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?*Mastigoteuthis* B Clarke, 1980, is a junior synonym of *Asperoteuthis acanthoderma* (Lu, 1977) (Cephalopoda, Oegopsida, Chiroteuthidae), a rare cosmopolitan deep-sea squid

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Abstract
The present work resolved the long-standing taxonomic problem associated with the enigmatic ?*Mastigoteuthis* B Clarke, 1980, by demonstrating that these lower beaks correspond to those of the large deep-sea chiroteuthid *Asperoteuthis acanthoderma* (Lu, 1977). A review of the existing literature listed 22 specimens of *A. acanthoderma*, but synonymizing ?*Mastigoteuthis* B with *A. acanthoderma* increased 14 times the species record worldwide. Pooling the data from both specimens and beaks (a total of 329 individuals) indicates that the species has a circumglobal distribution, since it occurs in tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans. The synonymization also highlights trophic relationships of the species as a prey of top marine predators. Lower beaks of *A. acanthoderma* were mostly found in stomachs of sperm whales, but a few beaks were also recorded from stomach contents of sharks, swordfish and the wandering albatross.

Keywords Biogeography · Cephalopods · Distribution · Predators · Squid · Taxonomy · Trophic relationships

Introduction

A peculiar species of chiroteuthid, "*Chiroteuthis*" *acanthoderma*, was described by Lu (1977) from two specimens collected in the Celebes Sea and northwest of New Guinea. A few years later, the species was incorrectly synonymized with the incompletely described "*Chiroteuthis*" *famelica* (now *Echinoteuthis famelica* (Berry, 1909)), and the new genus *Asperoteuthis* was erected for it because it was different from all the other members of the genus *Chiroteuthis* (Nesis 1980). Subsequently, "*Chiroteuthis*" *acanthoderma* and "*Chiroteuthis*" *famelica* were recognized as different taxa, and the type species of the genus *Asperoteuthis* is considered today to be "*Chiroteuthis*" *acanthoderma* Lu, 1977 in place of "*Chiroteuthis*" *famelica* (Berry, 1909) (Young 1991; Young et al. 2007). Currently, the genus *Asperoteuthis* includes three valid species, namely, *A. acanthoderma* (Lu, 1977), *A. lui* Salcedo-Vargas, 1999, which was described from a single head obtained from the stomach of a pink cusk-eel *Genypterus blacodes* (Bloch and Schneider, 1801) caught in New Zealand (Salcedo-Vargas 1999), and *A. mangoldae* Young, Vecchione and Roper, 2007, which was described from specimens caught in nets in Hawaiian waters (Young et al. 2007). *Asperoteuthis* species are rarely recorded deep-sea squids. For example, I found no citation of additional records of *A. mangoldae* since its original description based on 18 specimens (Young et al. 2007) and 12 specimens of *A. lui* were listed in a recent taxonomic revision of the species, most of them being damaged or very incomplete (Braid 2017).

Identification of cephalopod prey of marine predators by using the morphology of their chitinized beaks that accumulate in consumers' stomach was initiated in the 1960s and subsequently developed with an initial focus on the feeding habits of sperm whales *Physeter macrocephalus* Linnaeus, 1758 (Clarke 1972, 1986). In his seminal and beautifully illustrated monograph, Clarke (1980) detailed two new mastigoteuthids, ?*Mastigoteuthis* A and ?*Mastigoteuthis* B, from stomach contents of sperm whales caught in the Southern Hemisphere. ?*Mastigoteuthis* A was described from

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two incomplete specimens collected in South Georgia, and the typical beaks of the species were also recorded elsewhere in the southern Atlantic (Clarke 1980). Twenty-eight years later, Arkhipkin and Laptikhovsky (2008) suggested that ?*Mastigoteuthis* A corresponds to the newly described chiroteuthid *Asperoteuthis nesisi*. The hypothesis was confirmed in an elegant integrative taxonomic investigation using a combination of morphology and DNA analysis by Braid (2017), which synonymized ?*Mastigoteuthis* A and *A. nesisi* with *A. lui*. A close examination of the beaks of *A. nesisi* (= *A. lui*) revealed that they were identical to those of ?*Mastigoteuthis* A, and a subsequent review of the literature on cephalopod prey of marine predators increased the number of records of the species, whose beaks had been identified in stomach contents of seabirds, pinnipeds and odontocetes (Cherel 2020). *A. lui* is now considered a circumpolar Southern Ocean meso-bathypelagic endemic that occurs occasionally into the subtropics (Clarke 1980; Braid 2017; Cherel 2020).

