

CEPHALPOD BEAK GUIDE FOR THE SOUTHERN OCEAN: an update on taxonomy

J. C. Xavier & Y. Cherel





**British
Antarctic Survey**

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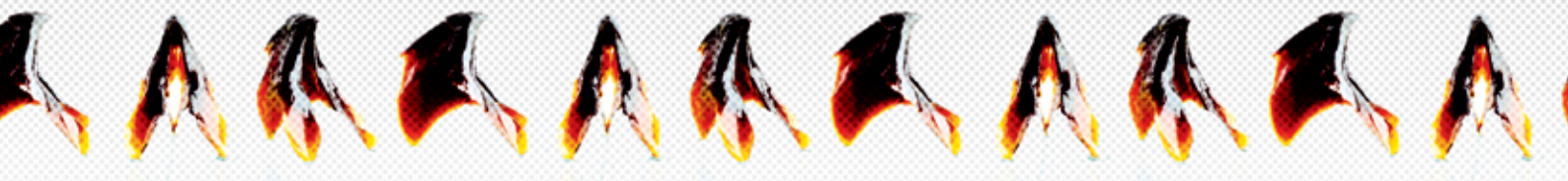
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“This book is dedicated to Malcolm Clarke”



CEPHALOPOD BEAK GUIDE FOR THE SOUTHERN OCEAN: an update on taxonomy

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Cover: the chiroteuthid squid *Chiroteuthis veranyi*

Chapters: the gonatid squid *Gonatus antarcticus*

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INTRODUCTORY NOTE

The research in Southern Ocean cephalopods is always an ongoing work. There were three main reasons to publish an updated book on beaks from Southern Ocean cephalopods: Firstly, our motivation is that the guide is used in the future without providing confusion on species taxonomy, Secondly, various mistakes on the original printed version of this book were identified and needed correction; and finally, there were considerable changes in the taxonomy of various species recently updated (see Cherel 2020). Therefore, this new guide revisits the names of many beaks of cephalopods from the Southern Ocean (see Table 3), whose backbone of the structure of the book is untouched. We encourage colleagues to keep inform us on their research in this field, on new allometric equations for specific species and any further that can contribute to a later version of this book in the future.

José Xavier & Yves Cherel (March 2021)

PREFACE

Cephalopods play a key role in global marine ecosystems. They occupy a wide range of habitats, are voracious predators and are important in the diet of numerous higher predators. To understand the feeding ecology of their predators, it is essential to identify the indigestible cephalopod beaks in the predator gut contents. Early research on beaks was based on material collected from whales during the industrial whaling era in the first half of the 20th century and the field was led by Malcolm Clarke at the National Institute of Oceanography, working largely with material from the Southern Ocean.

Clarke's book on identifying cephalopod beaks was published more than 35 years ago and since then much new knowledge has emerged. There is therefore a need for an updated catalogue for identification purposes, that includes all the new material. This book was written during the International Polar Year (IPY) 2007-08 and arose from two core projects: Integrating Climate and Ecosystem Dynamics (ICED) and the Census of Antarctic Marine Life (CAML), which included work on cephalopod beaks from the Southern Ocean. It's scope is comprehensive and circumpolar; it updates methods of identification and includes detailed 3-D images of the key species. Until now most research has focussed on the lower beak for identification purposes. This book includes data on both upper and lower beaks

providing new and useful information. It also includes an up to date review of the role of cephalopods in the diet of Southern Ocean predators including seals, whales, penguins, albatrosses and fish.

This new guide will be an essential identification tool for ecologists working on the diets of higher predators. Nevertheless it is clear that there are still cephalopod beaks being found in predator diets that belong to species that are unknown to science. There is therefore a continuing need for shipboard scientific cruises using innovative methods to catch bigger and faster cephalopods to complement data obtained from predators. In recent years development of satellite tracking techniques for marine predators has made it possible to determine the distribution of cephalopods caught by these predators. This has advanced our knowledge, particularly of poorly known species. It is now necessary to develop integrated research projects, focused on inter-disciplinary science, to understand the response of ecosystems to global climate change. Shipboard research cruises combined with higher predator tracking studies and carefully executed dietary analyses will continue to make important contributions in this field.

This book will make an essential contribution to the development of knowledge about the role of cephalopods in the Southern

Ocean ecosystem and will stimulate further research in this exciting field of marine ecology.

Prof. Paul Rodhouse
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INTRODUCTION

Cephalopods play an important role in the Antarctic ecosystem, being consumed by a wide range of predators such as whales, fish, seals, albatrosses and penguins. To understand predator-prey interactions between top predators and cephalopods, effort has been put into the development of methods to determine the identity and size of world cephalopods using beaks since the 1950s (Clarke 1962a, b; Clarke 1966; Clarke 1977; Clarke 1980; Clarke 1986; Kubodera & Furuhashi 1987; Fiscus 1991; Smale *et al.* 1993; Xavier *et al.* 2007). The most used beak guide worldwide (Clarke 1986) is now out of print and is in need of urgent revision with additional material (Santos *et al.* 2001). Also, several new cephalopod species for the Southern Ocean have been recently described taxonomically, whose beaks need to be described and/or included in a guide (e.g. Collins & Henriques 2000; Lipinski 2001; Allcock & Piertney 2002).

New efforts in the Southern Hemisphere allowed a new cephalopod beak guide to be produced (Lu & Ickeringill 2002), covering 75 species of cephalopods in Australian waters. Also new internet technology has been used to create a website to aid beak identification (<http://research.kahaku.go.jp/zoology/Beak-E/index.htm>) for Japanese waters.

However, a cephalopod beak guide for the entire Southern Ocean is nonexistent and urgently needed.

Here, we specifically aim to describe the main cephalopod beaks from species found in the diet of predators from the Southern Ocean (defined as south of the Subtropical Front) and adjacent waters in order to assist scientists and students interested in identifying cephalopods by the means of their beaks. Special attention was paid to providing photographs of typical beaks found in the diets of adults and juveniles when relevant. As a new tool applied to marine ecology, 3-D computer images of the most important lower beaks are also provided, where it is possible to rotate each beak 360 degrees and zoom in and out of particular key features of beaks in three dimensions. In addition, a review of the allometric regressions available is provided in order to relate cephalopod beak size to mantle length and mass as well as a review of the predators feeding on those cephalopod species.

PROCEDURE FOR SORTING AND IDENTIFYING BEAKS

Each cephalopod researcher has his own way to sort and identify beaks (for instructions for the collection and preservation of cephalopod beaks see Clarke (1986)). Identifying cephalopod beaks is an arduous task that requires spending a long time analyzing the morphological characteristics of beaks, comparing your beaks with others in reference collections and using guides. Identification keys can be used to help identify cephalopod beaks (Clarke 1986) but some researchers do not use them, and others, as they get more familiar with the species that they encounter in their region, prefer to use their beak collection, and beak guide photos, to confirm identification. Be aware, nevertheless, that even with this guide, it is extremely important to compare your beaks with beaks from reference collections and to get expert advice, before attributing a name to a beak.

To become familiar in sorting and identifying beaks from your region, here are a few suggested steps to follow.

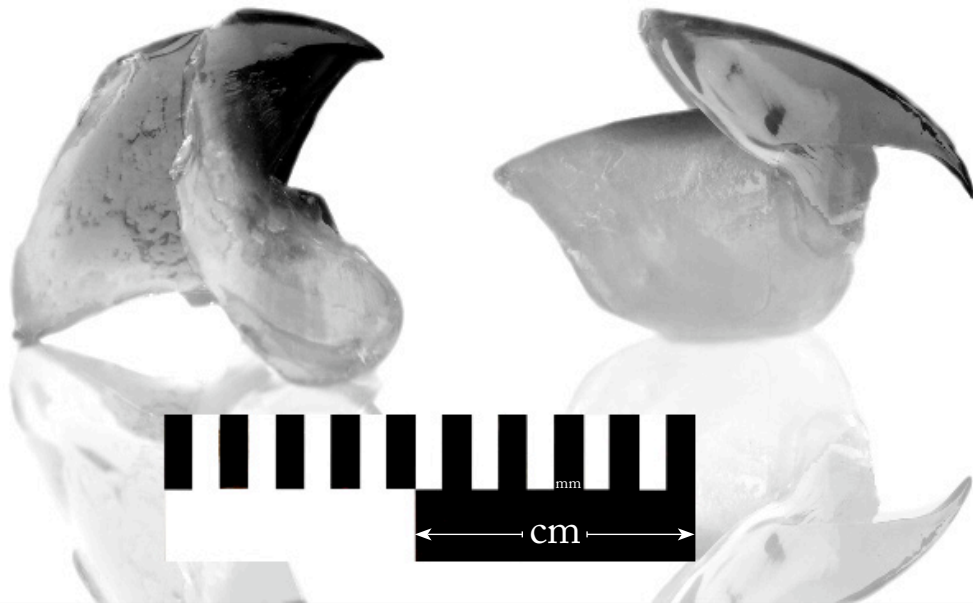
Firstly, have access to a large number of beaks, ideally from the diet of a single predator species that feeds on large cephalopods (larger beaks are easier to identify). It is advisable to register fresh beaks (e.g. beaks recently consumed by predators that still have flesh attached,

beaks in buccal masses or from complete or partially completed specimens. See examples of fresh beaks in Figure 1 and of old, eroded beaks of *Histioteuthis macrohista* in Figure 13) in order to assess if those beaks were consumed recently or not.

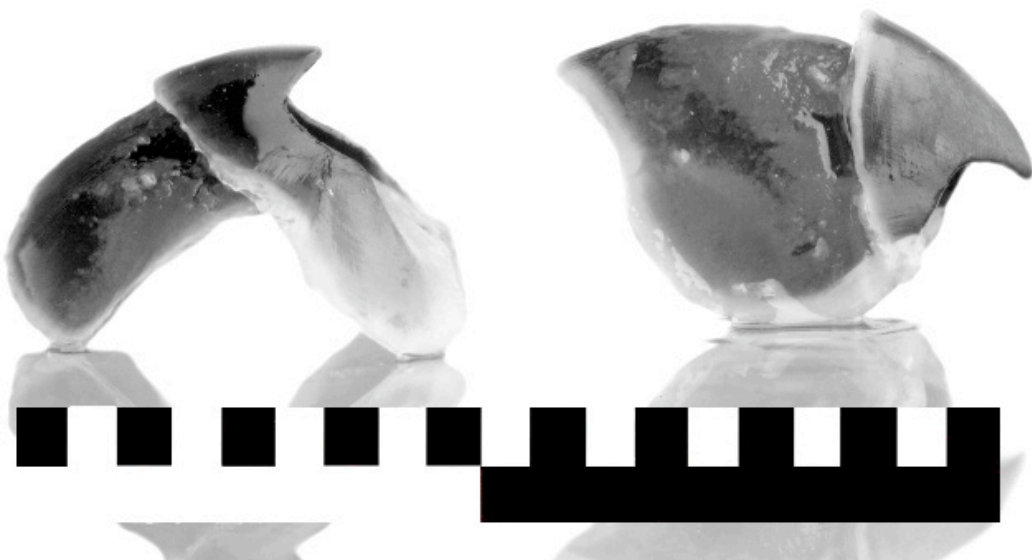
If possible, keep buccal masses because:

1. they have a radula, which may be useful in identifying the cephalopod species;
2. they can be used for genetic analysis (if frozen or fixed in ethanol; to confirm identification) or stable isotopic studies (for food web dynamics); and
3. they enable one to relate both upper and lower beaks (see more below), important for identification studies when beaks of cephalopod species can be found loose in the diet of predators;

When dealing with buccal masses or loose beaks, it is very important to spend considerable amount of time on separating the beaks according to their morphology, in order to get your eyes familiar with the features of the beaks. As a first step, separate upper and lower beaks (Figure 1). Then, within those, group beaks of similar morphology together. At present, most of the identification work is done on lower beaks due to their more obvious features (Clarke 1986) but upper beak identification can also be used.



• Lower (on the left) and upper (on the right) squid beaks. *Todarodes* sp.



• Lower (on the left) and upper (on the right) octopus beaks. *Pareledone turqueti*

Figure 1. Profiles of upper and lower beaks of cephalopods. Scale, which should be applied for all cephalopod photo images, is also shown. For fresh loose beaks, look at the outer parts of the beaks (i.e. edges of the wings, lateral wall and hood), which should be transparent.

Secondly, try to identify each group to a species level (where possible) using cephalopod beak guides, reference collections, biodiversity information of the cephalopod fauna and distribution atlases (e.g. Xavier *et al.* 1999) and information

about the biology of the cephalopod species of the study region (Tables 1, 2). It is not unusual to be unable to give a name to a beak. Indeed, a great majority of studies (if not all!), include unidentifiable or immeasurable beaks. Getting beaks from

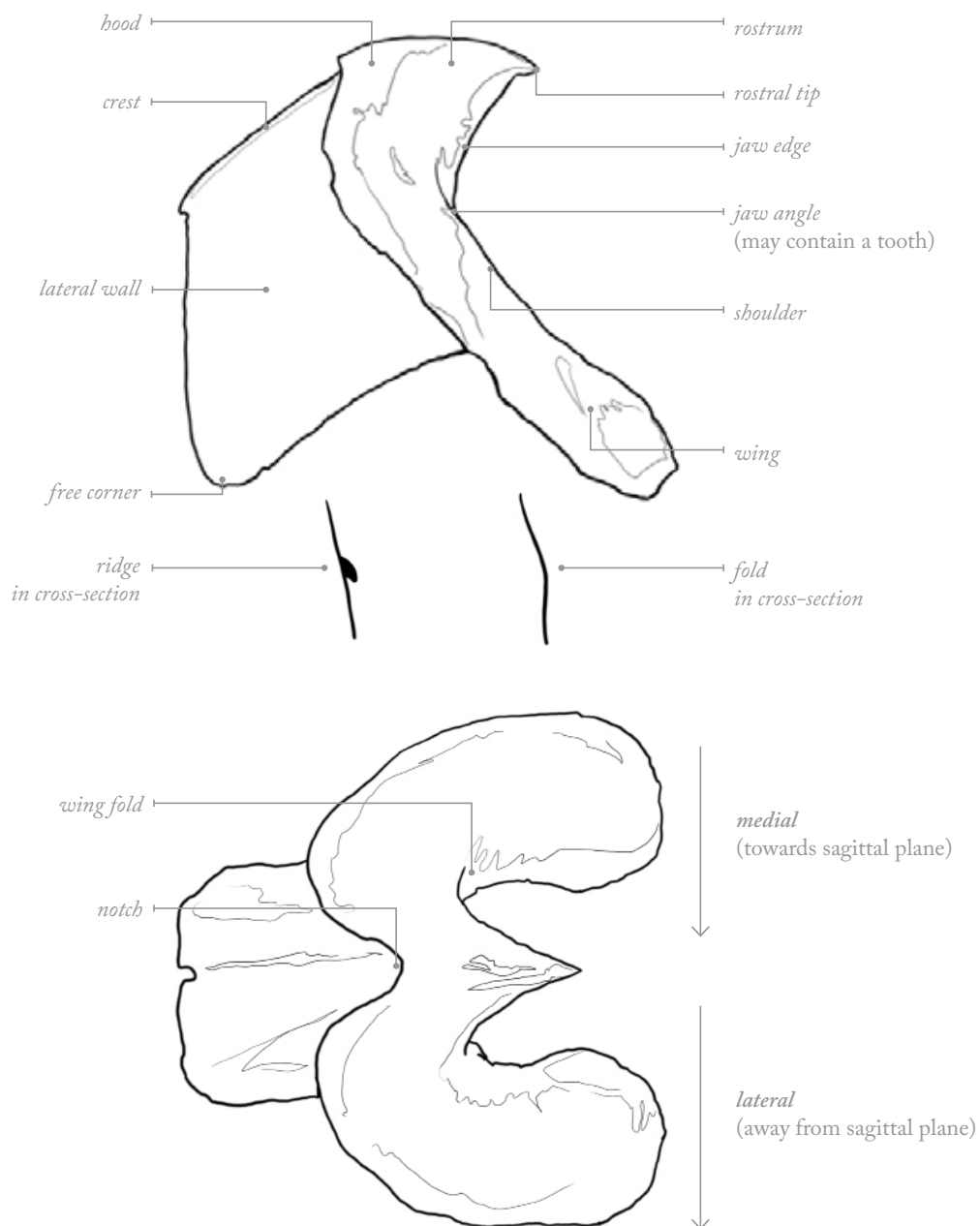


Figure 2. Principal terms used to characterize decapod beaks (following Clarke 1986).

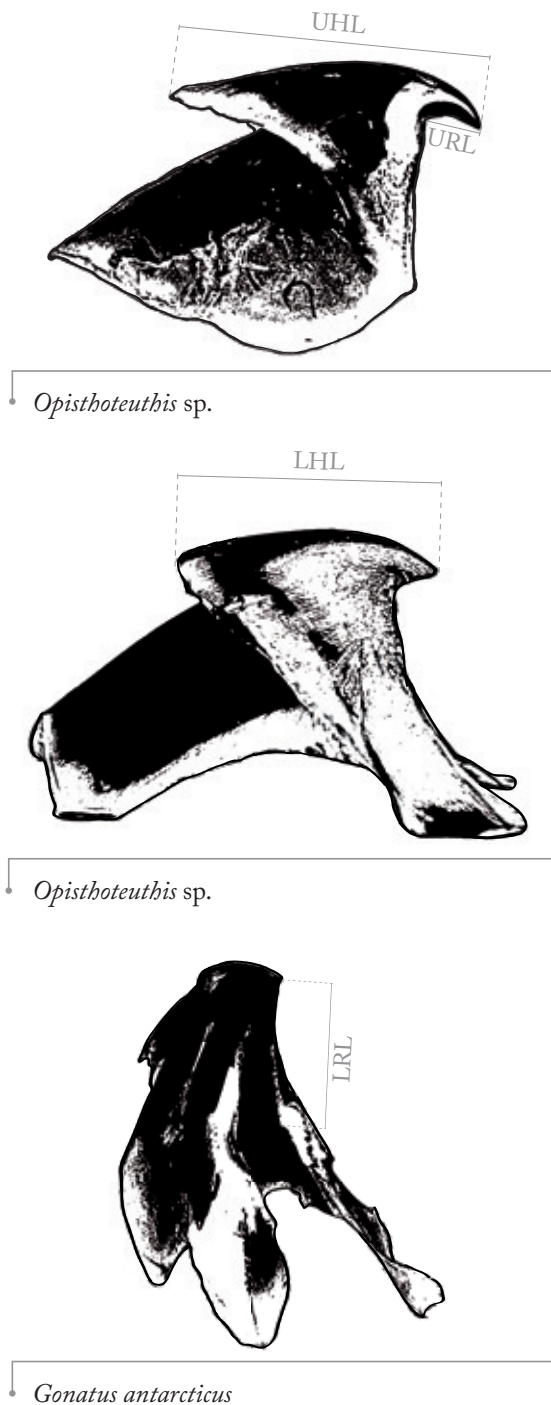


Figure 3. Key measurements of cephalopod beaks. Squid lower beaks are usually measured using the lower rostral length (LRL), from the rostral tip to the jaw angle. Octopod and sepiolid lower beaks are usually measured by the lower hood length (LHL), from the rostral tip to the edge of the hood. For upper beaks, the upper hood length (UHL) and upper rostral length (URL) are mostly used.

other cephalopod predators from the same study region can be useful as an unknown eroded beak in the diet of one predator can be a very common beak in the diet of another predator.

