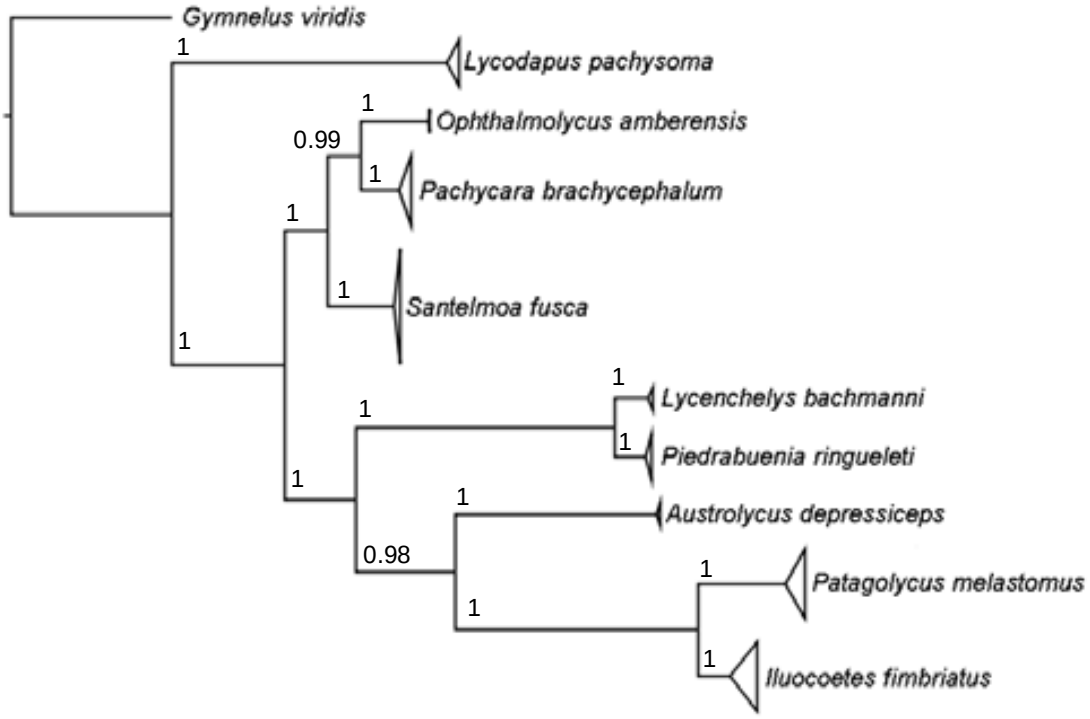


Figure 38. Bayesian inference tree of the combined COI and CR dataset. Magellan province and Antarctic species group. Values at nodes are posterior probabilities.

The delimitation of species in zoarcids is difficult because some genera are described on the basis of a combination of characters and in some cases with few specimens. Some descriptions do not include osteologic characters and are described by means of external characters (lateral line, teeth, scales, cephalic pores, colour, etc.) and meristic and morphometric characters. Counts and measurements are often not enough to delimitate species and the same issue can be found even in the genera. Several Lycodinae species inhabit in deep sea waters and this extreme environmental condition might impose stabilizing selection on morphology reducing morphological change (Bickford *et al*., 2007). In this type of environment such as Arctic tundra (Grundt *et al*., 2006), underwater karst (Lefébure *et al*., 2006) and deep sea environments (Vrijenhoek *et al*., 1994), a large number of cryptic species have been found (Bickford *et al*., 2007). In these cases, molecular data can help taxonomists to detect new species.

7.1 FUTURE OUTLOOKS

There is still a long way to go about knowledge of the subfamily Lycodinae. But there are three main lines of research that are most likely the next step in the Lycodinae study. First, it is necessary to clarify the taxonomy of some genera. *Pachycara* is a chaotic genus and a complete review is required with an anatomic and a molecular study of all species.

Secondly, the most important remaining task in Lycodinae study is probably a complete phylogenetic study. Lycodinae is a specious subfamily with a wide distribution, and obtaining samples from all species is very difficult. Therefore, to carry out this project, cooperation among researchers from different countries would be required to get the maximum number of samples. Mitochondrial and nuclear sequences should be amplified and a phylogenetic analysis would be carried out using inference Bayesian and Maximum Likelihood. The results will probably reveal taxonomic problems and cryptic species.

Last but not least, using the same information, the absolute time of divergence of Zoarcidae will be studied. Some authors have tried to study the time of divergence using “molecular clock” but there are evidences that the results that have been obtained are not completely correct. The “calibration points” method could be the best method to estimate the divergence time. But in Lycodinae, it is more difficult because no fossils exist. The use of biogeographical evidence and the time of divergence in close families to Zoarcidae can provide information of the absolute time of divergence of Zoarcidae.

CONCLUSIONS

7 Conclusions

1. A new genus and species (*Patagolycus melastomus* Matallanas and Corbella, 2012) from Magellan province has been described.

2. Genus *Iluocoetes* Jenyns, 1842 has been redescribed.

3. A new genus (*Argentinolycus* Matallanas and Corbella, 2012) has been proposed for *Iluocoetes elongatus* (Smitt, 1898).

4. Two new species of *Santelmoa* have been described (*Santelmoa fusca* Matallanas, Corbella and Møller, 2012 and *Santelmoa antarctica* Matallanas, Corbella and Møller, 2012).

5. A new species, *Pachycara matallanasi* sp.nov. (Corbella and Møller, in process) has been described from the Solomon Sea. It is the second record from Western South Pacific.

6. Osteologic characters are essential for the description of Lycodinae species.

7. COI, Citb and CR fragment sequence was obtained for the first time from several species recently described (*Patagolycus melastomus*, *Pachycara matallanasi*, *Pachycara priedei* and *Santelmoa fusca*).

8. Phylogenetic analyses show that a complete review of genera *Pachycara* and *Lycenchelys* is required.

9. For the first time, a molecular phylogenetic study has been carried out with these species of subfamily Lycodinae. This study will be the basis for further studies.

10. *Lycodapus pachysoma* is the most divergent species, with high values of genetic distances and with many synapomorphic characters.

11. Resulting trees of phylogenetic analyses show that *Patagolycus melastomus* and *Iluocoetes fimbriatus* form two separated groups, and this is congruent with the osteologic variation observed. Further molecular studies are needed to test more molecular markers.

12. Resulting trees of phylogenetic analyses show two clusters that correspond to Magellan species and Antarctic species, respectively.

7 Conclusions

1. S'ha descrit un nou gènere i una nova espècie (*Patagolycus melastomus* Matallanas and Corbella, 2012) de la província de Magallanes.

2. S'ha redescrit el gènere *Iluocoetes* Jenyns, 1842.

3. S'ha proposat un nou gènere (*Argentinolycus* Matallanas and Corbella, 2012) per a l'espècie *Iluocoetes elongatus* (Smitt, 1898).

4. S'han descrit dues noves espècies del gènere *Santelmoa* (*Santelmoa fusca* Matallanas, Corbella and Møller, 2012 i *Santelmoa antarctica* Matallanas, Corbella and Møller, 2012).

5. S'ha descrit una nova espècie del gènere *Pachycara*, *Pachycara matallanasi* sp.nov. (Corbella and Møller, en procés) del mar de Solomon. És la segona espècie descrita del sud-oest de l'Oceà Pacific.

6. Una detallada descripció dels caràcters osteològics és essencial per la descripció de noves espècies de la subfamília Lycodinae.

7. Per primera vegada s'han seqüenciat fragments de COI, Citb i CR d'espècies descrites recentment (*Patagolycus melastomus, Pachycara matallanasi, Pachycara priedei* i *Santelmoa fusca*).

8. Les anàlisis filogenètiques han deixat al descobert la necessitat de realitzar revisions completes dels gèneres *Pachycara* i *Lycenchelys*.

9. Per primera vegada s'ha realitzat una anàlisi filogenètica amb aquestes espècies de la subfamília Lycodinae. Aquest estudi serà la base de futurs estudis de filogènia d'aquesta subfamília.

10. L'espècie *Lycodapus pachysoma* és la que presenta una grau de divergència més gran, amb valors alts de distància genètica amb les altres espècies estudiades i amb un nombre elevat de caràcters sinapomòrfics.

11. Els arbres obtinguts de l'anàlisi filogenètica mostren que *Pachycara melastomus* i *Iluocoetes fimbriatus* estan separats cosa que coincideix amb les diferències observades en caràcters osteològics. Tot i això, és necessari realitzar més estudis moleculars per trobar altres marcadors moleculars que ens acabin de confirmar aquesta divergència.