In contrast to ?*Mastigoteuthis* A, no flesh was available to establish the taxonomic affinity of ?*Mastigoteuthis* B, and the identification was tentative (Clarke 1980). ?*Mastigoteuthis* B beaks were initially identified from stomach contents of sperm whales caught off South Africa and western Australia, and, unlike ?*Mastigoteuthis* A, they were not recorded from whales caught in the Southern Ocean (Clarke 1980). ?*Mastigoteuthis* B was tentatively identified with the large mastigoteuthid *Idioteuthis cordiformis* (Chun, 1908) (Braid and Bolstad 2015), but lower beaks of the two species showed distinct morphological features that preclude synonymy. Hence, the identification of the enigmatic ?*Mastigoteuthis* B beaks is still unresolved, corresponding to those of either an already described but poorly known large-sized oceanic squid or to a species new to science.

Here, I show that ?*Mastigoteuthis* B beaks are those of the rarely recorded deep-sea chiroteuthid *A. acanthoderma* by examining and comparing beaks initially identified as ?*Mastigoteuthis* B, *Asperoteuthis* sp. and *A. acanthoderma*, with those from two *A. acanthoderma* specimens identified morphologically. Then, the scientific literature on cephalopods and cephalopod predators was reviewed to increase the number of records of *A. acanthoderma*, thus improving the species biogeography and trophic relationships.

Material and methods

Based on Clarke (1980, 1986), I identified ?*Mastigoteuthis* B beaks from dietary samples of several predators, including sharks, bony fishes and albatrosses. I also examined lower beaks that were identified by other scientists, including (i) one ?*Mastigoteuthis* B beak from the set of beaks that initiated the original description of the species (Clarke 1980), (ii) five *Asperoteuthis* sp. beaks from New Zealand (Gomez-Villota 2007) and two *A. acanthoderma* beaks from Singapore (identification by T. Kubodera; Chua et al. 2019). All were accumulated beaks sorted from stomach contents of sperm whales (Table 1). I also looked at both upper and lower beaks of two *A. acanthoderma* that were collected in the Indian Ocean and identified morphologically from the whole specimens (Table 2).

Two complementary data sets were combined to gather information on the genus *Asperoteuthis* and *A. acanthoderma*. Firstly the literature on *Asperoteuthis* taxonomy and biogeography since the description of "*Chiroteuthis*" (= *Asperoteuthis*) *acanthoderma* by Lu (1977) was thoroughly examined (Table 2), including general catalogues on squids worldwide (Nesis 1987; Jereb and Roper 2010; Okutani 2015; Young et al. 2019). Secondly, dietary investigations were reviewed since the original description of ?*Mastigoteuthis* B lower beaks collected from stomach contents of sperm whales by Clarke (1980) (Table 1).

Results

Lower beaks of ?*Mastigoteuthis* B were described in details and well illustrated (Fig. 1) (Clarke 1980, 1986). Drawings of lower and upper beaks of the holotype of "*Chiroteuthis*" *acanthoderma* were included in the original description of the species (Lu 1977), and helpful photos of *Asperoteuthis acanthoderma* beaks are available in publications and on the web (Fig. 2) (Tsuchiya and Okutani 1993; Okutani et al. 2005; Young et al. 2019). Based on Clarke (1980, 1986), the main features distinguishing these lower beaks are:

1. Their overall large size when compared to those of most squid species, with lower rostral length (LRL) of beaks with darkened wings being in the range 5.0–13.3 mm.
2. The rostral edge is curved in profile and about half as long as the wing length.
3. A prominent high wing fold obscures the jaw angle from the side.
4. A well-marked wing fold runs to about the middle of the posterior edge of the lateral wall.
5. The hood is shallowly notched and measures about half the crest length.

Beaks of *A. acanthoderma* are larger than those of *A. lui* which they resemble superficially, but lower beaks of *A. lui* have longer shoulder and a more backward sloping rostral edge (Clarke 1980, 1986). All *A. acanthoderma* upper beaks examined had a relatively short rostrum and long lateral walls. Beaks of the smaller *A. mangoldae* were not examined in the present study.