Thirdly, work with an experienced beak expert to confirm or correct your identifications. It is advisable not to publish data without it being double checked by an expert. It is also important to go back and review which features you should be aware of when looking at a specific species beak, using specific beak terminology (Figure 2), when new beaks from other collections are available. For further discussion on the terminology used to describe the characteristics of cephalopod beaks see Clarke (1986).

To facilitate the identification of beaks, it is valuable to assess first the general shape, rostrum shape, presence or absence of a fold or ridge on the lateral wall, shapes of the beak behind the hood/groove and the characteristics of the jaw and level of darkening of the beaks (to assess if it is from a juvenile/sub-adult or adult; useful to determine if that particular species reaches large sizes; Table 2), comparing beaks of the same size is useful if there is access to a reference collection. Checking maximum species sizes, and known geographical position, is also helpful to exclude species of the same family (e.g. within histioteuthids). The lower rostral length (LRL) of the

lower beaks of squid and lower hood length (LHL) of octopods, and upper hood length (UHL) or upper rostral length (URL) from squids and octopods for upper beaks, are usually measured (Figure 3). Attention should be paid when measuring the LRL, as it should be measured from the inside of the lower beak rather than from the outside (Figure 3). When measuring beaks, it poses an excellent opportunity to double-check the identification of the cephalopods.

Fourthly, after confirming the identification of the cephalopod beaks with an expert, it is good to exchange beaks with colleagues to improve your own collection and double check identifications. Therefore it is essential to go back to the laboratory regularly to identify beaks so that you do not lose touch with identifying them (it is so easy to forget after being away for months!) even if you have really good notes. Also, do not discard them as they can be important for future studies (e.g. to double-check identifications, for new reference collections, and for stable isotopic studies).

Although upper beaks are less for identification, their overall shape and morphology can be species specific and very distinctive (e.g. *Architeuthis*, *Taonius notalia*), and can provide valuable biological information. In species that do not feed heavily on cephalopods, upper and lower

beaks may come in pairs and can provide immediately provide good information for future identification studies on how the upper or lower beaks of a certain species looks (ideally when in buccal masses). Also, as the number of upper and lower beaks differ in the diets of predators (when they should be the same), it is relevant to understand which mechanisms are affecting the presence of beaks in the diets (Cherel *et al.* 2004; Xavier *et al.* 2005).

THE STRUCTURE OF THE BOOK

Families are ordered alphabetically. The general family beak identification characteristics are based on the lower beaks of the most important cephalopod species that are present in the diet of predators from the Southern Ocean only. The photos of lower and upper beaks are provided to further assist in identification of these type of beaks. In addition, 3-D images of beaks of key cephalopod species are also provided.

The image features three cephalopod skulls, likely from the genus Nautilus, arranged in a horizontal line. The skulls are shown in profile, facing right. The first skull on the left is the largest and most detailed, showing the internal structure of the nautilus chamber, including the siphon and the eye. The second skull in the middle is smaller and less detailed, and the third skull on the right is the smallest and most faded. The background is a light, neutral color, and the skulls are rendered in a dark, muted tone, creating a sense of depth and focus on the anatomical details.

CEPHALPOD TAXONOMY

DECAPODA

- » FAMILY ANCISTROCHEIRIDAE
- » FAMILY ARCHITEUTHIDAE
- » FAMILY BATHYTEUTHIDAE
- » FAMILY BATOTEUTHIDAE
- » FAMILY BRACHIOTEUTHIDAE
- » FAMILY CHIROTEUTHIDAE
- » FAMILY CRANCHIIDAE
- » FAMILY CYCLOTEUTHIDAE
- » FAMILY GONATIDAE
- » FAMILY HISTIOTEUTHIDAE
- » FAMILY LEPIDOTEUTHIDAE
- » FAMILY LOLIGINIDAE
- » FAMILY LYCOTEUTHIDAE
- » FAMILY MASTIGOTEUTHIDAE
- » FAMILY NEOTEUTHIDAE
- » FAMILY OCTOPOTEUTHIDAE
- » FAMILY OMMASTREPHIDAE
- » FAMILY ONYCHOTEUTHIDAE
- » FAMILY PHOLIDOTEUTHIDAE
- » FAMILY PSYCHROTEUTHIDAE
- » FAMILY SEPIOLIDAE

FAMILY ANCISTROCHEIRIDAE Figure 4 | pages 53 & 83

Family identification:

- » Obtuse jaw angle
- » Broadly rounded
- » Small rostrum which often has a protruding tip
- » Prominent fold in the lateral wall, running to about halfway between the crest and the free corner
- » Broad, and often curled-up, wings

The only species likely to be found is:

Ancistrocheirus lesueurii

$ML = -41.3 + 40.75LRL$; $\ln M = -0.194 + 3.56 \ln LRL$ (n=23 for ML, n=21 for M) (Clarke 1986)

The subtropical squid species *A. lesueurii* is found in small numbers in the diet of sperm whales, albatrosses and petrels (Table 1).

Practical procedures to differentiate the lower beaks of this species:

Ancistrocheirus lesueurii. Easily identifiable by its medium-large size, long wings, very small hood and well defined fold in the lateral wall. Often large, potential for confusion with *M. longimana*, but its hood is much shorter than the crest, with a deep broad notch, very long broad wings, “pulled forward” so flat when seen from the front and has a fold on lateral walls running to posterior edge.

FAMILY ARCHITEUTHIDAE Figure 5 | pages 53 & 83

Family identification:

- » Smooth lateral wall with no ridge or marked fold
- » Very broad hood
- » Thickened crest
- » Long wings
- » Has a shoulder tooth
- » Short rostrum with often a slightly curved rostral tip
- » Beaks can reach large sizes
- » Beaks are soft, not very dark and generally flexible

The only species likely to be found is:

Architeuthis dux

$ML = -55.6 + 59.31LRL$; $\ln M = -1.773 + 4.57 \ln LRL$ ($n=11$ for ML ; $n=9$ for M) (Clarke 1986)
 For relationships between ML and LRL , $ML = 10^{(\log ML = (LRL + 19.3)/11.2)}$ ($n=43$) might be better (Roeleveld 2000) with ML = mantle length (in mm), M = mass (in g) and LRL = lower rostral length (in mm).

This subtropical/temperate species occurs in small numbers in the diet of predators from South Georgia and Kerguelen, including wandering albatrosses and sharks (Table 1) (Xavier *et al.* 2003b; Cherel & Duhamel 2004).

Practical procedures to differentiate the lower beaks of this species:

Architeuthis dux. Easily identifiable by its large size, darkens at a large size (Table 2), by the large shoulder tooth and by having a broad hood. It is not very dark when mature, unlike *Mesonychoteuthis hamiltoni*.

FAMILY BATHYTEUTHIDAE Figure 6 | pages 54 & 84

Family identification:

- » Obtuse jaw angle
- » Broad hood with no notch
- » Lateral walls with no fold or ridge

The only species likely to be found is:

Bathyteuthis abyssicola

$ML=1.68+51.59LRL$; $\ln M=2.855+3.38\ln LRL$ (n=17 for both ML and M) (Clarke 1986)

This deep-sea species is cosmopolitan in its distribution and is extremely rare in the diets of top predators (Sekiguchi *et al.* 1993; Clarke & Goodall 1994).

Practical procedures to differentiate the lower beaks of this species:

Bathyteuthis abyssicola lower beak is easily identifiable by having a broad hood and by being generally a small beak. Drawings of beaks of this species appear in Clarke (1986) and Lu & Ickeringill (2002).

FAMILY BATOTEUTHIDAE Figure 7 | pages 54 & 84

Family identification:

- » Sharp slightly thickened fold at the lateral wall
- » Narrow beak

The only species likely to be found is:

***Batoteuthis skolops* (no specific equations)**

May use formulas for close families

$ML = 11.4 + 24.46LRL$; $\ln M = -0.241 + 2.7 \ln LRL$ (n=23 for ML, n=14 for M) (Clarke 1986),
based on *Chiroteuthis* spp. formulas

$ML = -1.8 + 29.08LRL$; $\ln M = 0.184 + 2.88 \ln LRL$ (n=47 for ML, n=45 for M) (Clarke 1986),
based on *Mastigoteuthis* spp. formulas

This Antarctic circumpolar species is present in the diet of Patagonian toothfish (Xavier *et al.* 1999; Cherel *et al.* 2004), black-browed, grey-headed and yellow-nosed albatrosses (Cherel *et al.* 2000, 2002c), but rarely in high numbers (Table 1).

Practical procedures to differentiate the lower beaks of this species:

Batoteuthis skolops. It has a short crest and a fold on the lateral wall, unlike *Mastigoteuthis psychrophila*, which has a very thickened fold (in certain cases looking like a ridge, mostly under the groove). Could be confused with *Chiroteuthis veranyi*, but the hood is much bigger in relation to the size of the crest (whereas in *C. veranyi*, the size of hood and crest is far more similar). It is characterized by having a unique jaw, which the “pseudo-tooth” never links to the shoulder of the beak, similar to a small channel. This does not occur in *M. psychrophila*.

FAMILY BRACHIOTEUTHIDAE Figure 8 | pages 55 & 85

This family is in need of revision world-wide. Beaks from brachioteuthid squids were identified under various names until the preliminary description of two species from the Southern Ocean (Lipinski 2001). Examination of beaks from the two species allowed us to clarify their identification (Cherel *et al.* 2004).

Family identification:

- » Beaks are usually small (LRL usually < 4.0 mm; *Slosarczykovia circumantarctica* is generally smaller than *Brachioteuthis linkovskyi*)
- » Narrow rostrum
- » Distinctly thickened crest
- » Small wings
- » Hood slightly longer than crest
- » Curved rostral edge protruding forwards in sharp tip

Two species may be found and are provisionally referred to as:

***Brachioteuthis linkovskyi* (no specific equations)**

***Slosarczykovia circumantarctica* (no specific equations)**

ML= 16.31+20.18LRL; ln M=0.55+1.41ln LRL (n= 11 for both ML and M) (Clarke 1986) for the species of the family Brachioteuthidae

Both species are present in predators from the Indian and Atlantic sectors of the Southern Ocean, including in the diet of Patagonian toothfish, squids, Antarctic fur seals, gentoo and macaroni penguins, petrels and sharks (Cooper & Brown 1990; Ridoux 1994; Berrow & Croxall 1999; Daneri *et al.* 1999; Hoff 2001; Cherel & Duhamel 2003; Xavier *et al.* 2003b; Arata *et al.* 2004; Cherel & Duhamel 2004; Cherel *et al.* 2004; Lescroël *et al.* 2004; Xavier, unpublished data). *S. circumantarctica* is however commonly encountered in food samples from many predators, and from nets, around South Georgia (e.g. Rodhouse *et al.* 1996; Collins, Stowasser and Xavier, unpublished data), whereas *B. linkovskyi* has

not been caught in nets and specimens are rarer in diets (e.g. occasionally in wandering albatrosses breeding at South Georgia, Xavier *et al.* 2003b), suggesting that the latter species is distributed further north.

Practical procedures to differentiate the lower beaks of these species:

Beak from *B. linkovskyi* has a distinct thickened ridge running towards free corner of lateral wall whereas the beak of *S. circumantarctica* has a fold on the lateral wall, relatively less distinct (Rodhouse *et al.* 1992; Cherel *et al.* 2004). Also, *B. linkovskyi* is a much darker beak than *S. circumantarctica*. *S. circumantarctica* can be confused with cranchiids such as small *Galiteuthis glacialis*.

FAMILY CHIROTEUTHIDAE Figure 9 | pages 56 & 86

Description of beaks from this family is in need of revision world-wide. Beaks from several species of chiroteuthids were described under various names (e.g. Imber 1992), but only two species were definitely identified in the Southern Ocean (Rodhouse & Lu 1998; Cherel 2020). Thus, great care is needed when giving a species name.

Family identification:

- » Very short crest relative to its hood and beaks are thin in profile (e.g. *Chiroteuthis veranyi*)
- » Distinct thickened fold running to middle of posterior edge of lateral wall
- » Obtuse jaw angle hidden in profile
- » No shoulder tooth or groove
- » Hood broadly notched in midline
- » Hood lies close to the crest

At least two species are likely to be found:

***Asperoteuthis lui* (no specific equations)**

***Chiroteuthis veranyi* (no specific equations)**

$ML = 11.4 + 24.46LRL$; $\ln M = -0.241 + 2.7 \ln LRL$ (n=23 for ML, n=14 for M) (Clarke 1986), based on *Chiroteuthis* spp. formulas

The sub-Antarctic *C. veranyi* is present in the diet of a wide range of predators, but generally in low numbers, with the exception of the Patagonian toothfish at Kerguelen (Cherel *et al.* 2004) (Table 1).

Asperoteuthis lui is known to occur in the diet of sperm whales and wandering albatrosses from South Georgia (Clarke 1980; Xavier *et al.* 2003b).

Practical procedures to differentiate the lower beaks of these species:

C. veranyi rostrum is thinner, straighter, and has smaller crest than *Asperoteuthis lui* which is bigger and has a larger, but blunter, rostrum.

FAMILY CRANCHIIDAE Figure 10 | pages 57 & 87

Family identification:

» Wide range of characteristics and most beaks can be confused with other families (Clarke 1986)

Several species can be found in Southern Ocean waters:

Galiteuthis glacialis

ML=6.676+83.785LRL; $\log M = 0.415 + 2.20 \log LRL$ (n=25 for ML and M) (Lu & Williams 1994)

***Galiteuthis suhmi* (no specific equations)**

***Liguriella podophthalma* (no specific equations)**

Mesonychoteuthis hamiltoni

ML=-12.3+61.43LRL (n=72) (Rodhouse *et al.* 1990), although the relationship is weak and therefore evaluate carefully if it applies well to your data.

***Taonius expolitus* (no specific equations)**

***Taonius notalia* (no specific equations)**

ML=-12.3+61.43LRL; $\ln M = 0.786 + 2.19 \ln LRL$ (n=72 for ML, n=74 for M) (Rodhouse *et al.* 1990) based on *Taonius* spp. formulas

Teuthowenia pellucida

ML=22.27+29.90LRL; $\ln M = 0.71 + 1.94 \ln LRL$ (n=41 for ML and M) (Lu & Ickeringill 2002)

Although some species might have equations for M, in certain cases it might be better to apply the following allometric equation for all squids in this family: $\ln M = \ln 3.24 + 2.80 \ln LRL$ (Clarke 1962b).

The Antarctic circumpolar species *G. glacialis* is one of the most common squid species in the diet of Antarctic predators, particularly important in the diet of black-browed, grey-headed and light-mantled sooty albatrosses (Cherel & Klages 1998; Cherel *et al.* 2000, 2002c; Xavier *et al.* 2003a,c). The species *Taonius notalia* is one of the most important species in wandering albatrosses at South Georgia (Xavier *et al.* 2003b) and in Patagonian toothfish at Crozet (Cherel *et al.* 2004). Large sizes of the Antarctic circumpolar squid *M. hamiltoni* are found in sperm whales (Clarke 1980) and sleeper sharks (Cherel & Duhamel 2004) but rarely found in other predators (Table 1). *Taonius expolitus*, *Liguriella podophthalma* and *Galiteuthis submi* and *Teuthowenia pellucida* are not common prey species (Clarke 1986; Young *et al.* 1997; Tremblay *et al.* 2003; Cherel *et al.* 2004).

Practical procedures to differentiate the lower beaks of these species:

Galiteuthis glacialis is a rather plain beak, with few distinctive features (lacks a distinct fold on lateral wall, ridge or shoulder tooth), a broad rostrum, hood length roughly 1:1 with crest length. *Liguriella podophthalma*, typical of Subtropical Front region, have usually their lateral walls intact when found in predators stomachs, and is relatively bigger than *G. glacialis*. *Galiteuthis submi* has a little notch in the hood (not characteristic of *G. glacialis* nor *Liguriella podophthalma*) and is also considerably bigger than *G. glacialis*. *Taonius notalia* can be confused with *Gonatus antarcticus*. Similar in general shape, however the crest of the lower beak of *Taonius notalia* is straight (slightly curved in *G. antarcticus*), has a bigger, more “inflated” hood, has a fold in the lateral wall, the bottom edge of the lateral wall is quite straight and the free corner of lateral wall is more rounded and blunt. *Taonius expolitus* is similar to *Taonius notalia* but it is considerably smaller, with wings darkened at a small size (i.e. wings are found darkened at less than 5 mm LRL). *T. pellucida* is similar to *G. glacialis* but the former species has a distinctive lateral wall fold and a smaller crest in comparison to the total length of the lateral wall. *M. hamiltoni* has a broad hood, is often large, darker and potentially confused with *M. longimana*. The key differences are the lack of a distinctive fold in the lateral wall and the more “inflated” hood in *M. hamiltoni*. The beak of *M. hamiltoni* is very dark when compared to most other squids and its lower beaks darken at large sizes (Table 2).