12. Les anàlisis filogenètiques mostren dos clusters clarament separats, un format per espècies de la província de Magallanes i l'altre per espècies Antàrtiques.

REFERENCES

8 REFERENCES

Amaoka, K., Nakaya, K. and Yabe, M. (1995) The Fishes of Northern Japan. *Kita-Nihon Kaijo Center, Sapporo, Hokkaido, Japan.*

Anderson, M.E. (1981) Aspects of the natural history of the midwater fish *Lycodapus mandibularis* (Zoarcidae) in Monterey Bay, California. *Pacific Science*, 34(2): 181-194.

Anderson, M.E. (1982) Revision of the fish genera *Gymnelus* Reinhardt and *Gymnelopsis* Soldatov (Zoarcidae), with two new species and comparative osteology of *Gymnelus viridis*. *National Museum*, *Natural Science Publications, Zoology*, 17: 1-76.

Anderson, M.E. (1984) Zoarcidae: Development and relationships. In Moser, H.G. (Ed.), *Ontogeny and systematics of fishes.American Society of Ichthyologists and Herpetologists*, *Special Publication*, 1: 578-582.

Anderson, M.E. (1988a) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. I. The Antarctic and subantarctic regions. *Antarctic Research Series*, 47: 59-113

Anderson, M.E. (1988b) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. II. Two new genera and a new species from the temperate South America. *Proceedings of the California Academy of Sciences*, 45: 267-276.

Andreson, M.E. (1988c) *Eucryphycus*, a new genus of California eelpout (Teleostei:Zoarcidae) based on *Maynea californica* Starks and Mann, 1911. *Proceedings of the California Academy of Sciences*, 45(5): 89-96.

Anderson, M.E. (1989) Review of the eelpout genus *Pachycara* Zugmayer, 1911 (Teleostei: Zoarcidae), with descriptions of six new species. *Proceedings of the California Academy of Sciences*, 46 (10): 221–242.

Anderson, M.E. (1990) Studies on the Zoarcidae, (Teleostei: Perciformes) of the southern hemisphere. III. The southwestern Pacific. *JLB Smith Institute of Ichthyology, Special Publications*, 50: 1–17.

Anderson, M.E. (1991) Studies on the Zoarcidae (Teleostei: Perciformes) of the Southern Hemisphere. V. Two new species from the Weddell Sea, Antarctica. *Cybium*, 15 (2): 151–158.

Anderson, M.E. (1994) Systematics and osteology of the Zoarcidae (Teleostei: Perciformes). *J.L.B. Smith Institute of Ichthyology*, *Ichthyological Bulletin*, 60: 1-120.

Anderson, M.E. (2006) Studies on the Zoarcidae of the Southern hemisphere. X. New records from western Antarctica. *Zootaxa*, 1110: 1-15.

Anderson, M.E. and Bluhm, H. (1997) Description of a new species of *Pachycara* Zugmayer 1911 from the abyssal south-eastern Pacific and redescription of *P. thermophilum* Geistdoerfer, 1994, with a new key to the species. *Transactions of the Royal Society of South Africa*, 51: 219-227.

Anderson, M.E. and Fedorov, V.V. (2004) Family Zoarcidae Swainson 1839, eelpouts. *California Academy of Sciences*, *Annotated Checklists of Fishes*, 34: 1-58.

Anderson, M.E. and Gosztonyi, A.E. (1991) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. IV. New records and a new species from the Magellan Province of South America. *J.L.B. Smith Institute of Ichthyology, Ichthyological Bulletin*, 55: 1-16.

Anderson, M.E. and Hubbs, C.L. (1981) Redescription and osteology of the northeastern Pacific fish *Derepodichthys alepidotus* (Zoarcidae). *Copeia*, 1981(2): 341-352.

Anderson, M.E. and Mincarone, M.M. (2006) Studies on the Zoarcidae (Teleostei:Perciformes) of the southern hemisphere. IX. A new species of Pachycara from the southwestern Atlantic. *Zootaxa*, 1177: 21-26.

Anderson, M.E. and Peden, A.E. (1988) The eelpout genus *Pachycara* (Teleostei: Zoarcidae) in the northeastern Pacific Ocean, with descriptions of two new species. *Proceedings of the California Academy of Sciences*, (ser. 4) 46 (3): 83-94.

Andriashev, A. P. (1939) Essay on the zoogeography and origin of the fish fauna of the Bering Sea and adjacent waters. *Izdanie Leningradskogo Gosudarstvenogo Universiteta, Leningrad.* 1-187. (In Russian with English summary (pp. 181–185). English translation by A. Merrivale. [i–iv] + 1-284).

Andriashev, A. P. (1952) A new deep-sea fish of the eelpout family (Pisces, Zoarcidae) from the Bering Sea. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, 12: 415-417. (English translation in 1963)

Andriashev, A.P. (1953) Ancient deep-water and secondary deep-water fishes and their importance in a zoogeographical analysis. In note on special problems of ichthyology. *Okeanologii Institut, Akademiy Nauk SSSR, Izdatel'stvo Nauk, Moskva*, 58-64. (English translation. U.S. Bureau of Commercial Fisheries, Washington, D.C).

Andriashev, A.P. (1954) Fishes of the Northern seas of the USSR. Academy of Sciences of the Union of Soviet Socialist Republics, Moscow, Leningrad. (Translated from Russian by Israel program for scientific translations Jerusalem, 1964).

Andriashev, A.P. (1965) A general review of Antarctic fish fauna. In: van Oye P, van Mieghen J (eds) Biogeography and ecology in Antarctica. *Elsevier*, 491-550.

Andriashev, A.P. (1979) On the occurrence of fishes belonging to the families Zoarcidae and Liparidae off the Kerguelen Island. *Biologia Morya*, 1979 (6): 28-34. (In Russian. English translation in *Soviet Journal of Marine Biology*., 5 (6): 481-486 with somewhat different title).

Andriashev, A.P. (1987) A general review of the Antarctic bottom fish fauna. In: Kullander SO, Fernholm B (eds) *Proceeding of fifth congress of European ichthyologists*, Stockholm, 1985.

Andriashev, A. P. (1991) New species of liparidid fishes of the genus *Careproctus* (Scorpaeniformes, Liparididae) from Patagonia. Second Report. *Voprosy Ikhtiologii*, 31 (5): 707-116. (In Russian. English translation *in Journal of Ichthyology*, 1992, 32 (1): 38-49).

Andriashev, A.P. (1998) A review of recent studies of southern ocean Liparidae (Teleostei:Scorpaeniformes). *Cybium*, 22(3): 255:266.

Arntz, W.E., Gutt, J. and Klages M (1997) Antarctic marine biodiversity: an overview. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure and survival. *Cambridge University Press*, Cambridge, 3-14

Balushkin, A.V (1994) Fossil notothenioid, and not gadiform, fish Proeleginops grandeastmanorum gen.nov.sp.nov. (Perciformes, Notothenioidei, Eleginopidae) from the late Eocene found in Seymour Island (Antarctica). *Voprosy Ikhtiologii*, 34: 298-307.

Barnes D.K.A. and Conlan, K.E. (2007) Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362: 11-38.

Bean, T. H. (1890) New fishes collected off the coast of Alaska and the adjacent region southward. In: Scientific results of explorations by the U. S. Fish Commission steamer *Albatross. Proceedings of The United States National Museum*, 13 (795): 37-45.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. and Das, I. (2007) Cryptic species as a window on diversity and conservation. *Trends in Ecology and Evolution*, 22: 148-155.

Biscoito, M and Almeida, A.J. (2004) New species of *Pachycara* Zugmayer (Pisces: Zoarcidae) from the Rainbow Hydrothermal Vent Fielf (Mid-Atlantic Ridge). *Copeia*, 3: 562-568.

Bleeker, P. (1874) Type nonnulli generic piscium neglecti. *Verslagen van de Gewone Vergaderingen der Wis en Natuurkundige Afdeeling. Konink Akademie van Wetenschapen, Amsterdam*, (ser. 2), 8: 367-371.

Bloch, M. E. (1785). *Ichtyologie ou Histoire naturelle, générale et particulière des poissons.* Berlin, Paris et Londres: Louis Philippe Wegener pour l'auteur, chez Didot, White & fils, 1785-1788.

Bond, C. E. and Stein, D.L. (1984) *Opaeophacus acrogeneius,* a new genus and species of Zoarcidae (Pisces: Osteichthyes) from the Bering Sea. *Proceedings of the Biological Society of Washington*, 97 (3): 522-525.

Brandt, A. (1999) On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). *Scientia Marina*, (63 Supplement) 1: 261- 274.

Briggs, J.C. (1974) Marine Zoogeography. *McGraw-Hill Book Company*, New York, 475.

Briggs, J.C. (2000) Centrifugal speciation and centres of origin. *Journal Biogeography*, 27: 1183-1188.

Bromham, L. and Penny, D. (2003) The modern molecular clock. *Nature Review Genetics*, 4: 216-224.

Brown WM (1985) The mitochondrial genome of animals. *In: MacIntyre RJ (ed*) *Molecular evolutionary genetics. Plenum Press, New York*, 95-130

Brown, J.W., Miller, S.E. and Horak, M. (2003) Studies on New Guinea moths. 2. Description of a new species of *Xenothictis* Meyrick (Lepidoptera: Tortricidae: Archipini). *Proceeding of the Entomological Society of Washington*, 105: 1043-1050.

Bull, J.J., Badgett, M.R., Wichman, H.R., Huelsenbeck, J.P., Hillis, D.M., Gulati, A., Ho, C., and Molineux, I.J. (1997) Exceptional convergent evolution in a virus. *Genetics*, 147: 1497-1507.

Cano, R. J., Poinar, H. (1993) Rapid isolation of DNA from fossil and museum specimens suitable for PCR. *BioTechniques*, 15: 432-435.

Chakraborty, A., Sakai, M. and Iwatsuki, Y. (2006) Museum fish specimens and molecular taxonomy: A comparative study on DNA extraction protocols and preservation techniques. *Journal of Applied Ichthyology*, 22(2006): 160-166.

Chase, M. R., Etter, R. J., Rex, M. A., Quattro, J. M. (1998) Extraction and amplification of mitochondrial DNA from formalin-fixed deep-sea molluscs. *BioTechniques*, 24: 243-247.

Chen, W.J., Bonillo, C. and Lecointre G. (2003) Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. *Molecular Biology and Evolution*, 26: 262-288.

Chereshnev, I.A., Nazarkin, M.V. and Shestakov, A.V. (2005). Marine and freshwater fishes of Tauiskaya Bay, in Biologicheskoe raznoobrazie rauiskoi guby okhotskogo morya. (Biological diversity of Tauiskaya Bay of the Sea of Okhotsk). *Vladivostok. Dal'nauka*, 545-575.

Clarke, A. and Johnston, I.A. (1996) Evolution and adaptative radiation of Antarctic fishes. *Trends in Ecology and Evolution*, 11:212-218.

Cunningham, R. O. (1871) Notes on the reptiles, amphibia, fishes, mollusca, and crustacea obtained during the voyage of H. M. S. 'Nassau' in the years 1866-69. *Transactions of the Linnean Society of London*, 27: 465-502.

Cuvier, G. (1829) Le Regne Animal Distribué d'après son Organisation, por Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction a l'Anatomie Comparée, Second Edition, 2:122-406.

Darwin, C. (1859) On the origin of species. Facsimile of the 1st edition. *Harvard, University Press*, Cambridge, Massachusetts.

Dayrat, B. (2005) Towards integrative taxonomy. *Biological Journal of the Linnean Society*, 85**:** 407-415.

Dettai, A., Lautredou, A.C., Bonillo, C., Goimbault, E., Busson, F., Causse, R., Couloux, A., Cruaud, C., Duhamel, G., Denys, G., Hautecoeur, M., Iglesias, S., Koubbi, P., Lecointre, G., Moteki, M., Pruvost, P., Tercerie, S. and Ozouf-Costaz, C. (2011) The

actinopterygian diversity of the CEAMARC cruises: Barcoding and molecular taxonomy as a multi-level tool for new findings. *Deep-Sea Research II*, 58: 250-263.

Dettaï, A. and Lecointre, G. (2004). In search of notothenioid (Teleostei) relatives. *Antarctic Science*, 16(1): 71-85.

Dettaï, A. and Lecointre, G. (2005). Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *Comptes rendus Biologies*, 328: 674-689.

DeWitt, H.H. (1962) A new genus and species of zoarcid fish from McMurdo Sound, Antarctica. *Copeias*, 1962: 819-826.

DeWitt, H.H. (1971) Coastal and deep-water benthic fishes of the Antarctic. *Antarctic Map Folio Series*, 15: 1-10.

DeWitt, H. H. (1977) A new genus and species of eelpout (Pisces, Zoarcidae) from the Gulf of Mexico. *United States National Marine Fisheries Service Fishery Bulletin*, 75 (4): 789-793

Eastman, J.T. (2005) The nature of the diversity of Antarctic fishes. *Polar Biology* 28: 93-107.

Eastman, J.T. and Grande, L. (1991) Late Eocene gadiform (Teleostei) skull from Seymour-Island, Antarctic Peninsula. *Antarctic Science*, 3: 87-95.

Eastman, J.T. and McCune, A.R. (2000). Fishes on the Antarctic continental shelf: evolution of a marine species flock? *Journal of Fish Biology*, 57: 84-102.

Emery, W.J. (1977) Antarctic Polar Frontal Zone from Australia to the Drake Passage. *Journal of Physical Oceanography*, 7: 811-822.

Fedorov, V. V. (1975) Description of a new genus and species of a zoarcid fish *Puzanovia rubra,* gen. et sp. n. (Pisces, Zoarcidae) from the northern part of the Pacific Ocean. *Voprosy Ikhtiol*, 15 (4): 587-591. (English translation in *Journal of Ichthyology*, 15 (4): 527-541.

Fedorov, V. V. (1982) A new eelpout, *Hadropogonichthys lindbergi* Fedorov, gen. et sp. nov. (Zoarcidae), from the bathyal depths of the Fourth Kuril Strait. Voprosy Ikhtiologii, 22 (5): 722-729. (In Russian. English translation in *Journal of Ichthyology*, 22 (5): 16-23)

Fedorov, V.V. (2004) An annotated catalogue of fishlike vertebrates and fishes of the Seas of Russian and adjacent countries: 6 Suborder Zoacidae. *Journal of Ichthyology*, 44 (1): S73-S128.

Fedorov, V.V., Chereshnev, I.A., Nazarkin, M.V., Shestakov, A.V. and Volobuev, V.V. (2003) Catalogue of marine and freshwater fishes of the Northem Sea of Okhotsk. *Vladivostok:* D*al'nauka*, 204.

Fedorov, V. V. and Neyelov, A.V (1978) A new genus and species of eelpout, *Andriashevia aptera* gen. et sp. n. (Perciformes, Zoarcidae). Voprosy Ikhtiol, 18 (5): 952-955. (In Russian. English translation in J. Ichthyol, 18 (5): 846-849)

Fedorov, V.V and Parin, N.V. (1998). Pelagic and Benthopelagic Fish from Pacific Waters of Russian (VNIRO, Moscow).

Foster, T.D. and Middleton, J.H. (1984) The oceanographic structure of the Eastern Scotia Sea. I. Physical oceanography. *Deep-Sea Research*, 31: 529-550.

Garman, S. (1899) XXVI. The fishes. In: Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U. S. N.,commanding. *Memoirs of the Museum of Comparative Zoology*, 24: 1-431.

Geistdoerfer, P. (1994) *Pachycara thermophilum*, une nouvelle espèce de poisson Zoarcidae des sites hydrothermaux de la dorsale médio- Atlantique. *Cybium*, 18: 109-115.

Gilbert, C. H. (1890) A preliminary report on the fishes collected by the steamer *Albatross* on the Pacific coast of North America during the year 1889, with

descriptions of twelve new genera and ninetytwo new species. *Proceedings of the United States National Museum*, 13 (797): 49-126.

Gilbert, C. H. (1896) The ichthyological collections of the steamer Albatross during the years 1890 and 1891. *Report of the United States Fish Commission*, 19 (for 1893): 393-476.

Gill, T.N. (1862) Catalogue of the fishes of the eastern coast of North America from Greenland to Georgia. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 13 (sup): 1-63.

Gill, T. N. (1863) Synopsis of the family of Lycodoidae. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 15: 254-262.

Gill, T.N. (1884) On the anacanthine fishes. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 36: 167-183.

Gill, T.N. (1893) Families and subfamilies of fishes. *Memoirs of the National Academy of Sciences*, 6: 127-138.

Givnish, T. J., and Sytsma, K.J. (1997) Homoplasy in molecular vs. morphological data: The likelihood of correct phylogenetic inference. Pages 55-101 *in* Molecular evolution and adaptive radiation (T. J. Givnish and K. J. Sytsma, eds.). *Cambridge University Press, Cambridge*, U.K.

Godfray, H.C.J. and Knapp, S. (2004) Introduction. Philosophica. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, 359: 559-569.