FAMILY CYCLOTEUTHIDAE Figure 11 | pages 60 & 90

Family identification:

- » Narrow fold at lateral wall
- » Often curved wings
- » No step at jaw edge
- » Narrow distinctive crest
- » Distinctive rostrum tip

The only species likely to be found is:

Cycloteuthis sirventi

ML= 31LRL; $\ln M = 1.89 + 1.95 \ln LRL$ (Clarke 1986)

The species is a regular prey of wandering albatrosses breeding in the Indian Ocean (Cherel & Weimerskirch 1999) (Table 1).

Practical procedures to differentiate the lower beaks of this species:

Similar to *M. longimana* but *C. sirventi* has not step on the jaw edge, it has a typical tip of the rostrum and a lighter fold in the lateral wall.

FAMILY GONATIDAE Figure 12 | pages 61 & 91

Family identification:

- » Distinctively laterally compressed beak when found in diets: lateral walls are usually close together
- » A tall beak (LRL longer than hood)
- » Fold in lateral wall (sometimes this is not well developed)
- » Bottom edge of lateral wall strongly curved
- » Hood curved, follows crest, which is also slightly curved

Two species likely to be found are:

***Gonatus antarcticus* (no specific equations)**

$ML = -43.4 + 42.87LRL$; $\ln M = -0.655 + 3.33 \ln LRL$ (n=17 for ML, n=20 for M) (Clarke 1986) based on *Gonatus* spp. formulas

The following equations is better for small beaks/specimens:

$ML = 12.82 + 19.02LRL$; $\ln M = 0.086 + 2.13 \ln LRL$ (Clarke 1986)

The Antarctic/sub-Antarctic squid *G. antarcticus* is commonly found in predator diets of the Southern Ocean, particularly in the diet of Patagonian toothfish, rockhopper and king penguins, wandering albatrosses and southern right-whale dolphins (Goodall & Galeazzi 1985; Rodhouse *et al.* 1996; Cherel & Klages, 1998; Cherel & Kooyman 1998; Xavier *et al.* 1999; Cherel *et al.* 2002b,c; Xavier *et al.* 2003b; Cherel *et al.* 2004).

***Gonatopsis octopedatus* (no allometric equations available)**

From a single lower beak found in the diet of sooty albatrosses collected at Marion Island, Imber (1978) described a new species, *Gonatus phoebetriae*, which is now *Gonatopsis octopedatus* (Cherel 2020). Drawings of beaks of this species appear in Cherel *et al.* (2020) (Figure 25).

Gonatopsis octopedatus is a rare prey of Patagonian toothfish at Crozet (Cherel *et al.* 2004).

Practical procedures to differentiate the lower beaks of this species:

Gonatus antarcticus. Can be confused with *Taonius notalia*. Free corner of lateral wall more pointed than in *Taonius notalia*. Also tall, but rather different shape, *G. antarcticus* has a less “inflated” hood, the bottom edge of the lateral wall curved, free corner of lateral wall less rounded and the crest is longer and more curved than in *Taonius notalia*. Note also that upper beaks of the two species are quite different, with the upper beak of *Taonius notalia* having a very typical long and curved rostrum. The lower beak of *G. octopedatus* is less narrow than that of *G. antarcticus*. It has a well-defined inner-wing notch, which is an obvious diagnostic feature from above and in a frontal view.

FAMILY HISTIOTEUTHIDAE Figure 13 | pages 62 & 92

Family identification:

- » Distinct, or shallow, notch in the posterior dorsal edge of hood
- » Have a well developed ridge (*Histioteuthis* A) or weakly developed ridge (*Histioteuthis* B) along the lateral wall - Rostrum tip is typically curved
- » Beaks are usually small - medium in size

This family comprises various species in the Southern Ocean that are divided into two types of beaks, A and B (see Clarke 1986):

- » *Histioteuthis* A, which has a deep notch in back of hood and a well-developed ridge running to free corner of lateral wall:

***H. arcturi* (no specific equations)**

H. bonnellii corpuscula

ML=17.1+8.99LRL (n=19) (Clarke 1986)

ML=1.82+15.24LRL; ln M= 1.16+2.70lnLRL (n=21 for ML and M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

H. macrobista

ML=2.36+14.46LRL; ln M= 1.16+2.72lnLRL (n=8 for ML and for M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

H. miranda

ML=-7.0+25.82LRL; ln M=1.783+2.44ln LRL (n=27 for ML, n=14 for M) (Clarke 1986)

ML=-26.51+34.21LRL; ln M= 0.86+3.04lnLRL (n=31 for ML, n=22 for M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

» *Histioteuthis B* has a shallow notch in back of hood and a weakly-developed ridge under the hood (evident in *H. atlantica* juveniles) that becomes a slight fold running to free corner of lateral wall:

H. atlantica

$ML = -10.42 + 25.66LRL$; $\ln M = 1.49 + 2.45\ln LRL$ (n=21 for ML, n=19 for M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

H. eltaninae

$ML = -3.65 + 24.48LRL$; $\ln M = 0.33 + 3.11\ln LRL$ (n=6 for ML, n=5 for M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

Histioteuthis arcturi occurs in Atlantic sector of the Southern Ocean waters (also known as *Histioteuthis A5* (Clarke, 1986)) and *Histioteuthis hoylei* might occur in Indian sector of the Southern Ocean waters. These species can be confused with *Histioteuthis bonnellii bonnellii*, which does not occur in the Southern Ocean (Voss *et al.* 1998).

Within the histioteuthids, the Antarctic/sub-Antarctic circumpolar squid *H. eltaninae* is far more common in predators, being important in the diet of wandering, grey-headed, sooty and light-mantled sooty albatrosses (Cherel & Klages 1998). The sub-Antarctic circumpolar *H. atlantica* is an important prey of porbeagle sharks at Kerguelen (Cherel & Duhamel 2004). The other species are less common in predators and mostly distributed north of the Subtropical Front (STF) (Imber 1992; Xavier *et al.* 1999).

Practical procedures to differentiate the lower beaks of these species:

Histioteuthis A.

Histioteuthis miranda is similar to *H. macrohista* but the former species has a distinct shoulder groove and a ridge of the lateral wall that goes continuously to the end of the free corner of the lateral wall. *H. miranda* reaches a larger size than *H. macrohista*. *H. macrohista* has a more curved rostral tip than *H. bonnellii corpuscula*. *H. arcturi* tends to be more deeper than longer, with a very obvious ridge (also called a keel) under the hood.

***Histioteuthis* B.**

Beaks of *Histioteuthis eltaninae* and *H. atlantica* are easily confused. *H. eltaninae* is rounded in profile whereas *H. atlantica* is taller, has a small ridge in the lateral wall beneath the hood, jaw edge is straighter and crest is generally longer. Although the lower beaks of both species overlap in size, *H. atlantica* is usually bigger (Clarke 1986; Rodhouse *et al.* 1987). Note that small beaks of *H. atlantica* have a distinct ridge on the lateral wall under the hood, thus looking like, from a first quick glance from inexperienced eyes, beaks of *Histioteuthis* A.

FAMILY LEPIDOTEUTHIDAE Figure 14 | page 64

Family identification:

- » Very low wing (and thickened) fold
- » Narrow rostrum
- » Long jaw angle
- » Hood deeply notched
- » Shallow groove at hood's surface
- » Lateral wall with a deep notch to the sides of the crest and a prominent, slightly thickened fold.

The only species likely to be found is:

Lepidoteuthis grimaldii

ML=36.2LRL; $\ln M = -0.17 + 3.0 \ln \text{LRL}$ (British Antarctic Survey, unpublished data)

ML=-10.60+50.57LRL (n=2, using total weight of preserved specimens) (Lu & Ickeringill 2002) but this relationship is obviously not strong.

The tropical/subtropical squid *L. grimaldii* is rarely found in high numbers in the diet of Southern Ocean predators (Table 1).

Practical procedures to differentiate the lower beaks of this species:

Lepidoteuthis grimaldii. Can be confused with *M. longimana* and *T. danae*. It has a thickened fold (unlike *M. longimana*), has a large notch in posterior edge of lateral wall and a shallow groove in rostrum that mirrors the underlying thickened fold in lateral wall (unlike *T. danae*).

FAMILY LOLIGINIDAE Figure 15 | pages 65 & 94

Family identification:

- » Obtuse jaw angle
- » Broad rostrum
- » No distinct fold or ridge on lateral wall
- » Jaw edge with sometimes indentation, particularly in smaller sizes

The only species likely to be found is:

Doryteuthis gahi

$\ln ML = 4.23 + 1.01 \ln LRL$; $\ln M = 2.25 + 2.39 \ln LRL$ (n=446) (British Antarctic Survey, unpublished data)

This sub-Antarctic species is particularly important in predators foraging at the Patagonian shelf (South America) such as black-browed albatrosses, sea lions, penguins and Commerson's dolphins (Thompson 1992; Clarke & Goodall 1994; Alonso *et al.* 2000; Clausen & Pütz 2003; Xavier *et al.* 2003b; Herling *et al.* 2005).

Practical procedures to differentiate the lower beaks of this species:

Doryteuthis gahi is generally a very small beak, easily identifiable by the indentated jaw angle.

FAMILY LYCOTEUTHIDAE Figure 16 | pages 65 & 95

Family identification:

- » Thick, well developed lateral wall ridge
- » Beaks usually dark in adults
- » Shoulder forming a slight tooth
- » Short crest

The only species likely to be found is:

Lycoteuthis lorigera

$ML = -13.04 + 34.56LRL$; $\ln M = 0.32 + 3.00 \ln LRL$ (n=45 for ML and M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

This subtropical species is present in the diet of predators from the Indian, Pacific and Atlantic Oceans, including catsharks in South Africa, tuna in the Tasman sea, and elephant seals and whales in Brazil (Young *et al.* 1997, Richardson *et al.* 2000; Aguiar & Haimovici 2001).

Practical procedures to differentiate the lower beaks of this species:

Lycoteuthis lorigera. This species is distinguishable from other species by the dark aspect of the beak and by the well-developed ridge in the lateral wall.

FAMILY MASTIGOTEUTHIDAE Figure 17 | pages 66 & 95

Family identification:

- » Very high, and very well defined, thick fold (in certain cases becoming a ridge mostly under the hood)
- » Very broad wings
- » Hood with broad notch

The only species likely to be found is:

Mastigoteuthis psychrophila

ML=94.424+6.203LRL; ln M=0.701+1.779lnLRL (n=19 for ML and M) (British Antarctic Survey, unpublished data)

Mastigoteuthis psychrophila is an Antarctic species that is common in a wide range of Southern Ocean predators, but only in high numbers in the diet of the Patagonian toothfish and occasionally in the diet of lanternsharks, southern elephant seals and toothed whales (Cherel *et al.* 2004; Cherel & Duhamel 2004).

Practical procedures to differentiate the lower beaks of this species:

Mastigoteuthis psychrophila. Similar to *Batoteuthis skolops*, but it has a distinct, and well defined, thickened fold in lateral wall (closer to the hood) and a shoulder tooth.

FAMILY NEOTEUTHIDAE Figure 18 | pages 66 & 96

Family identification:

- » Shoulder forms a distinct hook-like tooth
- » Lateral wall lacks a ridge or distinct fold (though a slight infold may be present)
- » Recessed jaw angle from the side
- » A distinctively wide, squat, but attractively proportioned beak when viewed from the front
- » Frequently encountered in small numbers in albatross diets

The species likely to be found are:

Alluroteuthis antarcticus

ML=-4.301+34.99LRL; $\ln M=1.229+2.944\ln LRL$ (n=22) (Piatkowski *et al.* 2001).

Nototeuthis dimegacotyle (no specific equations)

The Antarctic circumpolar species *A. antarcticus* can be found in the diet of a wide range of predators, but rarely in high numbers (Table 1). The poorly known subantarctic *N. dimegacotyle* is a regular prey of predators, but it has been previously misidentified (Cherel *et al.* 2004) (Table 1).

Practical procedures to differentiate the lower beaks of these species:

Alluroteuthis antarcticus. Easily identifiable for its broad shoulder groove. *N. dimegacotyle* has a shoulder that forms a distinct tooth, has a pale strip inside jaw angle, no true fold or ridge, but lateral walls “pinched” to form overhang/suggestion of fold, wings generally folds backwards and has a shallow notch in hood. The rostrum resembles *Doryteuthis gahi* but *D. gahi* is mostly distributed at the Patagonian shelf (South America, Hatfield & Rodhouse 1994) whereas *A. antarcticus* is distributed in the Southern Ocean (Xavier *et al.* 1999). Unlike *N. dimegacotyle*, *D. gahi* lacks an “overhang” in lateral wall, darkening of beak extends below jaw angle and jaw edge is slightly jagged or indentated. Drawings of beaks of *N. dimegacotyle* appear in Cherel *et al.* (2004).

FAMILY OCTOPOTEUTHIDAE Figure 19 | pages 67 & 97

Family identification:

- » Very low wing fold
- » Broad rostrum
- » Little-thickened jaw edge
- » No groove in hood's surface

The species likely to be found are:

Taningia danae

ML=-556.9+75.22LRL; $\ln M = -0.874 + 3.42 \ln \text{LRL}$ (n=15 for ML and M) (Clarke 1986)

***Octopoteuthis* sp.**

ML=-0.4+17.33LRL; $\ln M = 0.166 + 2.31 \ln \text{LRL}$ (n=30 for ML, n=22 M) (Clarke 1986)

The large *T. danae* is relatively rare in Southern Ocean predators, probably with the exception of sperm whales (Table 1) and sleeper sharks (Cherel & Duhamel 2004).

Practical procedures to differentiate the lower beaks of these species:

Taningia danae. Often large, potential for confusion with *Moroteuthopsis longimana* and *Lepidoteuthis grimaldii*. *T. danae* has a well-defined low wing fold (unlike *M. longimana*) and has a notch in posterior edge of the lateral wall. The key feature to differentiate *T. danae* from *L. grimaldii* is the absence of groove in the rostrum of *T. danae*. The beaks of *Octopoteuthis* sp. has a sharper tip in the rostrum and darken at an earlier size (e.g. wings are found dark at less than 14 mm LRL) in comparison with *T. danae*. At 14 mm LRL the wings of *T. danae* are not dark, has no rostrum tip and, in most instances, has cartilage present at the jaw. The lower beaks of this species darken at large sizes (Table 2).

FAMILY OMMASTREPHIDAE Figure 20 | pages 68 & 98

Family identification:

- » Large shoulder tooth present
- » Transparent strip below jaw angle (not always present in older beaks)
- » Low wing fold or no wing fold
- » Broad hood with a notch
- » Rostrum curved and relatively long rostral edge
- » Rather “square” profile
- » Lateral wall fold runs to point above half way between crest and free corner of lateral wall, or no fold at all

The species likely to be found are:

Martialia hyadesi

ML= 102.0+29.47LRL; $\ln M=2.405+2.012 \ln LRL$ (n=67 for ML and M) (Rodhouse & Yeatman 1990)

Illex argentinus

ML=-12.228+55.187LRL; $M=2.2750 LRL^{3.1210}$ (n=131 for ML and M) (Santos & Haimovici 2000)

***Todarodes* sp. (no specific equations)**

ML=-11.3+41.36LRL; $\ln M=0.783+2.83 \ln LRL$ (Clarke 1986), based on *Todarodes* spp. formulas

The Antarctic/sub-Antarctic circumpolar squid *M. hyadesi* is commonly found in the diet of grey-headed, black-browed and yellow-nosed albatrosses and white-chinned petrels (Croxall *et al.* 1995; Cherel & Klages 1998; Waugh *et al.* 1999; Xavier *et al.* 2003a). It is also present in the diet of other albatrosses, petrels, penguins, fish, whales and sharks (Table 1). The sub-Antarctic squid *I. argentinus* occurs in a wide range of predators feeding at the Patagonian shelf (South America) such the albatrosses, penguins, whales, dolphins, fish, sea lions and white-chinned petrels (Thompson 1992; Garcia de la Rosa *et al.* 1997; Cherel

& Klages 1998; Berrow & Croxall 1999; Alonso *et al.* 2000; Santos & Haimovici 2000; Clausen & Pütz 2003; Piatkowski *et al.* 2001; Cherel *et al.* 2002b; Xavier *et al.* 2003a,b). This species can be found in the diet of large procellariiforms outside its geographical range because it is a common bait used by longliners (Catard *et al.* 2000). Finally, *Todarodes* sp. is common in Kerguelen waters only, where it is consumed by many predators (Cherel & Weimerskirch 1995; Cherel *et al.* 2000, 2002c; Cherel *et al.* 2004; Cherel & Duhamel 2004).

Practical procedures to differentiate the lower beaks of these species:

M. hyadesi has more acutely pointed rostrum than *I. argentinus*, with distinctive “pickaxe” shape even when missing wings. *Todarodes* sp. is narrow like *M. hyadesi*, less acutely pointed rostrum like *I. argentinus*, usually larger (LRL > 10 mm) and wings do not darken until LRL of 5–9 mm (darken at < 4 mm in *M. hyadesi* and *I. argentinus*). *Pholidoteuthis massyae*, which also possess a large shoulder tooth, is easily differentiable amongst ommastrephids by the very prominent, and curved, rostrum, and deep hood notch (see Figure 22).

FAMILY ONYCHOTEUTHIDAE Figure 21 | pages 70 & 99

Some species of this family are well known, but some beaks probably belong to undescribed species (e.g. *Moroteuthopsis* sp. B (Imber)).