Goode, G. B. and T. H. Bean. (1883) Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the U. S. coast survey steamer “Blake,” Commander J. R. Bartlett, U. S. N., commanding. *Bulletin of the Museum of Comparative Zoology*, 10 (5): 183-226.

Gosline, W.A. (1968) The Suborders of Perciform fishes. *Proceeding of the United States National Museum*, 124: 1-78.

Gosztonyi, A.E. (1977) Results of the research cruises of FRV "Walther Herwig" to South America. XLVIII. Revision of the South American Zoarcidae (Osteichthyes, Blennioidei) with the description of three new genera and five new species. *Archiv für Fischereiwissenschaft*, 27: 191-249.

Gosztonyi, A.E. (1981) Results of the research cruises of FRV “Walther Herwig” to South America. LIX. *Lycodonus malvinensis* n. sp. (Pisces, Blennioidei), another new zoarcid fish from western South Atlantic Ocean. *Archiv für Fischereiwissenschaft*, 31 (3): 151-159.

Gosztonyi, A.E. (1984) Tooth replacement in South American Zoarcidae (Pisces, Teleostei). *Physis (Buenos Aires),* Sección A, 42: 63-69.

Gosztonyi, A.E. (1988) The intercalar bone in the eel-pout family Zoarcidae (Osteichthyes). *Zoological Anzeiger*, 221: 134-144.

Greenwood, P.H., Rosen, D.E., Weitzman, S.H. and Myers G.S. (1966) Phyletic studies of teleostean fishes, with a provisional classification of living forms. *American Museum of Natural History Bulletin*, 131(4): 399-456.

Gronow, L. T. (1760) Animalium in Belgio habitantium centuria prima. *Acta Helvetica* 4:243-270.

Grundt, H.H., Kjølner, S., Borgen, L., Rieseberg and Brochmann (2006) High biological species diversity in the arctic flora. *Proceedings of the national Academy of Sciences of the United States of America*, 103: 972-975.

Günther, A. (1862) Catalogue of the fishes in the British Museum. 4. Catalogue of the Acanthopterygii Pharyngognathi and Anacanthini in the collection of the British Museum. London. I-xxi + 1-534.

Günther, A. (1881) Reptiles, batrachians, and fishes. In: Account of the zoological collections made during the survey of H. M. S. ‘Alert’ in the Straits of Magellan and on the coast of Patagonia. *Proceedings of the* Zoological *Society of London 1881*, 1: 18-22.

Hall, T.A. (1999). Bioedit: a user-friendly biological sequence alignment editor and anslysis program for windows 95/98/NT. *Nucleic Acids. Symposium*, 41:95-98.

Hanson, J.D. and Gordon, J.E. (1998) Antarctic Environments and Resources: a geographic perspective. New York: Longman, 1-402.

Hebert, P.D.N., Cywinska, A., Ball, S.L., deWaard, J.R. (2003) Biological identifi cations through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences*, 270: 313-322.

Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H., and Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United State of America*, 101: 14812- 14817.

Hedges, S. B. and Maxson, L.R. (1996) Molecules and morphology in amniote phylogeny. *Molecular Phylogenetics and Evolution*, 6:312-314.

Hedges, S.B. and Sibley, C.G. (1994) Molecules vs. morphology in avian evolution. The case of “pelecaniform” birds. *Proceedings of the National Academy of Sciences of the United State of America*, 91: 9861-9865.

Henning, W. (1966) Phylogenetic systematic. *University of Illinois Preess*, *Urbana*.

Herman, Y. and Hubkins, D.M. (1980) Arctic oceanic climate in late Cenozoic time. *Science*, 209: 557-562.

Hillis, D. M. and Wiens J.J. (2000) Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. Pages 1-19 in Phylogenetic analysis of morphological data (J. J. Wiens, ed.) *Smithsonian Institution Press, Washington, DC.*

Hoar, W.S. (1969) Reproduction. *In* Hoar, W.S. and Randall, D.L. (Eds.), *Fish physiology*. *Academic Press*, London, 3: 1-72.

Hoelzel, A.R., Hancock, J.M. and Dover, G.A. (1991) Evolution of the cetacean mitochondrial D-Loop region. *Molecular Biology and Evolution*, 8(3): 475493.

Hollar, L.J. and Springer, M.S. (1997) Old World fruitbat phylogeny: Evidence for convergent evolution and an endemic African clade. *Proceedings of the National Academy of Sciences of the United State of America*, 94: 5716-5721.

Hubbs, C. (1952) A contribution to the classification of the Blennioid fishes of the Family Clinidae, with a partial revision of the Eastern Pacific forms. *Stanford Ichthyology Bulletin*, 4(2): 41-165.

Iglésias, S.P., Dettai, A., Ozouf-Costaz, C. (2012) *Barbapellis pterygalces*,new genus and new species of a singular eelpout (Zoarcidae:Teleostei) from the Antarctic deep waters. *Polar Biology*, 35:215-220.

Jensen, A.S. (1902). Ichthyologiske studier. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 1901:191- 214.

Jenyns, L. (1842) The zoology of the voyage of H. M. S. Beagle, under the command of Captain Fitzroy, R. N., during the years 1832 to 1836. IV. *Fish.* Smith, Elder and Co., London, 4: 97-172.

Jordan, D.S. and Gilbert, C.G. (1883) Synopsis of the fishes of North America. *Bulletin of the United States National Museum*, 16: lvi+1-1018.

Jordan, D. S. and C. L. Hubbs. (1925) Record of fishes obtained by David Starr Jordan in Japan, 1922. *Memoirs of the Carnegie Museum*, 10 (2): 93–346.

Kaup, J.J. (1856) Einiges über die Unterfamilie Ophidinae. *Archiv für Naturgeschichte*, 22(1): 93-100.

Kawahara, R., Miya, M., Mabuchi, K., Lavoué, S., Inoue, J.G., Satoh, T.P., Kawaguchi, A. and Nishida M. (2008) Interrelationships of the 11 gasterosteiform families (sticklebacks, pipefishes, and their relatives): A new perspective based on whole mitogenome sequences from 75 higher teleosts. *Molecular Biology and Evolution*, 46: 224-236.

Kennett, J.P. (1982) Marine geology. Englewood Cliffs, NJ: Prentice- Hall, 813.

Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16: 111-120.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S.F., Villablanca, F.X. and Wilson, A.C., (1989). Dynamics of mtDNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America*, 86: 6196-6200.

Lahille, F. (1908) Nota sobre los zoárcidos argentinos. *Anales del Museo Nacional de Historia Natural de Buenos Aires*, 16: 403-441.

Lauder, G.V. and Liem, K.F. (1983) The evolution and interrelationships of the Actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology*, 150: 95-197.

Lee, W.J., Conroy, J., Howell, W.H. and Kocher, T.D. (1995) Structure and evolution of teleost mitochondrial control regions. *Journal of Molecular Evolution*, 41(1): 54-66.

Lefébure, T., Douady,C.J., Gouy, M., Trontelj, P, and Gibert., J (2006) Phylogeography of a subterranean amphipod reveals cryptic diversity and dynamic evolution in extreme environments. *Molecular Ecology*, 15: 1797-1806.

Leviton, A.E., Gibbs, R.H.Jr., Heal, E. and Dawson, C.E. (1985) Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, 1985: 802-832.

Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M. and Lecointre, G., (2009) RNF213, a new nuclear marker for acanthomorph phylogeny. *Molecular Biology and Evolution*, 50: 345-363.

Linnaeus, C. (1758) Systema Naturae, ed. X. (Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.) *Holmiae* Stockholm. i–ii + 1-824.

Lipscomb, D., Platnick, N. and Wheeler (2003) The intellectual content of taxonomy: a comment on DNA taxonomy. *Trends in Ecology and Evolution*, 18: 65-66.

Lloris, D. and Rucabado, J. (1987) *Iluocoetes facali* sp. n. (Osteichthyes, Zoarcidae), una nueva especie para la ictiofauna argentina. *Thalassas*, 5: 53-56.

Loeb, V.J., Kellermann, A.K., Koubbi, P., North, A.W. and White, M.G. (1993) Antarctic larval fish assemblages: a review. *Bulletin of Marine Science*, 53(2): 416-49.

Machida, Y. and Hashimoto, J. (2002) *Pyrolycus manusanus*, a new genus and species of deep-sea eelpout from a hydrothermal vent field in the Manus Basin, Papua New Guinea (Zoarcidae, Lycodinae). *Ichthyological Research*, 49: 1-6.

Makushok, V.M. (1958) The morphology and classification of the northern Blennioid fishes (Stichaeidae, Blennioidei, Pisces). *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, 25: 3-129.