Family identification:

- » Distinct jaw angle ridge
- » Fold or a ridge on lateral wall (*Moroteuthopsis ingens*, *Moroteuthopsis* sp. B (Imber), and *Onychoteuthis banksii* complex)
- » Beaks are often large, particularly *Moroteuthopsis longimana*

The species likely to be found are:

Moroteuthopsis longimana

ML=-22.348+37.318LRL; M=0.713LRL^{3.152} (n=13 for ML; n=22 for M) (Brown & Klages 1987)

Moroteuthopsis ingens

It is provided the mean value between estimates obtained using equations for males and females (Jackson 1995):

Males: ML= 98.59+24.40LRL (n=82); females: ML=-27.84+44.63LRL (n=68)

Males: logM= 1.22+1.80logLRL (n=82); females: logM= 0.15+3.25logLRL (n=68)

Moroteuthis sp. B (Imber) (no specific equations)

Filippovia knipovitchi

ML=-105.707+62.369LRL; ln M=-0.881+3.798lnLRL (n=7 for ML, n=5 for M) (Cherel, unpublished data)

Onykia robsoni

ML=-652.91+151.03LRL; ln M= -9.15+8.07lnLRL (n=8 for ML, n=6 for M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

***Onychoteuthis banksii* complex**

ML=2.31+32.75LRL; $\ln M = -0.04 + 2.80 \ln LRL$ (n=10 for ML and M, using total weight of preserved specimens) (Lu & Ickeringill 2002)

Other very rare species that might occur are *Walvisteuthis rancureli*, and *Notonykia africanae*. Most recently, another species of the genus *Moroteuthopsis* has been described, *Moroteuthopsis nigmatullini*, which is a junior synonym of *M. longimana*. (Laptikhovsky *et al.* 2008).

The Antarctic/sub-Antarctic circumpolar squid *M. longimana* is commonly found in the diet of albatrosses, penguins, bottlenose and sperm whales, and sleeper sharks (Clarke 1980; Brown & Klages 1987; Clarke & Goodall 1994; Cherel & Klages 1998; Green & Burton 1998; Cherel & Weimerskirch 1999; Arata & Xavier, 2003; Xavier, 2003a,b,c; Arata *et al.* 2004; Cherel & Duhamel 2004;). The Antarctic circumpolar squid *F. knipovitchi* is common in the diet of sperm whales and grey-headed, black-browed and wandering albatrosses in some years (Clarke 1980; Cherel & Klages 1998; Xavier *et al.* 2003a). The sub-Antarctic circumpolar squid *M. ingens* is common in the diet of king penguins, wandering and royal albatrosses, pilot whales and the southern opah (Clarke & Goodall 1994; Cherel *et al.* 1996; Cherel & Klages 1998; Cherel & Weimerskirch 1999; Jackson *et al.* 2000), whereas the warm-water circumpolar species *O. robsoni* and *O. banksii* complex are generally not very common in predator diets. Finally, the poorly known *Moroteuthopsis* sp. B (Imber) is a regular prey of Patagonian toothfish and king penguins in the southern Indian Ocean (Cherel *et al.* 2004, unpublished data).

Practical procedures to differentiate the lower beaks of this species:

M. longimana beaks are usually big, with a large rostrum and jaw angle step well defined. It also has a hood shorter than the crest that flares up from line of crest, long jaw edge, with distinct jaw angle, whereas *F. knipovitchi* has a hood that curves to follow line of crest, shorter jaw edge, and less distinct curved jaw angle when viewed from the side. Hood length equal to (or slightly shorter than) crest length. *F. knipovitchi* can be also confused with *O. robsoni*, but the latter has very long wings and hood doesn't curve following the line of the crest (i.e. fairly straight) and it reaches larger size. *M. ingens* can be easily

identified by having a concave shape and a curved ridge on the lateral wall (it becomes a fin close to the hood) in adults. Sexual dimorphism in the beaks of *M. ingens* has been described when they reach a large size (Bolstad 2006). The beaks of *M. sp. B* (Imber) darken at a smaller size, its ridge is straight and asperous (in comparison with *M. ingens*), with a coarse texture, that runs to the middle of posterior edge and extend much further than the hood in adults (unlike *M. ingens* and *O. banksii* complex). Drawings of beaks of this species appear in Cherel *et al.* (2004). *O. banksii* complex is a small species and therefore wings are already darkened at < 3 mm LRL, the lower beak has a very strong ridge all along the lateral wall. For juvenile squid, *M. longimana* and *M. ingens* have a long and narrow dark jaw, whereas *F. knipovitchi* and *O. robsoni* have a wide and broader dark jaw.

FAMILY PHOLIDOTEUTHIDAE Figure 22 | pages 74 & 102

Family identification:

- » Curved rostral tip
- » Shoulder tooth
- » Unthickened lateral wall fold
- » Crest narrow

The only species likely to be found is:

Pholidoteuthis massyae

ML=11.3+41.09LRL; $\ln M=0.976+2.83\ln LRL$ (n=12 for ML, n=15 for M) (Clarke 1986)

This subtropical/temperate species is present in a wide range of predator diets from the Atlantic, Indian and Pacific waters, including albatrosses, petrels, sperm whales and Patagonian toothfish, but always in low numbers (Clarke & MacLeod 1982b, Imber *et al.* 1995, Xavier *et al.* 2003b, Cherel *et al.* 2004). This species was previously named *Pholidoteuthis boschmai* (Table 3; O'Shea *et al.* 2007).

Practical procedures to differentiate the lower beaks of this species:

P. massyae can be confused with ommastrephids but it can be easily differentiated by the short step below the jaw angle (as in onychoteuthids) and the very prominent, and curved, rostrum and deep hood notch.

FAMILY PSYCHROTEUTHIDAE Figure 23 | pages 74 & 103

Family identification:

- » A distinctive square shoulder tooth
- » Very distinct thick ridge running to near, or just below the middle of posterior edge of the lateral wall
- » Hood length 1:1 with crest length
- » Hood stands high above crest
- » Obtuse jaw angle not (or possibly, in older specimens, just) hidden from the side by a low wing fold
- » Clear strip below jaw angle in young beaks
- » Beaks may be large (*Psychroteuthis glacialis*) or small (*Psychroteuthis* sp. B (Imber)), (i.e. usually two almost distinct beak size groups)

Two species are likely to be found:

Psychroteuthis glacialis

$ML = 50.6895LRL - 8.6008LRL^2 + 1.0823LRL^3 - 8.7019$ (n=211); $\ln M = 0.3422 + 2.1380 \ln LRL + 0.2214 \ln LRL^3$ (Gröger *et al.* 2000)

***Psychroteuthis* sp. B (Imber) (no specific equations)**

Psychroteuthis glacialis is an Antarctic circumpolar species that occurs particularly in high numbers in the diet of emperor penguins, sperm whales and elephant seals (Offredo *et al.* 1985; Piatkowski *et al.* 2002; Clarke 1980). *Psychroteuthis* sp. B (Imber) has a circumpolar distribution in the Southern Ocean (i.e. extending more north than *P. glacialis*) (Cherel 2020) and is rare in predator diets.

Practical procedures to differentiate the lower beaks of those species:

Psychroteuthis glacialis and *Psychroteuthis* sp. B (Imber) are easily identified by a shoulder tooth and ridge on the lateral wall, with *P. glacialis* having bigger beaks and *Psychroteuthis* sp. B (Imber) generally smaller. Both species can be confused with sub-adults of *M. ingens* and *Moroteuthopsis* sp. B (Imber). The beaks of both *Psychroteuthis* sp. B (Imber) and *P. glacialis* are usually dark.

FAMILY SEPIOLIDAE Figure 24 | pages 75 & 103

Family identification:

- » Jaw edge not S-shaped
- » No lateral wall fold
- » Deep groove or step in the sides of the hood
- » Obtuse jaw angle
- » Indefinite jaw angle

The only species likely to be found is:

cf. *Stoloteuthis leucoptera*

This species is present in the diet of Patagonian toothfish from the Indian Ocean, at Kerguelen Islands (Cherel *et al.* 2004).

Practical procedures to differentiate the lower beaks of this species:

cf. *Stoloteuthis leucoptera* is differentiable from other cephalopod species by its small size (i.e. they darken at small size), and the lack of a well-defined angle point of the jaw.

OCTOPODA

- » FAMILY ALLOPOSIDAE
- » FAMILY CIRROTEUTHIDAE
- » FAMILY OCTOPODIDAE
- » FAMILY OPISTHOTEUTHIDAE
- » FAMILY STAUROTEUTHIDAE

FAMILY ALLOPOSIDAE Figure 25 | page 77

Family identification:

- » Broad hood, fairly flat in profile
- » Acute jaw angle
- » Fold present

The only species likely to be found is:

Haliphron atlanticus

$\ln M = 2.5 + 1.45 \ln \text{LHL}$ (British Antarctic Survey, unpublished data)

This cosmopolitan species is regular in the diets of wandering albatrosses and great-winged petrels (Xavier *et al.* 2003b; Table 1).

Practical procedures to differentiate the lower beaks of this species:

Haliphron atlanticus. Different shape of lower beak cf. squid. No well-defined jaw angle, so measure lower hood length (LHL) instead of LRL. Definite large rostrum compared with other pelagic octopods but small compared with decapod (squid) beaks. Broad hood, fairly flat in profile, stands high above the crest posteriorly.

FAMILY CIRROTEUTHIDAE Figure 26 | pages 77 & 105

Family identification:

- » Long crest in relation to the size of the hood
- » Rostrum with small hook

The only species likely to be found is:

Cirrata sp. A (Cherel) (no allometric equations available)

This species is present in predators from the Indian Ocean, such as the Patagonian toothfish and sleeper sharks (Cherel *et al.* 2004; Cherel & Duhamel 2004).

Practical procedures to differentiate the lower beaks of this species:

Cirrata sp. A (Cherel). This large species has an identifiable rostrum with a small hook and a sharp rostrum.

FAMILY OCTOPODIDAE Figure 27 | pages 78 & 105

There are many species of endemic benthic octopods all around Antarctica and sub-Antarctic islands (review in Collins & Rodhouse, 2008), but they are usually reported in low numbers in predator diets. In terms of identifying beaks from Antarctic octopodids, numerous species have very similar beaks (e.g. *Thaumeledone* spp.; Allcock *et al.* 2004), making the identification to a species level difficult. Below are beaks of octopod species that have been found regularly in the diet of predators and have features that makes them identifiable.

Family identification:

- » No fold or ridge on lateral wall
- » No hood notch
- » Shoulder tooth absent
- » Angle point absent
- » Free corners of lateral walls widely spread
- » Rostrum tip blunt

The numerous species present in this family include:

Pareledone turqueti

ML=17.70487+ 13.32812LHL; $\ln M = 0.689269 + 2.542938 \ln LHL$ (n=7 for ML, n=23 for M), where LHL= lower hood length (in mm) (Collins, unpublished data)

Adelieledone polymorpha

ML= -7,426229508+25,16393443LHL; $\ln M = 1,077552 + 3,200449 \ln LHL$ (n=3 for ML, n= 39 for M) (Collins, unpublished data)

Muusoctopus thielei

ML = 7.398+12.569LHL; $\ln M = 0.471 + 2.706 \ln LHL$ (n=48 for ML and M) (Cherel, unpublished data)

Graneledone gonzalezi

ML = $5.047 + 13.004 \text{LHL}$; $\ln M = 0.288 + 2.967 \ln \text{LHL}$ (n=54 for ML and M) (Cherel, unpublished data)

The Antarctic species *P. turqueti* and *A. polymorpha*, mostly present in South Georgia waters, are common in the diet of the Patagonian toothfish, but also present in the diets of albatrosses and seals (Rodhouse & Prince 1993; Reid & Arnould 1996; Rodhouse *et al.* 1996; Croxall *et al.* 1997; Daneri *et al.* 2000; Rodhouse *et al.* 1992; Xavier *et al.* 2002). The Kerguelen endemic *M. thielei* is present in black-browed albatross diet and both *M. thielei* and *G. gonzalezi* in the food of Patagonian toothfish (Cherel *et al.* 2000, 2002c, 2004).

Practical procedures to differentiate the lower beaks of these species:

Octopods of the genus *Adelieledone* have a peculiar beak morphology, which contrasts with other genera of benthic octopods in the area in which the overall shape is similar, thus often precluding species identification. In South Georgia, *Pareledone turqueti* is easily differentiated from *A. polymorpha* by the latter species having a rostral tip sharp and pointed. On the other hand, there is no good way to differentiate the lower beaks of the two endemic species from the Kerguelen Plateau, *Muusoctopus thielei* and *Graneledone gonzalezi*.

FAMILY OPISTHOTEUTHIDAE Figure 28 | pages 80 & 107

Family identification:

» Jaw obtuse or absent

The identifiable species likely to be found is:

***Opisthoteuthis* sp.**

$ML = -26.0047 + 12.4858CL$; $\log M = 0.5893 + 0.2413CL$ (n= 13 for ML, n=9 for M) (Smale *et al.* 1993) where CL = Crest length (in mm)

This species is present in predators from the Indian Ocean, such as the Patagonian toothfish (Cherel *et al.* 2004).

Practical procedures to differentiate the lower beaks of this species:

This species has a typical curved rostrum and a short jaw edge. Drawings of beaks of that species appear in Cherel *et al.* (2004).

FAMILY STAUROTEUTHIDAE Figure 29 | pages 80 & 108

Family identification:

- » Sharp rostrum
- » Large hook
- » Straight crest

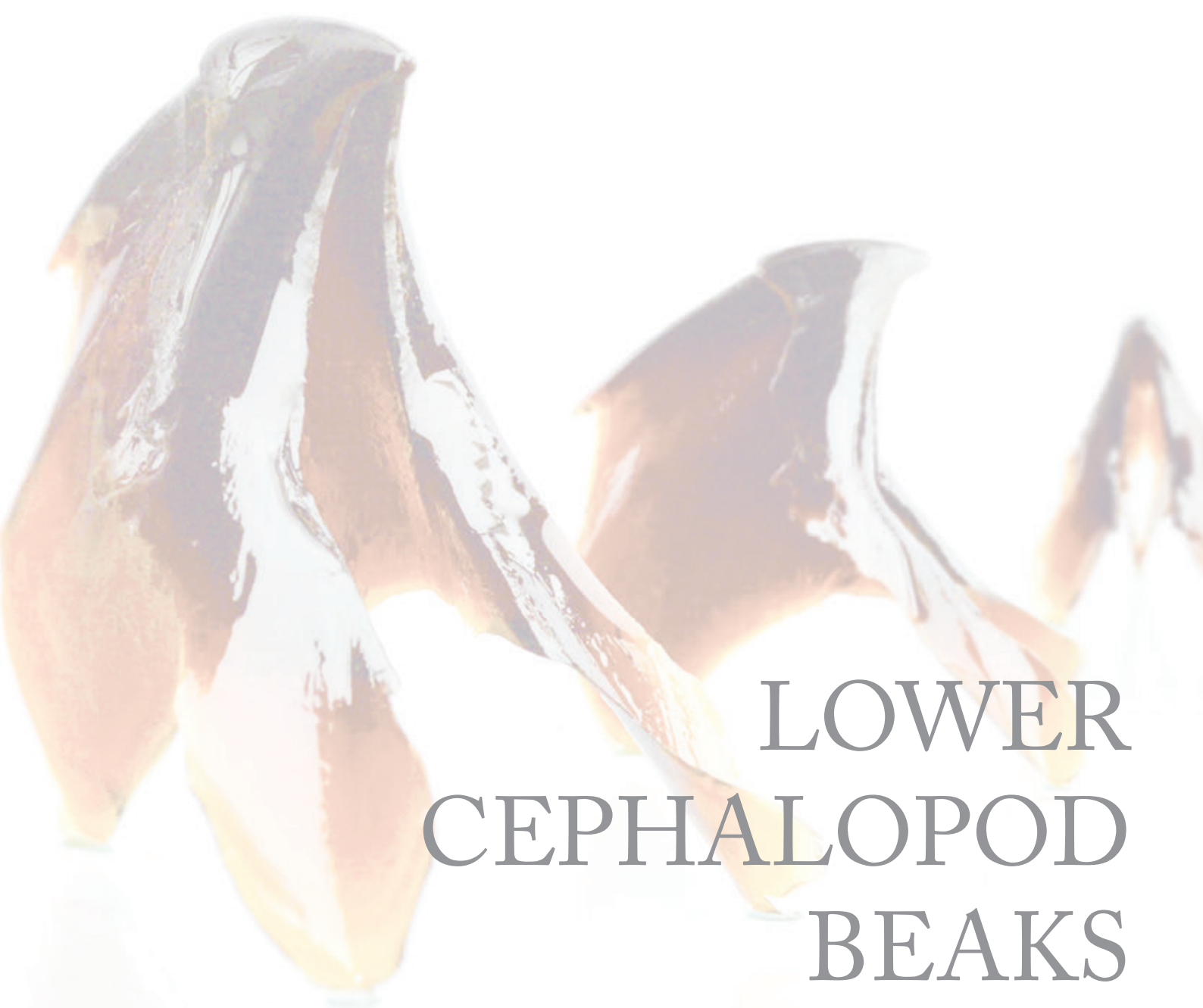
The identifiable species likely to be found is:

***Stauroteuthis gilchristi* (no allometric equations available)**

This species is present in predators from the Indian Ocean, such as the Patagonian toothfish (Cherel *et al.* 2004), although it is known to occur in southern Atlantic Ocean waters too (Collins & Henriques 2000).

Practical procedures to differentiate the lower beaks of this species:

Stauroteuthis gilchristi. Easily identifiable by the large hook at the tip of the rostrum. Drawings of beaks of this species appear in Cherel *et al.* (2004).