Mallet, J. and Willmott, K. (2003) Taxonomy: renaissance or Tower of Babel? Trends in Ecology and Evolution, 18: 57-59.

Markle, D.F. and Sedberry, G.R. (1978) A second specimen of the deep-sea fish, Pachycara obese, with a discussion of its classification and a checklist of other Zoarcidae of Virginia. *Copeia*, 1978 (1): 22-25.

Marshall, N. B. and Cohen, D.M. (1973) Order Anacanthini (Gadiformes). Characters and synopsis of families. *Memoirs of the Sears Foundation for Marine Research*, 1: 478-495.

Masuda, H., Amaoka, K., Araga, Y., Uyedo, T. and Yoshino, T. (1984) The fishes of the Japanese Archipelago, Vols. 1-2. *Tokai Spring Press*.

Matallanas, J. (2009a) Description of *Gosztonyia antarctica*, a new genus and species of Zoarcidae (Teleostei: Perciformes) from the Antarctic Ocean. *Polar Biology*, 32: 15-19.

Matallanas, J. (2009b) Description of a new genus and species of zoarcid fish, *Bellingshausenia olasoi*, from the Bellingshausen Sea (Southern Ocean). *Polar Biology*, 32: 873-878.

Matallanas, J. (2009c) Description of *Ophthalmolycus andersoni* sp. nov. (Pisces, Zoarcidae) from the Antarctic Ocean. *Zootaxa*, 2027: 55-62.

Matallanas, J. (2010) Description of two new genera, *Santelmoa* and *Bentartia*, and two new species of Zoarcidae (Teleostei,Perciformes) from the Southern Ocean. *Polar Biology*, 33: 659-672.

Matallanas, J. (2011a) Description of two new species of *Ophthalmolycus* (Teleostei: Zoarcidae) from the Southern Ocean and key to species of the genus. *Journal of the Marine Biological Association of the United Kingdom*, 91: 561-567.

Matallanas, J. (2011b) Description of *Santelmoa elvirae* sp. nov. (Teleostei: Zoarcidae) from the Southern Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 91: 1231-1235.

Matallanas, J. and Corbella, C. (2012) Redescription of *Iluocoetes* Jenyns, 1842, proposal of a new genus, *Argentinolycus*, for *Iluocoetes elongatus* (Smitt, 1898) and description of *Patagolycus melastomus*, gen. et sp. nov. (Teleostei, Zoarcidae). *Zootaxa*, 3296: 1-18.

Matallanas,J., Corbella, C. and Møller, P.R. (2012). Description of two new species of *Santelmoa*, *Santelmoa fusca* sp. nov. and *Santelmoa antarctica* sp. nov. (Teleostei, Zoarcidae) from the Southern Ocean. *Polar Biology*, 9: 1395-1405.

Matallanas, J. and Olaso, I. (2007) Fishes of the Bellingshausen Sea and Peter I Island. *Polar Biology*, 30: 333-341

Matallanas, J., Rucabado, J., Lloris, D. and Olivar, P. (1990) Early stages of development and reproductive biology of the South-American eelpout *Austrolycus depressiceps* Regan, 1913 (Teleostei: Zoarcidae). *Scientia Marina*, 54: 257-261.

Mayden, R. L. (1997) A hierarchy of species concepts: the denoument in the saga of the species problem. pp. 381- 423 *in* M. F. Claridge, H. A. Dawah and M. R. Wilson, eds. *Species: The units of diversity.* Chapman and Hall, London.

Mayr, E. (1942) Systematics and the origin of species from the viewpoint of a zoologist. *Columbia University Press*, New York.

McAllister, D. E. and Rees, E.I.S (1964) A revision of the eelpout genus *Melanostigma* with a new genus and with comments on *Maynea. Bulletin National Museum of Canada*, 199: 85-110.

McCracken, K. G., Harshman, J., Mcclellan, D.A. and Afton, A.D. (1999) Data set incongruence and correlated character evolution: An example of functional convergence in the hind-limbs of stifftail diving ducks. *Systematic Biology*, 48: 683-714.

McCracken, K.G. and Sheldon, F.H. (1998) Molecular and osteological analyses of heron phylogeny: Sources of incongruence. *Auk*, 115: 127-141.

Miller, S. A., Dykes, D. D. and Polesky, H. F. (1988) A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Research*, 16:1215.

Mincarone, M.M and Anderson, M.E. (2008) A new genus and species of eelpout (Teleostei: Zoarcidae) from Brazil. *Zootaxa*, 1852: 65-68.

Miya, M., Kawaguchi, A. and Nishida, M. (2001) Mitogenomic exploration of higher teleostean phylogenies: a case study for moderate-scale evolutionary genomics with 38 newly determined complete mitochondrial DNA sequences. *Molecular Biology and Evolution*, 18(11): 1993-2009.

Miya, M., Takeshima, H., Endo, H., Ishiguro, N.B., Inoue, J.G., Mukai, T., Satoh, T.P., Yamaguchi, M., Kawaguchi A., Mabuchi K., Shirai, S.M. and Nishida, M. (2003) Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular phylogenetics and evolution*, 26: 121-138.

Moritz, C. and Cicero, C. (2004) DNA barcoding: promise and pitfalls. *PLoS Biology*, 2: 1529-1531.

Müller, J. (1846) Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin*, 1844: 117-216.

Müller, K. (2005) SeqState: Primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinfformatics*, 4: 65-69.

Møller, P.R. (2000a) On the validity of the eelpouts *Lycodes terraenovae* Collett, 1896, (Pisces, Zoarcidae). *Copeia*, 200: 846-850.

Møller, P.R. (2000b) Restoration of the taxon, *Lycodes marisalbi*, with notes on its disjunct Arctic distribution. *Journal of Fish Biology*, 57: 1404-1415

Møller, P.R. (2001a) A new zoarcid, Lycodes mcallister from eastern Arctic Canada (Teleostei: Perciformes). *Ichthyological Research*, 48: 111-116.

Møller, P.R. (2001b) Redescription of the Lycodes pallidus species complex (Pisces, Zoarcidae), with a new species from the Arctic/North Atlantic Ocean. *Copeia* , 2001: 972-996.

Møller, P.R. (2003) Two New Species of Pachycara Zugmayer (Teleostei:Zoarcidae) from the Indian Ocean, with Redescription of *Pachycara shcherbachevi* Anderson. *Copeia*, 2003(2): 357-365.

Møller, P.R. and Anderson, M.E. (2000) Assignment *of Lycodes Microcephalum* Jensen, 1902 to Pachycara Zugmayer, 1911 (Teleostei:Zoarcidae). *Cybium*, 24(1): 61-65.

Møller, P.R. and Gravlund, P. (2003) Phylogeny of the Eelpout genus Lycodes (Pisces, Zoarcidae) as inferred from mitochondrial cytochrome b and 12S rDNA. *Molecular Phylogenetics and Evolution*, 26: 369-388.

Møller, P.R. and King, N. (2007). Two New Species of *Pachycara* (Teleostei:Zoarcidae) from the sub-Antarctic Southern Indian Ocean, and a Range Extension of *Lycenchelys Antarctica*. *Copeia*, 2007 (3): 586-593.

Møller, P.R. and Stewart, A.L. (2006) Two new species of eelpouts (Teleostei, Zoarcidae) of the genus *Seleniolycus* from the Ross Dependency, Antarctica. *Zootaxa*, 1376:53-67.

Nakabo, T. (2002) Fishes of Japan with Pictorial Keys to the Species, Engl. Ed. Vols. 1-2 (Tokai Univ. Press, Tokyo).

Nazarkin, M.V. (2000) Candidate's Dissertation in Biology (SPbGU, ST. Petersburg).

Near, T.J. (2004) Estimating divergence time of notothenioid fishes using a fossil-calibrated molecular clock. *Antarctic Science*, 16(1): 37- 44.

Nelson, J.S. (1994) Fishes of the world. 3rd edn. John Wiley and Sons, New York, 600.

Nelson, J.S. (2006) Fishes of the world. 4th ed. John Wiley and Sons, Inc. Hoboken, New Jersey, USA, 601.

Nilsson, S. (1832). Prodromus Ichthyologiae Scandinavicae. Lundae, i-iv + 1-124.

Norman, J.R. (1937) Coast fishes II. The Patagonian region. *Discovery Reports*, 16: 1-150.

Norman, J.R. (1938) Coast fishes III. The Antarctic region. *Discovery Reports*, 18: 1-104.

Norman, J.R. (1966) A Draft Synopsis of the Orders, Families and Genera of Recent Fishes and Fish-like Vertebrate. *British Museum* (*Natural History*), London; 649.

Orsi, A.H., Whitworth, T. and Nowlin, W.D. (1995) On the meridional extent and front of the Antarctic Circumpolar Current. *Deep-Sea Research I*, 42(5): 641-673.

Palumbi, S.R. (1996) Nucleic Acids II. The polymerase chain reaction. IN: Hillis, D.M., Moritz, C., Mable, B.K (eds), Molecular Systematics. Sinauer, Sunderland, MA. 205-247.

Pappenheim, P. (1911) Neue antarktische Fische. Nach dem Material der Deutschen Südpolarexpedition 1901–1903. *Sitzungsberichte der Gesellschaft Naturforschender Freunde Zu Berlin*, 8: 382-383.

Pappenheim, P. (1912) Die Fische der Deutschen Südpolar-Expedition 1901-1903. I. Die Fische der Antarktis und Subantarktis. *Deutsche Südpolar-Exped.* 1901-1903, 13 (Zool. 5): 163-182.

Peden, A. E. and M. E. Anderson. (1978) A systematic review of the fish genus *Lycodapus* (Zoarcidae) with descriptions of two new species. *Canadian Journal of Zoology*, 56 (9): 1925-1961.

Pérez, M. and Presa, P. (2011) FENOSALT: un método sintético para la extracción de ADN de peces y moluscos. In: Métodos y Técnicas de Investigación Marina. JM Estévez et al. (eds) Editorial TECNOS (Grupo Anaya S.A.) Chapter VII: 81-89, Spain. ISBN 978-84-309-5208-3.

Popov, A. M. (1931) On a new genus of fish *Davidijordania* (Zoarcidae, Pisces) from the Pacific. *Comptes Rendus de l'Academie des Sciences de Leningrad*, 1931: 210-215.

Popov, A.M. (1935) A new genus and species, *Lycozoarces hubbsi*, gen. n. sp. n. (Pisces, Zoarcidae), of the Okhotsk Sea. *Doklady Akademii Nauk SSSR,* 4, 303-304 (in Russian).

Poulin, E., Palma, A.T. and Feral, J.P. (2002) Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology and Evolution*, 17: 218-222.

Prendini L (2005) Comment on "Identifying spiders through DNA barcodes". *Canadian Journal of Zoology*, 83: 498-504.

Proudlove, G. and Wood, P.J. (2003) The blind leading the blind: cryptic subterranean species and DNA taxonomy. *Trends in Ecology and Evolution*, 18: 272-273.

Radchenko, O. A., Chereshnev, I. A., Petrovskaya, A. V., Nazarkin, M. V. and Chegodaeva, E. A. (2008a) Nucleotide Sequence Variation of the Mitochondrial *COI* Genein Several Eelpout Species of the Genus *Zoarces* (Zoarcidae, Pisces) *Russian Journal of Genetics*, 44 (7): 799-807.

Radchenko, *O*. A., Chereshnev, I. A., Nazarkin, M. V., Petrovskaya, A.V and Chegodaeva, E.A. (2008b) Restriction Fragment Variation of the Mitochondrial

Gene of Cytochrome b in Some Taxa of the Eelpout Family (Pisces, Perciformes, Zoarcidae) from the Northern Sea of Okhotsk, *Genetika*, 44 (1): 112-119.

Radchenko, O. A., Chereshnev, I. A., Nazarkin, M. V., Petrovskaya, A. V. and Chegodaeva, E. A. (2008c) Relationships Among Several Species of the Subfamily Gymnelinae (Zoarcidae) Inferred from Mitochondrial DNA Sequence Analysis. *Russian Journal of Marine Biology*, 34 (2): 126-130.

Radchenko, O.A., Chereshnev, I.A. and Petrovskaya, A.V. (2009) Relations and Divergence of Some Taxa of the Subfamily Lycodinae (Zoarcidae, Pices) Based on Molecular-Genetic and Morphological Data. *Journal of Ichthyology*, 49 (8): 585-598.

Regan, C.T. (1912) The classification of the blennioid fishes. *The Annals and Magazine of Natural History*, 10(ser. 8): 265-280.

Regan, C.T. (1913) The Antarctic fishes of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh*, 49: 229-292.

Regan, C.T. (1914) Fishes. British Antarctic Terranova Nova Expedition 1910. *Natural History Reports, Zoology*, 1: 1-54.

Reinhardt, J. C. H. (1831). Bidrag til vor Kundskab om Grönlands Fiske. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1830-31: 18-24.

Reinhardt, J. C. H. (1834) Om en Grönlandsk Ulkeart. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1831-32: 4.

Reinhardt, J.C.H. (1838) Ichthyologiske bidrag til den grønlandske fauna (Ichthyological contributions to the fauna of Greenland). *Det Kongelige Danske videnskabernes selskabs naturvidenskabelige og mathematiske afhandlinger,* 7: 83-196.

Ronquist, F. and Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19: 1572-1574.

Rosen, D.E. and Patterson, C. (1969) The structure and relationship of the Paracanthopterygian fishes. *Bulletin of the American Museum of Natural History*, 141(3): 357- 474.

Rosenblatt, R. H. and D. M. Cohen. (1986). Fishes living in deepsea thermal vents in the tropical eastern Pacific, with descriptions of a new genus and two new species of eelpouts (Zoarcidae). Transactions of the San Diego Natual History Society, 21 (4): 71-79.

Roule, L. (1916) Notice préliminaire sur quelques espèces nouvelles ou rares des poissons provenant des croisières de S. A. S. le Prince de Monaco. *Bulletin de l'Institute Océanographique,* 320: 1-32.

Sáez, A.G. and Lozano, E. (2005) Body doubles. *Nature*, 433: 111.

Sambrook, J., Fritsch, E. F. and Maniatis, T. (1998) Commonly used techniques in molecular cloning. In *Molecular Cloning: A Laboratory Manual*, 2nd ed.; Ford, N., Nolan, C., Ferguson, M., Eds.; *Cold Spring Harbor Laboratory Press*, pp E3-E4.

Schmidt, P. J. (1904) Fishes of the eastern seas of the Russian Empire. St. Petersburg. i–xi + 1–466, 6 pls.

Schmidt, P. J. (1936) On the genera *Davidojordania* Popov and *Bilabria* n. (Pisces, Zoarcidae). *Doklady Akademii nauk SSSR = Comptes rendus de l'Académie des sciences de l'URSS*, 1(2): 97-100.

Schmidt, P.Y. (1938) Three New Deepwater Fish from the Sea of Okhotsk. *Doklady Akademii Nauk SSSR*, 19(8): 653-656.

Schmidt, P.Y. (1950) Fish of the Sea of Okhotsk. *Akademii Nauk SSSR*, Moscow.

Schultz, L. P. (1967) A new genus and new species of zoarcid fish from the North Pacific Ocean. *Proceedings of the United States National Museum*, 122 (3598): 1-5.

Scoble, M.J. (2004) Unitary or unified taxonomy? *Philosophical Transactions of the Royal Society (Biological Sciences)*, 359: 699-710.

Seberg, O., Humphries, C.J., Knapp, S., Stevenson, D.W., Petersen, G., Scharff, N., and Andersen, N.M. (2003) Shortcuts in systematics? A commentary on DNA-based taxonomy. *Trends in Ecology and Evolution*, 18: 63–65.

Shaklee, J.B. and Whitt, G.S. (1981) Lactate dehydrogenase isozymes of Gadiform fishes: Divergent patterns of gene expression indicate a heterogeneous taxon. *Copeia*, 3: 563: 568.

Shedlock, A. M., Haygood, M. G., Pietsch, T. W., Bentzen, P. (1997) Enhanced DNA extraction and PCR amplification of mitochondrial genes from formalin-fixed museum specimens. *BioTechniques*, 22: 394-400.

Sheiko, B.A and Fedorov, V.V (2000) “Chapeter 1. Class Cephalaspidomorphi-Lampreys. Class Chondrich thyes-Cartilaginous Fish. Class Holocephali. Class Osteichthyes-Bony Fish,” in *Catalog of Vertebrates of Kamchatka and Adjacent Marine Water Areas* (Kam chat. Pechat. Dvor, Petropavlovsk Kamchatskii, 2000), pp. 7–69.

Shinohara, G. (2012) A New Deep-sea Eelpout, Pachycara moelleri (Perciformes: Zoarcidae) from Japan. *Bulletin of the National Museum of Natural Science,* (ser. A) 6: 51-58.

Shinohara, G., Nazarkin, M.V. and Chereshnev, I.A. (2004) *Magadania skopetsi*, a new genus and species of Zoarcidae (Teleostei: Perciformes) from the Sea of Okhotsk. *Ichthyological Research*, 51: 137-145.