LOWER
CEPHALPOD
BEAKS

DECAPODA

- » FAMILY ANCISTROCHEIRIDAE
- » FAMILY ARCHITEUTHIDAE
- » FAMILY BATHYTEUTHIDAE
- » FAMILY BATOTEUTHIDAE
- » FAMILY BRACHIOTEUTHIDAE
- » FAMILY CHIROTEUTHIDAE
- » FAMILY CRANCHIIDAE
- » FAMILY CYCLOTEUTHIDAE
- » FAMILY GONATIDAE
- » FAMILY HISTIOTEUTHIDAE
- » FAMILY LEPIDOTEUTHIDAE
- » FAMILY LOLIGINIDAE
- » FAMILY LYCOTEUTHIDAE
- » FAMILY MASTIGOTEUTHIDAE
- » FAMILY NEOTEUTHIDAE
- » FAMILY OCTOPOTEUTHIDAE
- » FAMILY OMMASTREPHIDAE
- » FAMILY ONYCHOTEUTHIDAE
- » FAMILY PHOLIDOTEUTHIDAE
- » FAMILY PSYCHROTEUTHIDAE
- » FAMILY SEPIOLIDAE

FAMILY ANCISTROCHEIRIDAE Figure 4 | pages 13 & 83

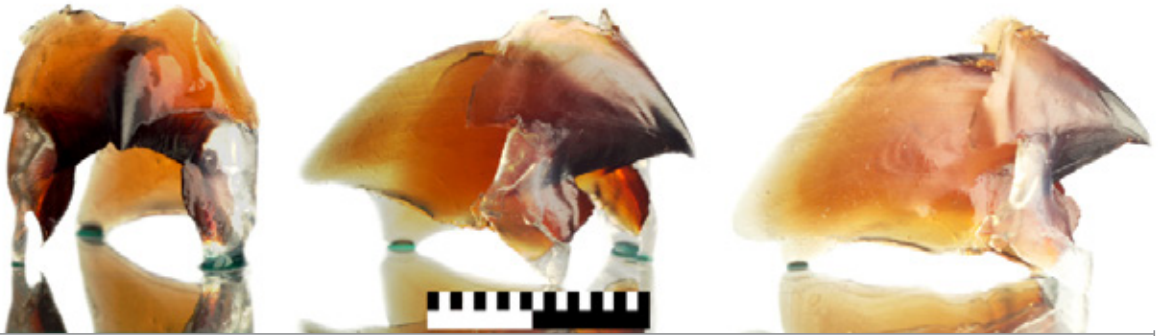


Ancistrocheirus lesueurii | from the diet of a Wandering albatross, South Georgia, 4.4 mm LRL

FAMILY ARCHITEUTHIDAE Figure 5 | pages 14 & 83



Architeuthis dux | adult | Sleeper shark, Kerguelen, 16.2 mm LRL



Architeuthis dux | juvenile | Sleeper shark, Kerguelen, 10.1 mm LRL

FAMILY BATHYTEUTHIDAE Figure 6 | pages 15 & 84



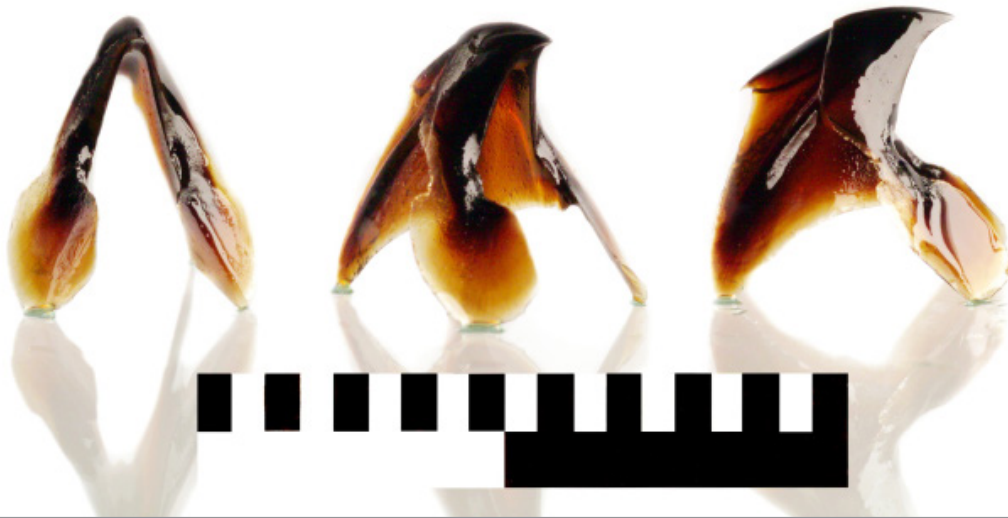
• *Bathyteuthis abyssicola* | from fresh specimen, South Georgia, 0.8 mm LRL

FAMILY BATOTEUTHIDAE Figure 7 | pages 16 & 84



• *Batoteuthis skolops* | Wandering albatross, South Georgia, 4.6 mm LRL

FAMILY BRACHIOTEUTHIDAE Figure 8 | pages 17 & 85

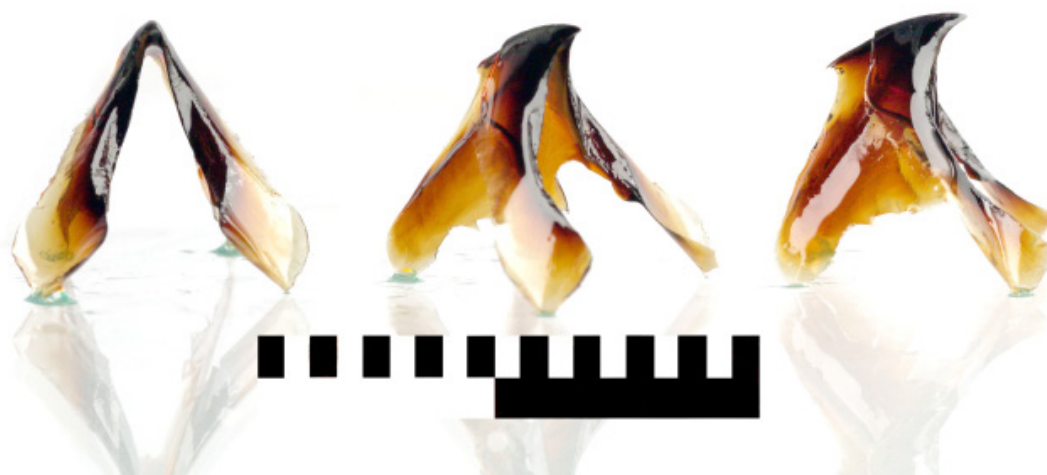


• *Brachioteuthis linkovskyi* | Grey-headed albatross, South Georgia, 4.8 mm LRL



• *Slosarczykovia circumantarctica* | Black-browed albatross, South Georgia, 2.0 mm LRL

FAMILY CHIROTEUTHIDAE Figure 9 | pages 19 & 86



• *Chiroteuthis veranyi* | Wandering albatross, South Georgia, 5.2 mm LRL



• *Asperoteuthis lui* | Wandering albatross, South Georgia, 6.7 mm LRL

FAMILY CRANCHIIDAE Figure 10 | pages 21 & 87



• *Galiteuthis glacialis* | Wandering albatross, South Georgia, 5.3 mm LRL



• *Galiteuthis submi* | Wandering albatross, Crozet, 8.3 mm LRL

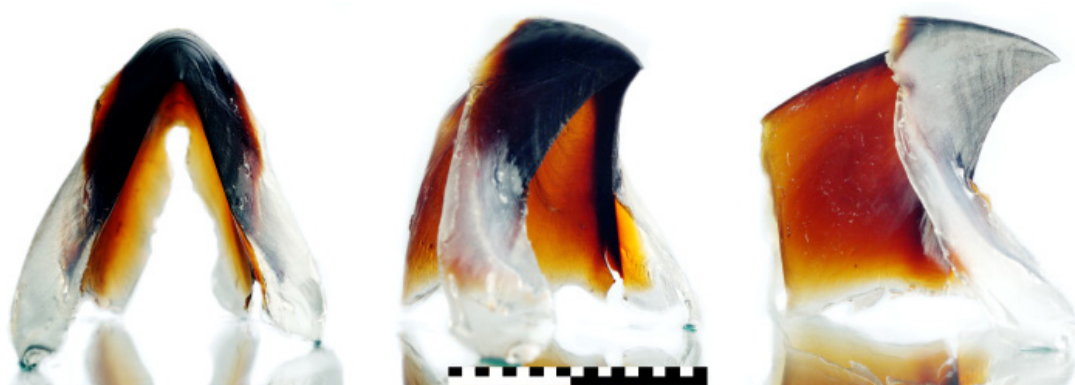


• *Liguriella podophtalma* | Wandering albatross, Crozet, 6.3 mm LRL

continue...



• *Mesonychoteuthis hamiltoni* | adult | Sleeper shark, Kerguelen, 23.6 mm LRL



• *Mesonychoteuthis hamiltoni* | juvenile | Sleeper shark, Kerguelen, 10.4 mm LRL



• *Taonius exopolitus* | Wandering albatross, Crozet, 5.0 mm LRL



• *Taonius notalia* | Wandering albatross, South Georgia, 8.9 mm LRL

continue...



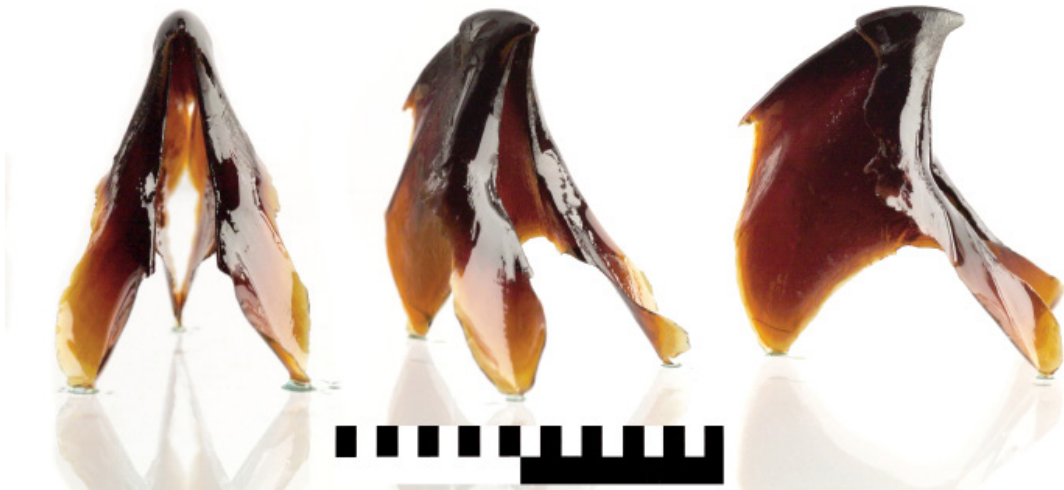
• *Teuthowenia pellucida* | Yellow-nosed albatross, Amsterdam, 5.0 mm LRL

FAMILY CYCLOTEUTHIDAE Figure 11 | pages 23 & 90



• *Cycloteuthis sirventi* | Wandering albatross, Crozet, 14.9 mm LRL

FAMILY GONATIDAE Figure 12 | pages 24 & 91



• *Gonatus antarcticus* | adult | Grey-headed albatross, South Georgia, 7.3 mm LRL



• *Gonatus antarcticus* | juvenile | King penguin, Falkand Islands, 2.5 mm LRL



• *Gonatopsis octopedatus* | = *Gonatus phoebetriae* (Imber); Patagonian toothfish, Crozet, 7.0 mm LRL

FAMILY HISTIOTEUTHIDAE Figure 13 | pages 26 & 92



• *Histioteuthis arcturi* | H. A5 in Clarke (1986); Wandering albatross, South Georgia, 10.3 mm LRL



• *Histioteuthis bonnellii corpuscula* | Wandering albatross, Crozet, 4.9 mm LRL



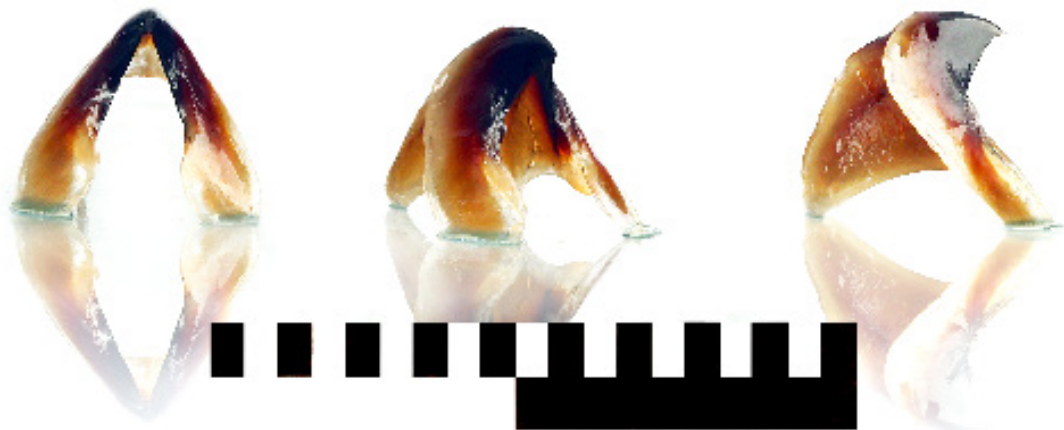
• *Histioteuthis macrohista* | Wandering albatross, South Georgia, 3.5 mm LRL



• *Histioteuthis miranda* | Wandering albatross, Crozet, 6.7 mm LRL

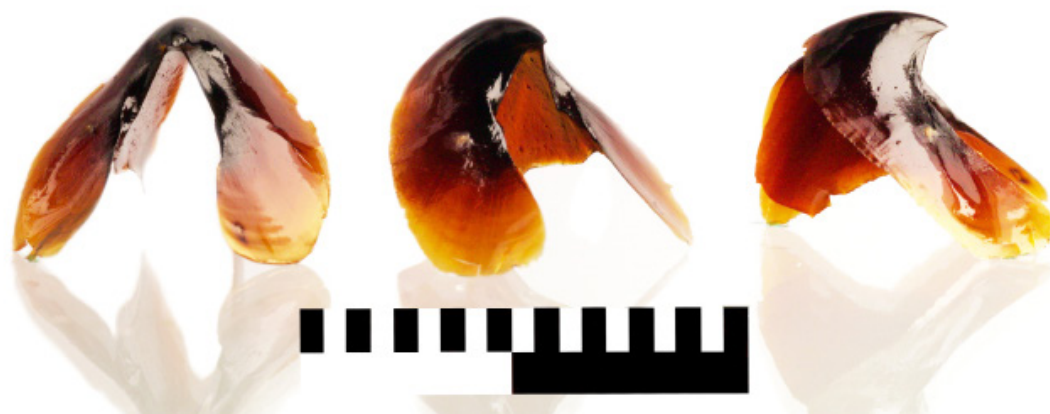


• *Histioteuthis atlantica* | adult | Wandering albatross, South Georgia, 5.3 mm LRL



• *Histioteuthis atlantica* | juvenile | Patagonian toothfish, Kerguelen, 2.2 mm LRL

continue...



• *Histioteuthis eltaninae* | Wandering albatross, South Georgia, 3.6 mm LRL

FAMILY LEPIDOTEUTHIDAE Figure 14 | page 29



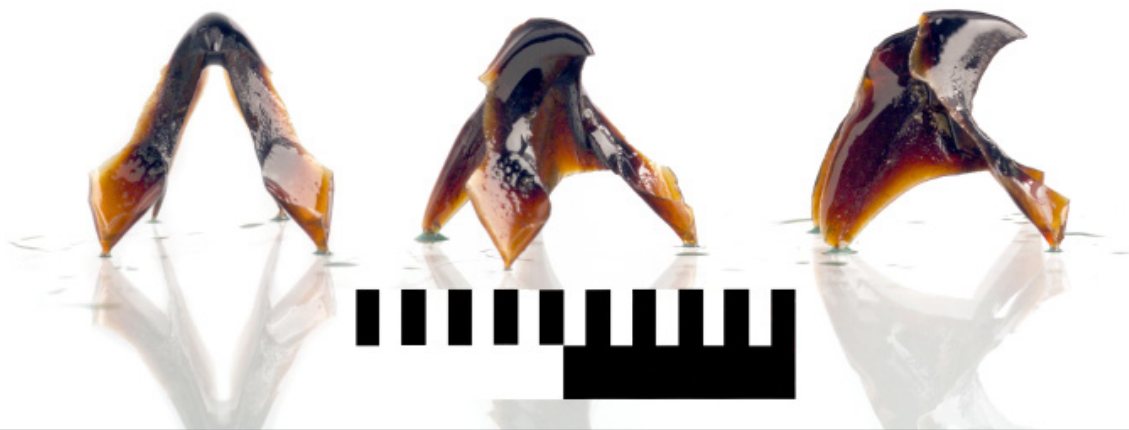
• *Lepidoteuthis grimaldii* | Wandering albatross, South Georgia, 15.9 mm LRL

FAMILY LOLIGINIDAE Figure 15 | pages 30 & 94



Doryteuthis gahi | Wandering albatross, South Georgia, 1.6 mm LRL

FAMILY LYCOTEUTHIDAE Figure 16 | pages 31 & 95



Lycoteuthis lorigera | Yellow-nosed albatross, Amsterdam, 4.3 mm LRL

FAMILY MASTIGOTEUTHIDAE Figure 17 | pages 32 & 95



• *Mastigoteuthis psychrophila* | Wandering albatross, South Georgia, 3.7 mm LRL

FAMILY NEOTEUTHIDAE Figure 18 | pages 33 & 96



• *Alluroteuthis antarcticus* | Wandering albatross, South Georgia, 5.4 mm LRL



• *Nototeuthis dimegacotyle* | Patagonian toothfish, Crozet, 3.1 mm LRL

FAMILY OCTOPOTEUTHIDAE Figure 19 | pages 34 & 97



• *Taningia danae* | Sleeper shark, Kerguelen, 16.6 mm LRL



• *Octopoteuthis* sp. | Wandering albatross, South Georgia, 14.5 mm LRL

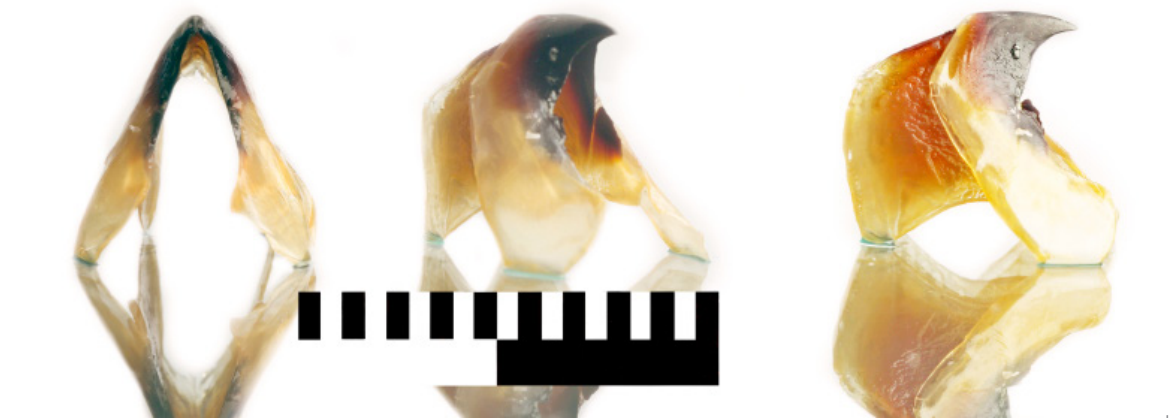
FAMILY OMMASTREPHIDAE Figure 20 | pages 35 & 98



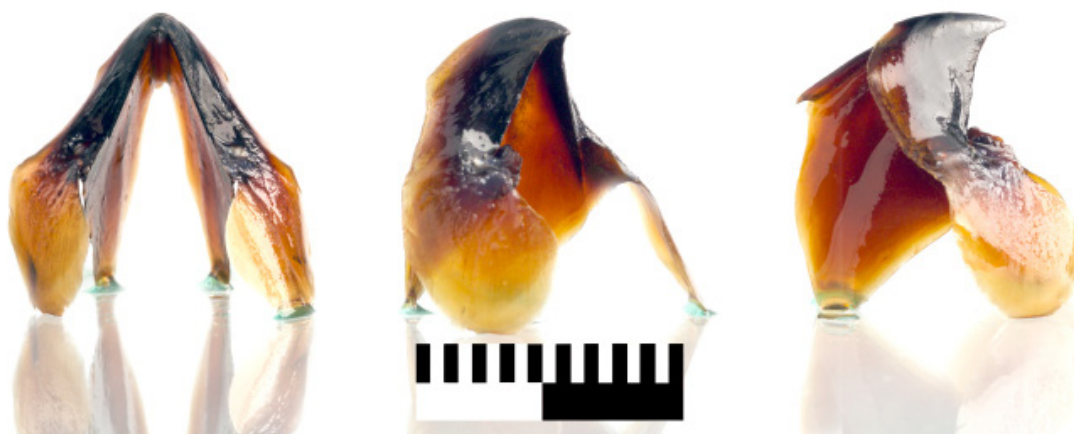
• *Illex argentinus* | Wandering albatross, South Georgia, 6.9 mm LRL



• *Martialia hyadesi* | adult | Wandering albatross, Crozet, 8.4 mm LRL



• *Martialia hyadesi* | juvenile | Black-browed albatross, Crozet, 4.7 mm LRL



• *Todarodes* sp. | adult | Black-browed albatross, Kerguelen, 10.1 mm LRL



• *Todarodes* sp. | juvenile | Grey-headed albatross, Kerguelen, 5.4 mm LRL

FAMILY ONYCHOTEUTHIDAE Figure 21 | pages 37 & 99



• *Moroteuthopsis longimana* | adult | Wandering albatross, South Georgia, 11.3 mm LRL



• *Moroteuthopsis longimana* | juvenile | Patagonian toothfish, Kerguelen, 3.7 mm LRL

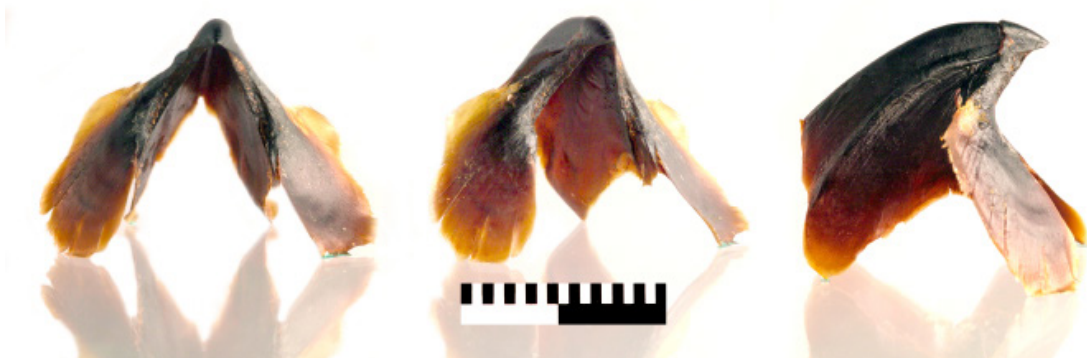


• *Filippovia knipovitchi* | adult | Wandering albatross, South Georgia, 6.3 mm LRL



• *Filippovia knipovitchi* | juvenile | King penguin, Crozet, 2.9 mm LRL

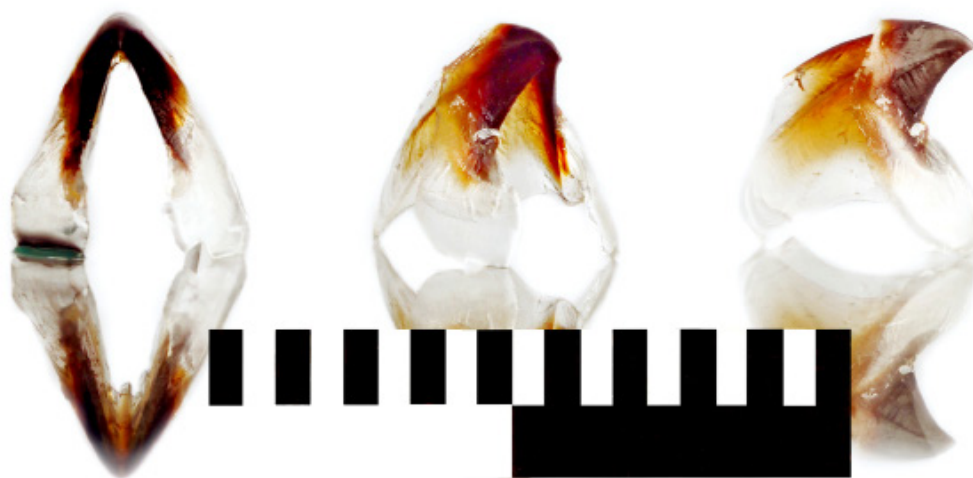
continue...



• *Moroteuthopsis ingens* | female adult | Wandering albatross, South Georgia, 10.2 mm LRL



• *Moroteuthopsis ingens* | male adult | Patagonian toothfish, Crozet, 8.7 mm LRL



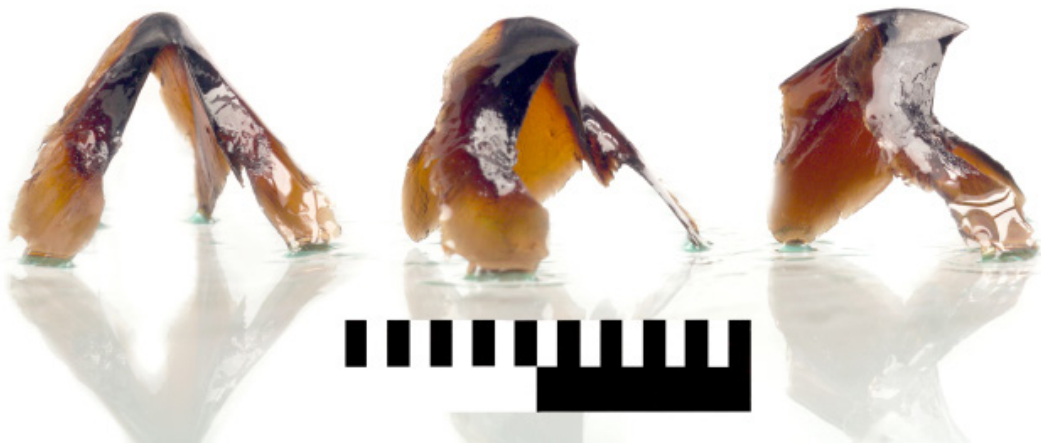
• *Moroteuthopsis ingens* | juvenile | Patagonian toothfish, Crozet, 3.0 mm LRL



• *Onykia robsoni* | Wandering albatross, South Georgia, 8.3 mm LRL

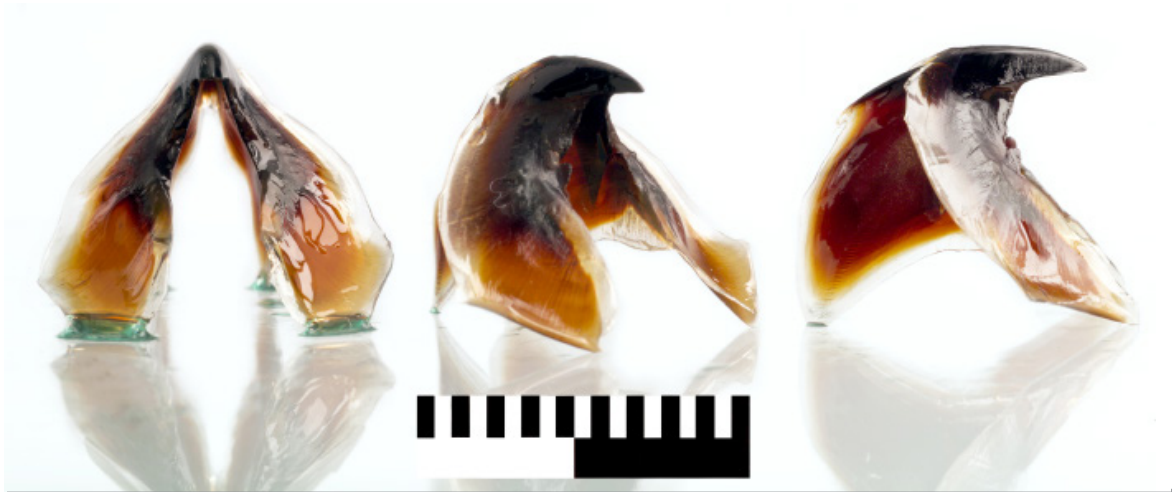


• *Onychoteuthis banksii* complex | Subantarctic fur seal, Amsterdam, 2.9 mm LRL



• *Moroteuthopsis* sp. B (Imber) | Patagonian toothfish, Kerguelen, 5.4 mm LRL

FAMILY PHOLIDOTEUTHIDAE Figure 22 | pages 40 & 102



• *Pholidoteuthis massyae* | Patagonian toothfish, Kerguelen, 6.5 mm LRL

FAMILY PSYCHROTEUTHIDAE Figure 23 | pages 41 & 103



• *Psychroteuthis glacialis* | adult | Wandering albatross, South Georgia, 7.7 mm LRL



• *Psychroteuthis glacialis* | juvenile | Emperor penguin, Adélie Land, Antarctica, 1.8 mm LRL

FAMILY SEPIOLIDAE Figure 24 | pages 43 & 103

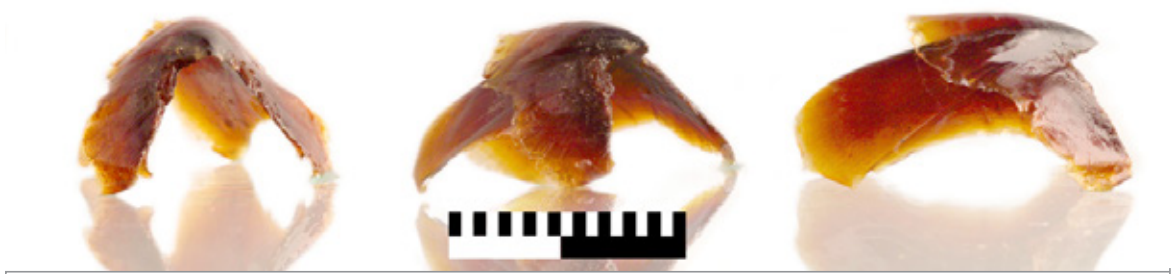


• *cf. Stoloteuthis leucoptera* | from fresh specimen, Kerguelen, 1.3 mm LRL

OCTOPODA

- » FAMILY ALLOPOSIDAE
- » FAMILY CIRROTEUTHIDAE
- » FAMILY OCTOPODIDAE
- » FAMILY OPISTHOTEUTHIDAE
- » FAMILY STAURITEUTHIDAE

FAMILY ALLOPOSIDAE Figure 25 | page 45



• *Haliphron atlanticus* | Wandering albatross, South Georgia, 15.9 LHL

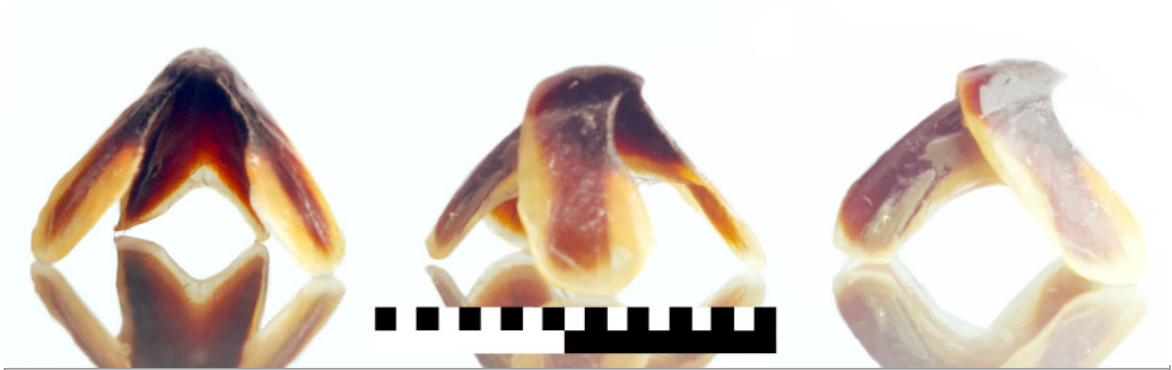
FAMILY CIRROTEUTHIDAE Figure 26 | pages 46 & 105



• *Cirrata* sp. A (Cherel) | Patagonian toothfish, Crozet, 6.6 mm LHL

FAMILY OCTOPODIDAE Figure 27 | pages 47 & 105





• *Graneledone gonzalezi* | from fresh specimen, Kerguelen, 5.7 mm LHL



• *Pareledone turqueti* | from fresh specimen, South Georgia, 3.8 mm LHL

FAMILY OPISTHOTEUTHIDAE Figure 28 | pages 49 & 107



• *Opisthoteuthis* sp. | Patagonian toothfish, Crozet, 5.8 mm LHL

FAMILY STAUROTEUTHIDAE Figure 29 | pages 50 & 108



• *Stauroteuthis gilchristi* | Patagonian toothfish, Crozet, 3.5 mm LHL



UPPER
CEPHALPOD
BEAKS

DECAPODA

- » FAMILY ANCISTROCHEIRIDAE
- » FAMILY ARCHITEUTHIDAE
- » FAMILY BATHYTEUTHIDAE
- » FAMILY BATOTEUTHIDAE
- » FAMILY BRACHIOTEUTHIDAE
- » FAMILY CHIROTEUTHIDAE
- » FAMILY CRANCHIIDAE
- » FAMILY CYCLOTEUTHIDAE
- » FAMILY GONATIDAE
- » FAMILY HISTIOTEUTHIDAE
- » FAMILY LEPIDOTEUTHIDAE
- » FAMILY LOLIGINIDAE
- » FAMILY LYCOTEUTHIDAE
- » FAMILY MASTIGOTEUTHIDAE
- » FAMILY NEOTEUTHIDAE
- » FAMILY OCTOPOTEUTHIDAE
- » FAMILY OMMASTREPHIDAE
- » FAMILY ONYCHOTEUTHIDAE
- » FAMILY PHOLIDOTEUTHIDAE
- » FAMILY PSYCHROTEUTHIDAE
- » FAMILY SEPIOLIDAE

FAMILY ANCISTROCHEIRIDAE Figure 4 | pages 13 & 53



• *Ancistrocheirus lesueurii* | Swordfish, Tropical Indian Ocean, 4.7 mm URL

FAMILY ARCHITEUTHIDAE Figure 5 | pages 14 & 53



• *Architeuthis dux* | from the diet of Sleeper shark, Kerguelen, 18.1 mm URL

FAMILY BATHYTEUTHIDAE Figure 6 | pages 15 & 54



• *Bathyteuthis abyssicola* | from fresh specimen, Falkland Islands, 1.8 mm URL

FAMILY BATOTEUTHIDAE Figure 7 | pages 16 & 54



• *Batoteuthis skolops* | Patagonian toothfish, Kerguelen, 3.3 mm URL

FAMILY BRACHIOTEUTHIDAE Figure 8 | pages 17 & 55



• *Brachioteuthis linkovskyi* | Patagonian toothfish, Kerguelen, 3.9 mm URL

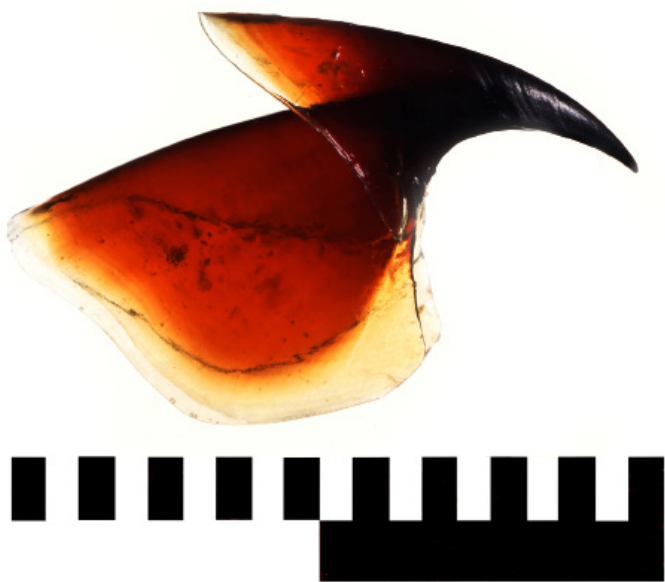


• *Slosarczykovia circumantarctica* | Patagonian toothfish, Kerguelen, 2.6 mm URL

FAMILY CHIROTEUTHIDAE Figure 9 | pages 19 & 56

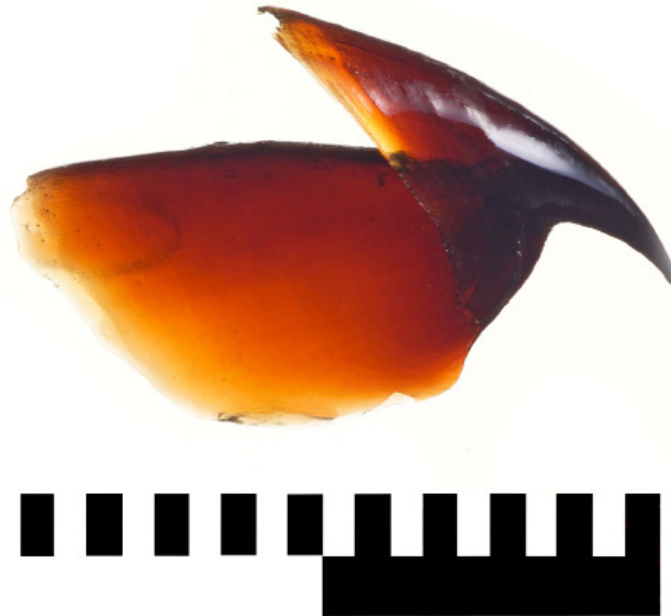


• *Asperoteuthis lui* | from specimen, Kerguelen, 5.3 mm URL



• *Chiroteuthis veranyi* | Patagonian toothfish, Kerguelen, 5.3 mm URL

FAMILY CRANCHIIDAE Figure 10 | pages 21 & 57



• *Galiteuthis glacialis* | Black-browed albatross, Crozet, 5.3 mm URL



• *Galiteuthis submi* | Yellow-nosed albatross, Amsterdam island, 6.5 mm URL

continue...