Shinohara, G., Sakurai, H and Machida, Y. (2002) *Japonolycodes,* a new genus for *Davidijordania abei* Matsubara, 1936 (Pisces: Zoarcidae). *Marine and Freshwater Research*, 53 (2): 297-301.

Shinohara, G. and Sakurai, H. (2006) *Ericandersonia sagamia*, a new genus and species of deep-water eelpouts (Perciformes : Zoarcidae) from Japan. *Ichtyological Research*, 53(2): 172-178.

Shiozawa, D. K., Kudo, J., Evans, R. P., Woodward, S. R., Williams, R. N. (1992) DNA extraction from preserved trout tissues, *Great Basin Naturalist*, 52: 29-34.

Smith, P. J., Steinke, D., Dettai, A., McMillan, P., Welsford, D., Stewart, A. and Ward, R.D. (2012) DNA barcodes and species identifcations in Ross Sea and Southern Ocean*, Polar Biology*, 35: 1297-1310.

Smitt, F.A. (1898) Poissons de l'expédition scientifique à la Terre de Feu. II. Bihang till Kongl. *Svenska vetenskaps-akademiens handlingar*, 24 (5): 1-80.

Soldatov, V. K. (1922) On a new genus and three new species of Zoarcidae. *Ezhegodnik Zoologicheskogo Muzeya Imp. Akademii Nauk SSSR*, 23 (2): 160-163.

Soldatov, V. K. and G. U. Lindberg. (1929) On a new genus and species of the family Zoarcidae (Pisces) from the Okhotsk Sea. *Ezhegodnik Zoologicheskogo Muzeya Imp. Akademii Nauk SSSR*, 1929: 39-42.

Springer, V.G. and Johnson, G.D. (2000) Use and advantages of ethanol solution of alizarin red S dye for staining bone in fishes. *Copeia*, 2000: 300-301.

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22(21): 2688-2690.

Stepien, C.A., Dillon, A.K., Brooks, M.J., Chase, K.L. and Hubers, A.N. (1997) The evolution of Blennioid fishes based on an analysis of mitochondrial 12s rDNA. *Molecular systematics of Fishes*, 245-270.

Suvorov, E. K. (1935) A new genus and two new species of fishes of the family Zoarcidae from the Okhotsk Sea*. Bulletin de l'Academie des Sciences de l'U.R.S.S., Classe des Sciences Mathématiques et Naturelles*, 1935: 435-440.

Swainson, W. (1839) The natural history and classification of fishes, amphibians, and reptiles, or monocardian animals. London, 2: i-vi + 1-448.

Swofford, D.L. (2002) PAUP* Phylogenetical Analysis Using Parsimony (*and Other Methods). *Sinauer Associates*, Sunderland, Massachusetts.

Tamura, K., Dudley, J., Nei, M. and Kumar, S. (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24: 1596-1599.

Tautz, D., Arctander, P., Minelli, A., Thomas, R.H., and Vogler, A.P. (2003). A plea for DNA taxonomy. *Trends in Ecology and Evolution*, 18: 70-74.

Teeling, E. C., Madsen, O., Van Den Bussche, R.A., De Jong, W.W., Stanhope, M.J. and Springer, M.S. (2002) Microbat paraphyly and the convergent evolution of a key innovation in the Old World rhinolophoid microbats. *Proceedings of the National Academy of Sciences of the United State of America*, 99: 1431-1436.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G. (1997) The Clustal_X windows interface: Xexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 25: 4876-4882.

Tomo, A. P., Marschoff, E and Torno, A.E. (1977) Nueva especie del genero *Lycenchelys* Gill (Pisces, Zoarcidae) hallado en proximidades de la Isla Amberes, peninsula Antartica. *Contribuciones del Instituto Antártico* Argentino, 221: 1-9.

Toyoshima, M. (1985) Taxonomy of the Subfamily Lycodinae (Family Zoarcidae) in Japan and Adjacent Waters. Memoirs of the Faculty of Fisheries Hokkaido University, 32(2): 131-234.

Valdecasas, A.G., Williams, D. and Wheeler, Q.D. (2008). "Integrative taxonomy" then and now: a response to Dayrat (2005). *Biological Journal of the Linnean Society*, 93: 211-216.

Voskoboinikova, O.S., Chegadaeva, E.A. and Nazarkin, M.V. (2010) Comparative osteology, relationships, and systematic of fish of the genus Zoarces (Zoarcidae: Perciformes). *Journal Ichthyology*, 50: 704-717.

Voskoboinikova, O.S. and Laius, D.L. (2003) Osteological development of European eelpout Zoarces viviparus (Zoarcidae). *Journal Ichthyology*, 43: 646–659.

Vrijenhoek, R.C., Schutz, S.J., Gustafson, R.G and Lutz, R.A (1994) Cryptic species of deep sea clams (Mollusca, Bivalvia, Vesicomyidae) from hydrothermal vent and

cold water seep environments. *Deep-Sea Research Part I: Oceanographic Research Papers*, 41: 1171-1189.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. and Hebert, P.D. (2005) DNA Barcoding of Australia's fish species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360: 1847-1857.

Weitzman, S.H. (1997) Systematics of deep-sea fishes. In: Deep-sea fishes. Randall D.J, and Farrell A.P. (eds). *Academic Press*, 43-77.

Wheeler, Q.D. (2004) Taxonomic triage and the poverty of phylogeny. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, 359: 571-583

Wheeler QD, Raven PH, Wilson EO. (2004) Taxonomy: impediment or expedient? *Science*, 303- 285.

Whitley, G. P. (1931) New names for Australian fishes. *Australian Zoologist* 6(4): 310-334.

Whitley, G. P. (1951) New fish names and records. *Proceedings of the Royal Zoological Society of New South Wales*, 1949 (50): 61-68.

Whitworth. T. (1980) Zonation and geostrophic flow of the Antarctic Circumpolar Current at Drake Passage. *Deep-Sea Research*, 27: 497-507.

Wiens, J.J., Chippindale, P.T. and Hillis, D,M. (2003) When Are Phylogenetic Analyses Misled by Convergence? A Case Study in Texas Cave Salamanders. *Systematic Biology*, 52(4): 501-514.

Wilkins, J. (2006) Species concepts in modern literature: summary of 26 species concepts. *Reports of NCSE* 26 (4).

Will, KW. and Rubinoff, D. (2004) Myth of the molecule: DNA barcodes for species cannot replace morphology for identification and classification. *Cladistics*, 20: 47-55.

Wu, C. I. and Li, W. H. (1985) Evidence for higher rates of nucleotide substitution in rodents than in man. *Proceedings of the National Academy of Sciences of the United State of America*, 82: 1741-1745.

Yarrell, W. (1841). A History of British Fishes, second edition John van Voorst, London, 1: xlvii + 464, 2: 628.

Yarrell, W. (1859). A History of British Fishes, third edition John van Voorst, London, 1: xxxviii+ 675, 2: 670.