• *Liguriella podophthalma* | Yellow-nosed albatross, Amsterdam island, 5.5 mm URL



• *Mesonychoteuthis hamiltoni* | Sleeper shark, Kerguelen, 27.7 mm URL



• *Taonius expositus* | Yellow-nosed albatross, Amsterdam island, 4.2 mm URL



• *Taonius notalia* | Patagonian toothfish, Crozet, 8.0 mm URL

continue...



• *Teuthowenia pellucida* | Yellow-nosed albatross, Amsterdam island, 3.4 mm URL

FAMILY CYCLOTEUTHIDAE Figure 11 | pages 23 & 60



• *Cycloteuthis sirventi* | Sleeper shark, Kerguelen, 13.7 mm URL

FAMILY GONATIDAE Figure 12 | pages 24 & 61



• *Gonatus antarcticus* | King penguin, Falkland Islands, 4.6 mm URL



• *Gonatopsis octopedatus* | Patagonian toothfish, Crozet, 5.8 mm URL

FAMILY HISTIOTEUTHIDAE Figure 13 | pages 26 & 62



• *Histioteuthis miranda* | Yellow-nosed albatross, Amsterdam island, 6.4 mm URL



• *Histioteuthis bonnellii corpuscula* | Yellow-nosed albatross, Amsterdam Island, 4.6 mm URL



• *Histiotteuthis macrobista* | Yellow-nosed albatross, Amsterdam Island, 2.5 mm URL



• *Histiotteuthis atlantica* | Yellow-nosed albatross, Amsterdam Island, 6.1 mm URL

continue...



• *Histioteuthis eltaninae* | Patagonian toothfish, Kerguelen, 2.5 mm URL

FAMILY LOLIGINIDAE Figure 15 | pages 30 & 65



• *Doryteuthis gahi* | from fresh specimen, Falkland Islands, 11.7 mm UHL

FAMILY LYCOTEUTHIDAE Figure 16 | pages 31 & 65



• *Lycoteuthis lorigera* | Yellow-nosed albatross, Amsterdam, 4.5 mm URL

FAMILY MASTIGOTEUTHIDAE Figure 17 | pages 32 & 66



• *Mastigoteuthis psychrophila* | Patagonian toothfish, Kerguelen, 3.7 mm URL

FAMILY NEOTEUTHIDAE Figure 18 | pages 33 & 66



• *Alluroteuthis antarcticus* | Patagonian toothfish, Crozet, 3.8 mm URL



• *Nototeuthis dimegacotyle* | Patagonian toothfish, Kerguelen, 2.7 mm URL

FAMILY OCTOPOTEUTHIDAE Figure 19 | pages 34 & 67



• *Taningia danae* | Sleeper shark, Kerguelen, 14.6 mm URL



• *Octopoteuthis* sp. | Sooty albatross, Amsterdam, 30.0 mm UHL

FAMILY OMMASTREPHIDAE Figure 20 | pages 35 & 68



• *Illex argentinus* | from fresh specimen, Falkand Islands, 18.0 mm UHL



• *Martialia hyadesi* | Patagonian toothfish, Crozet, 7.0 mm URL



• *Todarodes* sp. | Patagonian toothfish, Kerguelen, 11.4 mm URL

FAMILY ONYCHOTEUTHIDAE Figure 21 | pages 37 & 70



• *Moroteuthopsis longimana* | Patagonian toothfish, Kerguelen, 12.8 mm URL

continue...



• *Moroteuthopsis ingens* | Patagonian toothfish, Crozet, 7.6 mm URL



• *Moroteuthopsis* sp. B (Imber) | Patagonian toothfish, Kerguelen, 5.0 mm URL



• *Filippovia knipovitchi* | King penguin, Crozet, 6.2 mm URL



• *Onykia robsoni* | Patagonian toothfish, Kerguelen, 7.8 mm URL

continue...



• *Onychoteuthis banksii* complex | Subtropical fur seal, Amsterdam, 2.9 mm URL

FAMILY PHOLIDOTEUTHIDAE Figure 22 | pages 40 & 74



• *Pholidoteuthis massyae* | Patagonian toothfish, Kerguelen, 7.0 mm URL

FAMILY PSYCHROTEUTHIDAE Figure 23 | pages 41 & 74



• *Psychroteuthis glacialis* | Emperor penguin, Adelie Land, Antarctica, 6.9 mm URL

FAMILY SEPIOLIDAE Figure 24 | pages 43 & 75



• cf. *Stoloteuthis leucoptera* | from fresh specimen, Kerguelen, 1.3 mm UHL

OCTOPODA

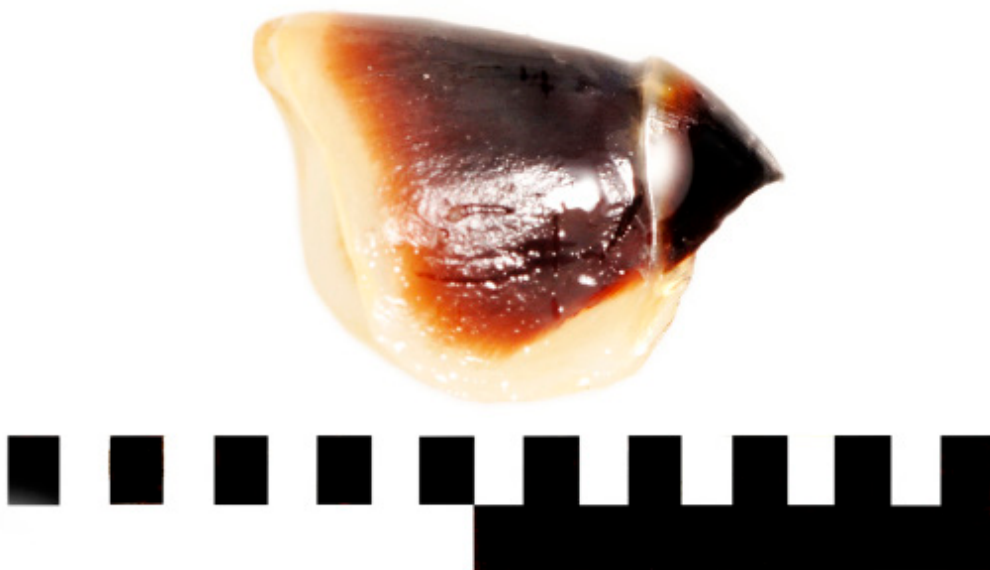
- » FAMILY ALLOPOSIDAE
- » FAMILY CIRROTEUTHIDAE
- » FAMILY OCTOPODIDAE
- » FAMILY OPISTHOTEUTHIDAE
- » FAMILY STAUROTEUTHIDAE

FAMILY CIRROTEUTHIDAE Figure 26 | pages 46 & 77



• *Cirrata* sp. A (Cherel) | Patagonian toothfish, Crozet, 13.1 mm UHL

FAMILY OCTOPODIDAE Figure 27 | pages 47 & 78



• *Adelieledone polymorpha* | from fresh specimen, South Georgia, 3.6 mm UHL

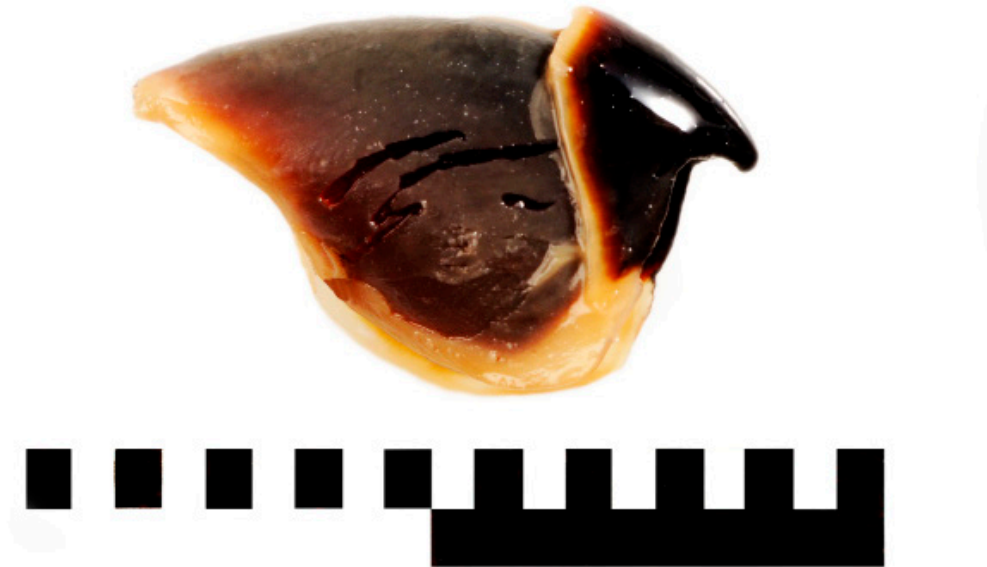
continue...



• *Muusoctopus thielei* | from fresh specimen, Kerguelen, 7.5 mm UHL



• *Graneledone gonzalezi* | from fresh specimen, Kerguelen, 6.5 mm UHL



• *Pareledone turqueti* | from fresh specimen, South Georgia, 5.2 mm UHL

FAMILY OPISTHOTEUTHIDAE Figure 28 | pages 49 & 80

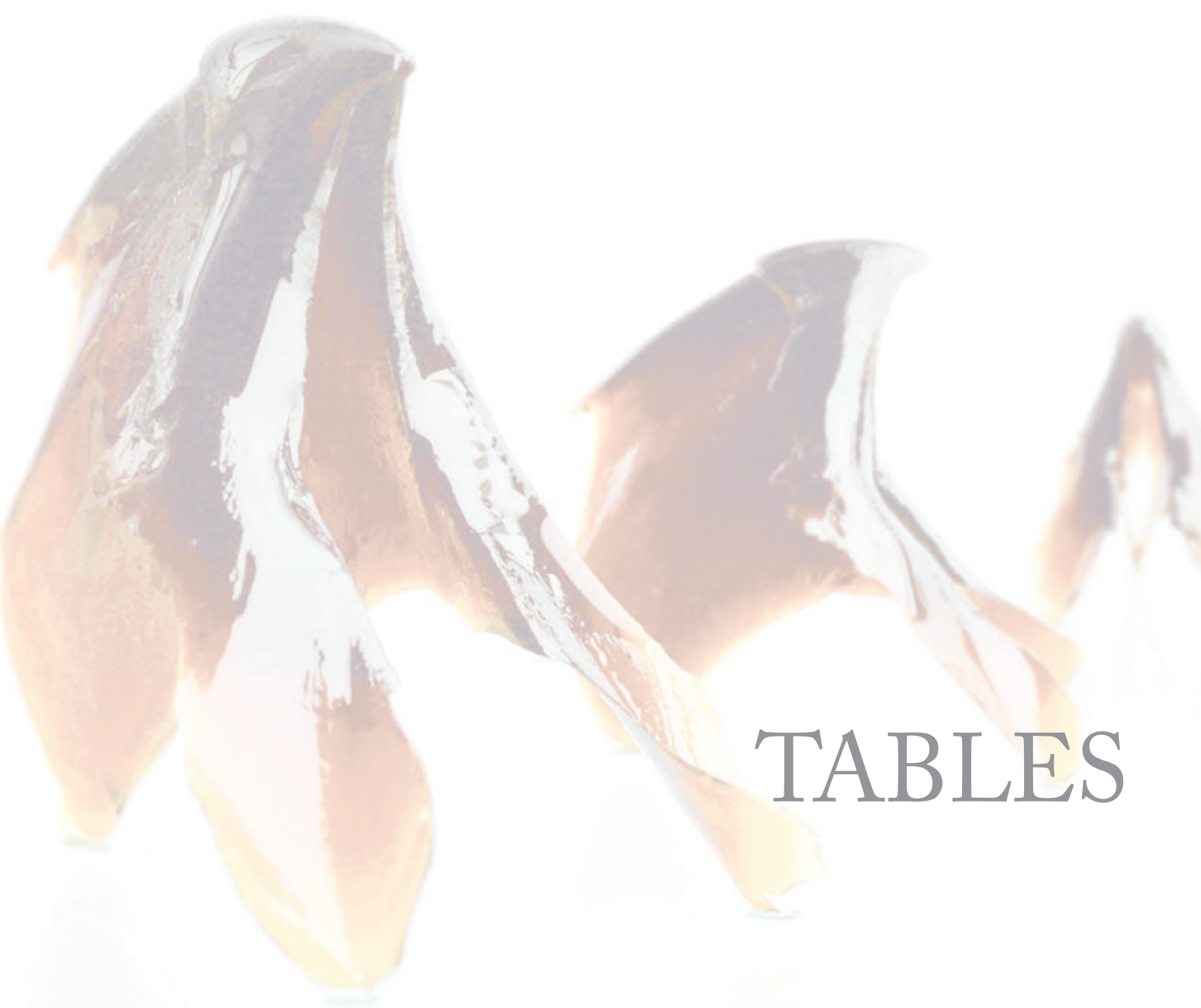


• *Opisthoteuthis* sp. | Patagonian toothfish, Crozet, 9.8 mm UHL

FAMILY STAUROTEUTHIDAE Figure 29 | pages 50 & 80



• *Stauroteuthis gilchristi* | Patagonian toothfish, Crozet, 7.5 mm UHL



TABLES

TABLE 1a. Main cephalopod taxa in the diet of albatrosses.

	Albatrosses									
Cephalopod taxa	Grey-headed	Black-browed	Wandering	Light-mantled	Sooty	Northern Royal	Southern Royal	Yellow-nosed	Buller's	
<i>Alluroteuthis antarcticus</i>	Cr, DR, PE, SG	K, SG	An, Au, Cr, G, Mac, PE, SG	C, Cr, H, Mac, PE, SG	Cr, PE	Cht				
<i>Ancistrocheirus lesueurii</i>	An, Au, Cr, G, Mac, PE, SG	SG		PE	Cr, PE	Cht	C	K	Ch, Sn	
<i>Batoteuthis skolops</i>	DR, K, SG	DR, K, SG	An, Au, Mac, PE, SG		PE	Cht	C	K		
<i>Chiroteuthis veranyi</i>	DR, K, SG	K, SG	SG		PE					
<i>Filippovia knipovitchi</i>	DR, PE, SG	K, SG	An, Au, Cr, G, Mac, PE, SG	Cr, Mac, PE	Cr, PE	Cht	C	PE		
<i>Galiteuthis glacialis</i>	C, Cr, DR, K, PE, SG	C, DR, K, SG	An, Au, Cr, G, Mac, PE, SG	C, Cr, K, Mac, PE, SG	Cr, PE	Cht		K		
<i>Gonatus antarcticus</i>	Cr, DR, K, PE, SG	Fl, K, SG	An, Au, Cr, G, Mac, PE, SG	Cr, H, Mac, PE, SG	Cr, PE	Cht	C	K		
<i>Haliphron atlanticus</i>	K	K	An, Au, G, Mac, PE, SG	PE	PE	Cht	C	K	Ch, Sn	
<i>Histioteuthis atlantica</i>	K	K	An, Au, G, Mac, PE, SG	PE	PE	Cht	C	K	Ch, Sn	
<i>Histioteuthis bonnellii corpuscula</i>	SG	SG	An, Au, G, PE, SG	PE	PE	Cht				
<i>Histioteuthis eltaninae</i>	Cr, K, PE, SG	K, SG	An, Au, Cr, Mac, PE, SG	Cr, H, Mac, PE, SG	Cr, PE	Cht	C	PE		
<i>Histioteuthis macrobista</i>	SG		An, Au, G, PE, SG			Cht			Ch, Sn	
<i>Histioteuthis miranda</i>			An, Au, G, PE, SG	PE	PE	Cht	C		Ch, Sn	
<i>Lepidoteuthis grimaldii</i>		SG	An, Cr, G, PE, SG	SG	Cr	Cht				
<i>Martialis byadesi</i>	C, Cr, DR, PE, SG	C, Cr, DR, Fl, K, SG	An, Mac, PE, SG	H, Mac, PE, SG	PE	Cht	C	Cr		
<i>Mastigoteuthis psychrophila</i>	DR, K, PE, SG	K, SG	An, Mac, SG							
<i>Mesonychoteuthis hamiltoni</i>	DR, SG	SG	An, Cr, Mac, PE, SG	Cr, Mac, PE	Cr, PE					
<i>Moroteuthopsis ingens</i>	DR, K, PE	K	An, Au, Cr, G, Mac, PE, SG	Cr, Mac	PE	Cht	C		Ch, Sn	
<i>Moroteuthopsis longimana</i>	Cr, DR, K, PE, SG	DR, K, SG	An, Au, Cr, G, Mac, PE, SG	H, Mac, PE, SG	Cr, PE	Cht	C	Cr, PE		
<i>Nototeuthis dimegacotyle</i>	DR, K	K	An, Au, G, Mac, PE, SG		PE	Cht	C			
<i>Onykia robsoni</i>	PE, SG	SG	An, Au, Cr, G, Mac, PE, SG	PE	Cr, PE	Cht	C	K, PE	Ch, Sn	
<i>Psychroteuthis glacialis</i>	Cr, DR, K, PE, SG	Cr, SG	An, Cr, Mac, PE, SG	C, Cr, Mac, PE, SG	PE					
<i>Taningia danae</i>	K, PE	K	An, Au, Cr, G, Mac, PE, SG	PE	Cr, PE		C	K		
<i>Taonius</i> spp.	Cr, DR, SG	SAf, SG	An, Au, Cr, G, Mac, PE, SG	H, Mac, PE, SG	Cr, PE				Ch, Sn	

(Legend: C-Campbell, K- Kerguelen, SG-South Georgia, DR-Diego Ramirez, Cr-Crozet, SA-South America, FI-Falkland Islands, Mac-Macquarie Island, PE-Prince Edward and Marion Islands, H- Heard Island, Ch-Chatham Islands, G-Gough Island, An-Antipodes, A-Antarctica (waters close to continent), SS-South Shetland Islands, T-Tasman Sea, Au-Auckland Islands, Sn-Snares Islands, NZ-New Zealand waters, Cht-Chatham Islands and Taiaroa Head, SAF-South African waters)

TABLE 1b. Main cephalopod taxa in the diet of petrels and prions.