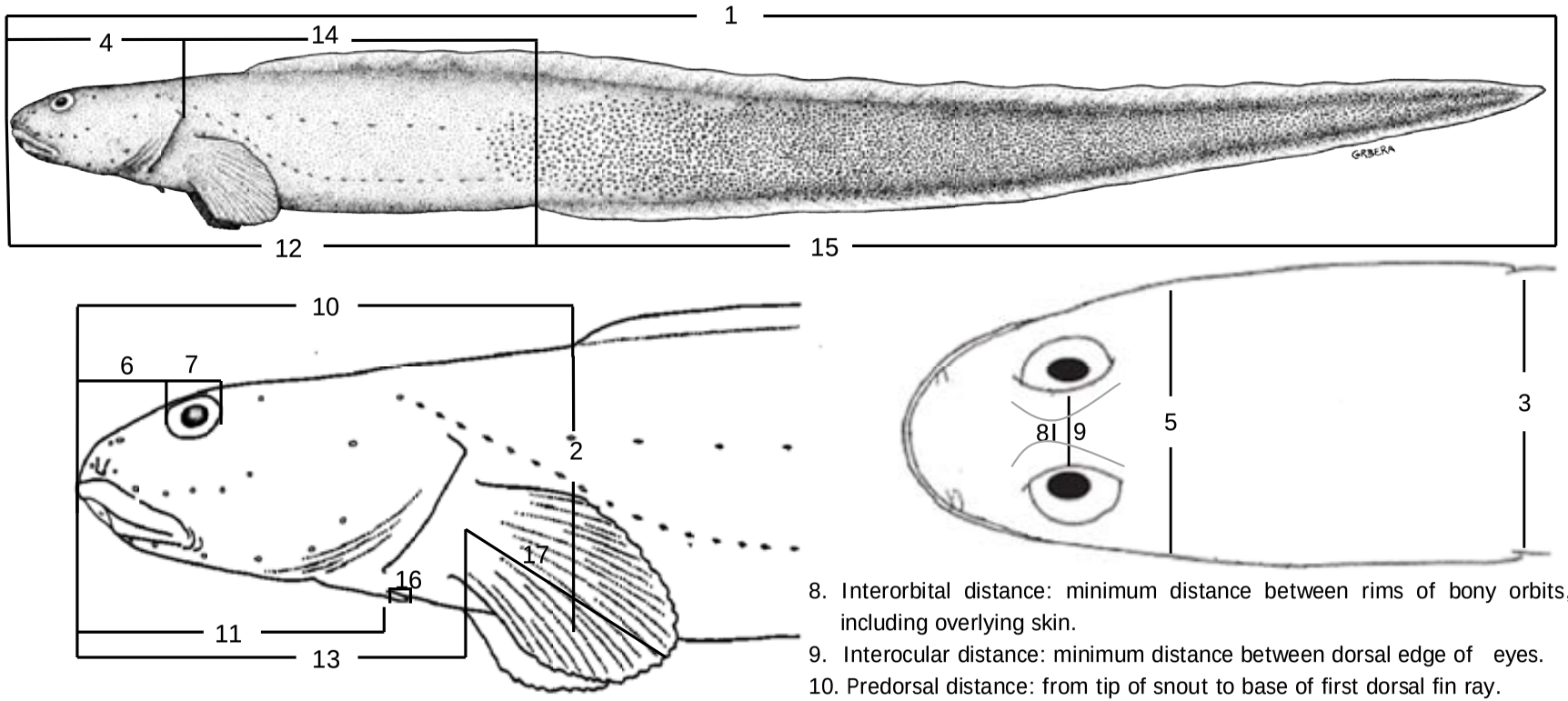
Zhuang, X. and Cheng, C.H.C (2010) ND6 gene "lost" and found: evolution of mitochondrial gene rearrangement in Antarctic Notothenioids. *Molecular Biology and Evolution*, 27(6): 1391-1403.

Zuckerkandl, E. and Pauling, L. (1965) Evolutionary divergence and convergence in proteins. Pages 97-166 in Evolving genes and proteins (V. Bryson, and H. Vogel, eds.). *Academic Press, New York.*

Zugmayer, E. (1911a) Diagnoses des poissons nouveaux provenant des campagnes du yacht "Princesse-Alice". (1901 à 1910). *Bulletin de l'Institute Océanographique*, 193: 1-14.

Zugmayer, E. (1911b) Poissons provenant des campagnes du yacht "Princesse-Alice". *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince*, 35: 1-174.

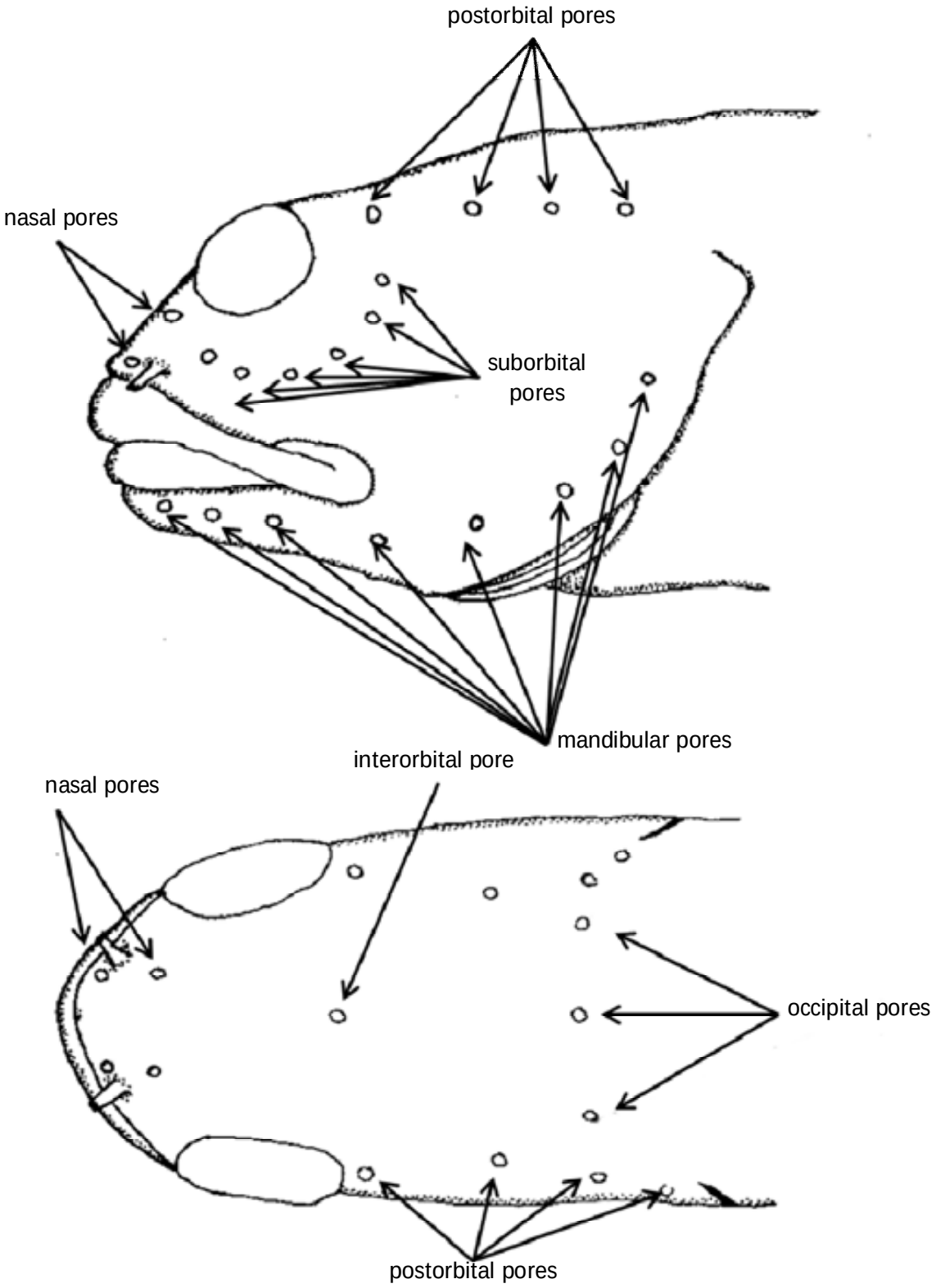
ANNEXES



Annex 1. Scheme of measurements used (Modified from Gosztonyi, 1977)

1. Total length: from tip of snout to end of caudal fin.
2. Body depth: maximum distance between dorsal and ventral profile of body.
3. Body width: horizontal distance through pectoral fin base.
4. Head length: from tip of snout to most posterior tip of gill cover.
5. Head width: maximum transverse horizontal distances across the cheeks.
6. Snout: from tip of snout to anterior vertical edge eye.
7. Eye length: maximum horizontal distance between anterior and posterior edge of eye.
8. Interorbital distance: minimum distance between rims of bony orbits, including overlying skin.
9. Interocular distance: minimum distance between dorsal edge of eyes.
10. Predorsal distance: from tip of snout to base of first dorsal fin ray.
11. Preventral distance: from tip of snout to a horizontal line joining the bases of the ventral fins.
12. Preanal distance: from tip of snout to base of first anal fin ray.
13. Prepectoral distance: from tip of snout to midpoint of pectoral fin base
14. Trunk length: from posterior end of gill cover to base of first anal fin ray
15. Tail: from base of first anal fin ray to end of caudal fin.
16. Ventral fin length: from insertion to distal tip.
17. Pectoral fin length: from mid point of base to end of longest ray.

ANNEX 2



Annex 2. Typical head pore pattern of Zoarcidae. (Modified from Anderson, 1982)

The aim of this thesis is to contribute to the knowledge of the diversity and the phylogeny of subfamily Lycodinae. Four studies have been carried out to achieve our specific goals.

After examining material collected in the Magellan Province. Two new genera (*Patagolycus* and *Argentinolycus*) have been described and *Iluocoetes* has been redescribed. Furthermore, three new species have been described, *Santelmoa fusca* and *Santelmoa antarctica* from the Southern Ocean, and *Pachycara matallanasi* from the Solomon Sea.

Finally, we present a phylogeny of Lycodinae using molecular and anatomical data.

UAB