Cephalopod taxa	Petrels										Prions	
	White-chinned	Northern Giant	Southern Giant	Great-winged	Grey	Westland black	Black	Kerguelen	Blue	Soft-plumaged	Antarctic	thin-billed
<i>Alluroteuthis antarcticus</i>	SAf, SG										SG	
<i>Ancistrocheirus lesueurii</i>				PE		NZ						
<i>Chiroteuthis veranyi</i>				PE			NZ					
<i>Filippovia knipovitchi</i>	Cr	Cr		PE							SG	K
<i>Galiteuthis glacialis</i>	Cr, SG	SG		PE								
<i>Gonatus antarcticus</i>	Cr, SG	Cr, Mac, PE, SG	PE	PE	Cr	NZ		PE		PE	SG	K
<i>Haliphron atlanticus</i>		PE		PE			NZ					
<i>Histioteuthis atlantica</i>		PE		PE			NZ					
<i>Histioteuthis eltaninae</i>	SG	PE			Cr	NZ	NZ	SAf	PE			
<i>Histioteuthis macrobista</i>				PE		NZ	NZ	PE				
<i>Histioteuthis miranda</i>				PE		NZ	NZ					
<i>Lepidoteuthis grimaldii</i>									SAf			
<i>Martialia hyadesi</i>	SG	SG										
<i>Mastigoteuthis psychrophila</i>	SG											
<i>Mesonychoteuthis hamiltoni</i>	SAf											
<i>Moroteuthopsis ingens</i>		Cr, PE	Cr, PE		Cr	NZ						
<i>Moroteuthopsis longimana</i>	Cr, SG	Cr, K, SG	Cr, Mac, PE, SG								SG	
<i>Onykia robsoni</i>			PE	PE								
<i>Psychroteuthis glacialis</i>	SG	SG		SAf								
<i>Taonius</i> spp.	Cr	PE		PE		NZ		PE				

TABLE 1c. Main cephalopod taxa in the diet of penguins.

	Penguins						
Cephalopod taxa	Gentoo	King	Adelie	Rockhopper	Royal	Macaroni	Emperor
<i>Aluroteuthis antarcticus</i>	Cr	Cr, FI, PE, SG		Cr		Cr	A
<i>Filippovia knipovitchi</i>	Cr	Cr, FI, SG		Mac, PE	Mac	Cr, PE	
<i>Galiteuthis glacialis</i>	Cr	Cr, PE					A
<i>Gonatus antarcticus</i>	Cr, FI, K	Cr, FI, PE, SG		FI		Cr	A
<i>Haliophron atlanticus</i>		Cr					
<i>Histioteuthis atlantica</i>		Cr					
<i>Histioteuthis eltaninae</i>		FI		Mac	Mac		
<i>Histioteuthis macrobista</i>		Cr					
<i>Martialia hyadesi</i>	Mac	Cr, FI, Mac, PE, SG		G, Mac,	Mac	SG	
<i>Mesonychoteuthis hamiltoni</i>		Cr	A				A
<i>Moroteuthopsis ingens</i>	FI	Cr, FI		Mac	Mac		A
<i>Moroteuthopsis longimana</i>	Cr, H, K, PE	Cr, FI, PE, SG		Cr, Mac, PE	Mac	Cr, PE, SG	A
<i>Psychroteuthis glacialis</i>		SG	A				A

TABLE 1d. Main cephalopod taxa in the diet of sharks, other fish, dolphins and whales.

Cephalopod taxa	Fish		Sharks		Dolphins			Whales	
	Patagonian toothfish	Porbeagle	Sleeper	Lantern	Southern right-whale	Long-finned pilot whale	Bottlenose	Pilot	Sperm
<i>Alluroteuthis antarcticus</i>	Cr, K, SG	K					SA	SA	
<i>Ancistrocheirus lesueurii</i>						SA			A, SA, SG, T
<i>Batoteuthis skolops</i>	Cr, K, SG			K			SA		
<i>Chiroteuthis veranyi</i>	Cr, K, SG	K					SA	SA	
<i>Filippovia knipovitchi</i>	Cr, K, Mac, SG	K	K				SA		A, SG
<i>Galioteuthis glacialis</i>	Cr, K, Mac, SG	K	K						A, SG
<i>Gonatus antarcticus</i>	Cr, K, Mac, SG	K	K		A		SA	SA	A, SA, SG
<i>Lepidoteuthis grimaldii</i>									A, SA, SG, T
<i>Haliphron atlanticus</i>	C, K	K	K	K					A, SA, SG
<i>Histioteuthis atlantica</i>	Cr, K	K	K	K					A, SA, SG
<i>Histioteuthis bonnellii corpuscula</i>									A, SA, SG
<i>Histioteuthis eltaninae</i>	Cr, K, Mac	K					SA	SA	A, SA, SG
<i>Histioteuthis macrohista</i>	C								
<i>Histioteuthis miranda</i>									A, SA, SG
<i>Martalia hyadesi</i>	Cr, K, SG	K					SA		A, SG
<i>Mastigoteuthis psychrophila</i>	C, K	K		K					A, SA, SG
<i>Mesonyboteuthis hamiltoni</i>	Cr, SG		K				SA	SA	A, SA, SG, T
<i>Moroteuthopsis ingens</i>	Cr, K, Mac	K	K				SA	SA	A, SA, SG
<i>Moroteuthopsis longimana</i>	Cr, K, Mac, SG	K	K				SA		A, SG, T
<i>Nototeuthis dimegacotyle</i>	Cr, K	K							
<i>Orykia roboni</i>	K		K						A, SA, SG, T
<i>Pycroteuthis glacialis</i>	Cr, K, SG								A, SG
<i>Tiningia danae</i>	Cr, K		K				SA		A, SA, SG, T
<i>Taonius</i> spp.	SG						SA		A, SA, SG, T

TABLE 1e. Main cephalopod taxa in the diet of seals.

Cephalopod taxa	Seals				
	Antarctic fur	Sub-Antarctic fur	Elephant	Weddell	Sea lion
<i>Alluroteuthis antarcticus</i>	SG, SA		A, SG, SS		SA
<i>Batoteuthis skolops</i>			SG		
<i>Chiroteuthis veranyi</i>			SS		
<i>Filippovia knipovitchi</i>	K, SG	G	A, SG, SS	SS	
<i>Galiteuthis glacialis</i>	SG		A, SG		
<i>Gonatus antarcticus</i>	K		A, Mac, SG, SS	SS	
<i>Martialia hyadesi</i>	SG, K		SG		
<i>Mastigoteuthis psychrophila</i>	SG				
<i>Mesonychoteuthis hamiltoni</i>			SG		
<i>Moroteuthopsis ingens</i>	K				
<i>Moroteuthopsis longimana</i>	SG		Mac, SG, SS, A	SS	
<i>Psychroteuthis glacialis</i>			A, SS, SG	A, SS	

References: Adams & Klages (1987), Aguiar dos Santos & Haimovici (2001), Alonso *et al.* (1998), Arata & Xavier (2003), Arata *et al.* (2004), Berrow & Croxall (1999), Bester & Laycock (1985), Brooke & Klages (1986), Brown & Klages (1987), Casaux *et al.* (1997), Casaux *et al.* (2003), Cherel & Duhamel (2003), Cherel & Duhamel (2004), Cherel & Klages (1998), Cherel & Kooyman (1998), Cherel & Weimerskirch (1995), Cherel & Weimerskirch (1999), Cherel *et al.* (2004), Cherel *et al.* (2002a,b,c), Cherel *et al.* (1996), Cherel *et al.* (2000), Clarke & Prince (1981), Clarke & MacLeod (1982a,b), Clarke & Goodall (1994), Clarke *et al.* (1976), Clarke *et al.* (1981), Clarke (1996), Clausen & Pütz (2003), Cooper & Brown (1990), Cooper & Klages (1995), Cooper *et al.* (1992), Croxall & Lishman (1987), Croxall *et al.* (1997), Croxall *et al.* (1995), Croxall *et al.* (1985), Croxall *et al.* (1999), Daneri *et al.* (2000), Daneri *et al.* (1999), Doidge & Croxall (1985), Garcia de la Rosa *et al.* (1997), Goldsworthy *et al.* (2001), Goldsworthy *et al.* (2002), Goodall & Galeazzi (1985), Green & Burton (1987), Green *et al.* (1998), Green & Wong (1992), Herling *et al.* (2005), Hoff (2001), Hoff *et al.* (2003), Hull (1999), Hunter (1983), Hunter & Klages (1989), Imber (1976), Imber (1992), Imber (1999), Imber & Russ (1975), Imber & Berruti (1981), Imber *et al.* (1995), Kent *et al.* (1998), Klages *et al.* (1988), Lea *et al.* (2002), Lescroët *et al.* (2004), Lipinski (2001), Lipinski & Jackson (1989), Lorentsen *et al.* (1998), Nel *et al.* (2000), Nel *et al.* (2001), North (1996), Offredo *et al.* (1985), Piatkowski *et al.* (2001), Piatkowski *et al.* (2002), Plötz (1986), Plötz *et al.* (1991), Prince (1980), Reid & Arnould (1996), Reid *et al.* (1997), Richardson *et al.* (2000), Ridoux (1994), Robertson *et al.* (1994), Rodhouse & Prince (1993), Rodhouse *et al.* (1987), Rodhouse *et al.* (1990), Rodhouse *et al.* (1992), Rodhouse *et al.* (1996), Rodhouse *et al.* (1998), Thomas (1992), Thompson (1992), Young *et al.* (1997), Waugh *et al.* (1999), Xavier *et al.* (2003a,b,c), Xavier *et al.* (2002), Xavier *et al.* (2004).

TABLE 2. Darkening of lower beaks (from the wings) of cephalopod species from the Southern Ocean and adjacent areas.

Species	Wings start darken (mm)		Reference
	Minimum	Maximum	
<i>Anicistrocheirus lesueurii</i>	<3.78	6.00	Clarke (1986), Lu & Ickeringill (2002)
<i>Architeuthis dux</i>	7.00	11.00	Clarke (1986)
<i>Bathyteuthis abyssicola</i>	0.55		Lu & Ickeringill (2002)
<i>Chiroteuthis veranyi</i>	3.00	4.00	Clarke (1986)
<i>Cycloteuthis sirventi</i>	8.00	12.00	Clarke (1986)
<i>Gonatus antarcticus</i>	<5.50		Clarke (1986)
<i>Histioteuthis atlantica</i>	2.54	3.50	Clarke (1986), Lu & Ickeringill (2002)
<i>Histioteuthis bonnellii corpuscula</i>	3.04		Clarke (1986), Lu & Ickeringill (2002)
<i>Histioteuthis eltaninae</i>	2.20		Clarke (1986), Lu & Ickeringill (2002)
<i>Histioteuthis macrobista</i>	1.50	3.20	Clarke (1986)
<i>Histioteuthis miranda</i>	>2.41	<5.40	Clarke (1986), Lu & Ickeringill (2002)
<i>Illex argentinus</i>		<4.00	Clarke (1986)
<i>Lepidoteuthis grimaldii</i>	7.50	17.00	Clarke (1986)
<i>Lycoteuthis lorigera</i>	> 2.56		Lu & Ickeringill (2002)
<i>Martidlia byadesi</i>	3.70		Clarke (1986)
<i>Mesonychoteuthis hamiltoni</i>	17.00	27.00	Clarke (1986)
<i>Moroteuthopsis ingens</i>	8.20	10.50	Clarke (1986)
<i>Moroteuthopsis longimana</i>	9.00	12.00	Clarke (1986)
<i>Onykia robsoni</i>	5.00	10.50	Clarke (1986)
<i>Onychoteuthis banksii</i> complex	2.02	2.36	Lu & Ickeringill (2002)
<i>Pholidoteuthis massyae</i>	5.00	6.00	Clarke (1986)
<i>Taningia danae</i>	9.00	16.00	Clarke (1986)
<i>Taonius notalia</i>	5.00	6.00	Clarke (1986)
<i>Teuthowenia pellucida</i>	2.66	3.14	Lu & Ickeringill (2002)

TABLE 3. Latest nomenclature of some Southern Ocean species.

Before	BAS collection	Xavier and Cherel (2009)	Cherel (2020)	Reference
<i>Chroteuthis</i> sp. C (Clarke 1980)	<i>Chroteuthis veranyi</i>	<i>Chroteuthis veranyi</i>		Clarke (1980), Xavier <i>et al.</i> (2003b)
	<i>Brachioleuthis ? picta</i> (Clarke 1986)	<i>Brachioleuthis linkowskyi</i>		Clarke (1986), Lipinski (2001)
	<i>Brachioleuthis ? picta</i> (Rodhouse <i>et al.</i> 1992)	<i>Slosarczykovia circumantarctica</i>		Rodhouse <i>et al.</i> (1992), Lipinski (2001)
	<i>Chroteuthis</i> sp.	? <i>Mastigoteuthis</i> A (Clarke 1986)	<i>Asperoteuthis lui</i>	Clarke (1986), Cherel (2020)
		<i>Galiteuthis</i> sp. 3 (Imber)	<i>Galiteuthis submi</i>	Cherel (2020)
		<i>Galiteuthis</i> stC sp. (Imber)	<i>Ligurolla podophthalma</i>	Cherel (2020)
		<i>Taonius</i> sp. (Clarke)	<i>Taonius exolitius</i>	Cherel (2020)
	<i>Taonius</i> sp. (cf. <i>pavo</i>)	<i>Taonius</i> sp. B (Voss)	<i>Taonius notalia</i>	Cherel (2020)
		<i>Cycloteuthis akimushkini</i>	<i>Cycloteuthis sirenti</i>	Cherel (2020)
		<i>Oegopsida</i> sp. A (Cherel)	<i>Gonatopsis octopedatus</i>	Cherel (2020)
<i>Histioteuthis</i> A2 (Clarke 1986)	<i>Histioteuthis corpuscula</i>	<i>H. bonnellii corpuscula</i>		
<i>Histioteuthis</i> A1 (Clarke 1986)	<i>Histioteuthis macrobista</i>	<i>H. macrobista</i>		Clarke (1986), Cherel <i>et al.</i> (2004)
<i>Histioteuthis</i> A3 (Clarke 1986)	<i>Histioteuthis miranda</i>	<i>H. miranda</i>		Clarke (1986), Xavier <i>et al.</i> (2003b)
<i>Histioteuthis</i> A5 (Clarke 1986)		<i>H. arcturi</i>		Clarke (1986)
<i>Histioteuthis</i> B1 (Clarke 1986)	<i>Histioteuthis elaninae</i>	<i>H. elaninae</i>		Clarke (1986)
<i>Histioteuthis</i> B3 (Clarke 1986)	<i>Histioteuthis atlantica</i>	<i>H. atlantica</i>		Clarke (1986)
		<i>Loligo gabi</i>	<i>Doryteuthis gabi</i>	Cherel (2020)
<i>Lycoteuthis diadema</i>		<i>Lycoteuthis lorigera</i>		
? <i>Cryptalloteuthis glacialis</i> (Clarke 1980)	<i>Alluroteuthis antarcticus</i>	<i>Alluroteuthis antarcticus</i>		Clarke (1980), Xavier <i>et al.</i> (2003b)
<i>Moroteuthis</i> A (Clarke 1980)		<i>Moroteuthis ingens</i> (Clarke 1986)	<i>Moroteuthopsis ingens</i>	Clarke (1980), Clarke (1986)
		<i>Moroteuthis knipovitchi</i>	<i>Filippovia knipovitchi</i>	Cherel (2020)
		<i>Kondakovia longimana</i>	<i>Moroteuthopsis longimana</i>	Cherel (2020)
		<i>Moroteuthis</i> sp. B (Imber)	<i>Moroteuthopsis</i> sp. B (Imber)	Cherel (2020)
		<i>Moroteuthis roboni</i>	<i>Onykia roboni</i>	Cherel (2020)
		<i>Onychoteuthis</i> sp. B (Imber)	<i>Notorykia africanae</i>	Cherel (2020)
		<i>Onychoteuthis banksii</i>	<i>Onychoteuthis banksii</i> complex	Cherel (2020)
		<i>Onychoteuthis</i> sp. C (Imber)	<i>Walvisteuthis rancureli</i>	Cherel (2020)
		<i>Psychroteuthis glacialis</i> (larger beaks)	<i>Psychroteuthis glacialis</i>	Cherel (2020)
		<i>Psychroteuthis glacialis</i> (smaller beaks)	<i>Psychroteuthis</i> sp. B (Imber)	Cherel (2020)
<i>Alloposus mollis</i> (Clarke 1980)	<i>Haliphron atlanticus</i>	<i>Haliphron atlanticus</i>		Clarke (1980), Xavier <i>et al.</i> (2003b)
		<i>Benthoctopus thielei</i>	<i>Musoctopus thielei</i>	Cherel (2020)

Legend: British Antarctic Survey – BAS, Centre d'Etudes Biologiques de Chizé – CEBC.



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