Table 1 Records of beaks of *Asperoteuthis acanthoderma* in the scientific literature

Location	Oceanic area	Initial identification	Number of specimens	Number of beaks		Source and comments	Sampling years	LRL (mm)	References
				Lower	Upper				
Atlantic Ocean									
Azores	Subtropical central	*Mastigoteuthis* sp. B	2	2	na	Sperm whale	1981–1984	na	Clarke et al. (1993)
South Africa (Donkergat)	Subtropical southeast	?*Mastigoteuthis* B	164	164	na	Sperm whale	1962–1963	na	Clarke (1980)
Indian Ocean									
South Africa (Durban)	Subtropical southwest	?*Mastigoteuthis* B	63	63	na	Sperm whale	1926–1969	na	Clarke (1980)*
Seychelles	Tropical western	?*Mastigoteuthis* B	1	1	1	Silky shark	2001	8.4	Y. Cherel unpublished data
Northern Mozambique Channel	Tropical western	?*Mastigoteuthis* B	1	1	1	Swordfish	2004	6.4	Y. Cherel unpublished data
Crozet	Southern	?*Mastigoteuthis* B	2	2	na	Wandering albatross	1992	5.3, 7.5	Y. Cherel unpublished data
Australia (Albany)	Subtropical southeast	?*Mastigoteuthis* B	6	6	na	Sperm whale	1955–1966	na	Clarke (1980)
Pacific Ocean									
Singapore	Tropical central	*A. acanthoderma*	25	25	na	Sperm whale	2015	7.8 ± 2.3 (4.5–11.2)	Chua et al. (2019)*
35–42°N, 155° E–178° W	Subtropical northwest	*A. acanthoderma*	1	1	na	Blue shark	2000	na	Kubodera et al. (2007)
Tasman Sea	Subtropical southwest	?*Mastigoteuthis* B	16	16	na	Sperm whale	1970	na	Clarke and MacLeod (1982)
New Zealand	Subtropical southwest	*Asperoteuthis* sp.	25	25	na	Sperm whale	2003	na	Gomez-Villota (2007)*
Canada (Vancouver Island)	Subarctic northeast	?*Mastigoteuthis* sp.	1	1	na	Sperm whale	No data	9.4	Clarke and MacLeod (1980)
Total			307						

LRL lower rostral length, *na* not applicable (in many cases, only lower beaks were examined and identified). * Some beaks were examined by the author

Table 2 Records of specimens of *Asperoteuthis acanthoderma* in the scientific literature

Location	Oceanic area	Number of specimens	Source and comments	Sampling years	Sex	Mantle length (cm)	References
Atlantic Ocean							
USA (Florida)	Tropical northwest	2	Floating at the surface	2007	Mature females	62.0*, 163.0	Judkins et al. (2009)
West Indies (Grand Cayman Island)	Tropical northwest	2	Floating at the surface	2006, 2009	No data	No data	Judkins et al. (2009), http://archive.caymannewsservice.com/2009/10/06/six-foot-squid-found-in-cayman-waters/
West Indies (Little Cayman Island)	Tropical northwest	1	Floating at the surface	2008	No data	152.4*	Judkins et al. (2009)
Gulf of Mexico	Tropical northwest	2	No data, pelagic trawl (0–1500 m)	2010, 2016	Mature male, no data	65, no data	Young et al. (2019)
No data	Western South	1	5.3 mm LRL	No data	No data	30.0	Young et al. (2019)
Indian Ocean							
South Africa	Subtropical southwest	2	Pelagic trawl	1991	No data	No data	Salcedo-Vargas (1999), F. Wayne personal communication
Arabian Sea (India)	Tropical northern	1	Pelagic trawl (350–400 m)	2013	No data	2.25	Rithin et al. (2015)
Australia (off western Australia)	Tropical southeast	1	ROV (580 m)	2005	No data	No data	Judkins et al. (2009)
No data	No data	1	11.8 mm LRL**	No data	Indeterminate	103.0	Braid (2017)
Seychelles	Tropical western Indian	1	Seafood market, 10.7 mm LRL**	2005	No data	No data	H. Braid personal communication
Pacific Ocean							
Celebes Sea and northwest of New Guinea	Tropical western	2	Pelagic trawl	1929	Immature females	18.8*, 14.4*	Lu (1977), Roper and Lu (1990), as "*Chiroteuthis" acanthoderma*
East of the Philippine Islands	Tropical western	1	Pelagic trawl (200 m)	1975	Immature, sex unknown	12.8	Nesis (1980), as "*Chiroteuthis" famelica*
Japan (Okinawa)	Tropical northwest	3	Seafood market	1991, 1993	Immature females	78*, 56*, 45*	Tsuchiya and Okutani (1993)
Hawaii	Tropical central	1	2.2 mm LRL	No data	Unknown	12.0	Young et al. (2019)
35°21′ N, 144°15′ E	Subtropical northern	1	Sperm whale stomach, 7.5 mm LRL	2001	No data	47.0	Okutani et al. (2005)
Total		22					

LRL lower rostral length. * Damaged, **beaks examined and measured by the author

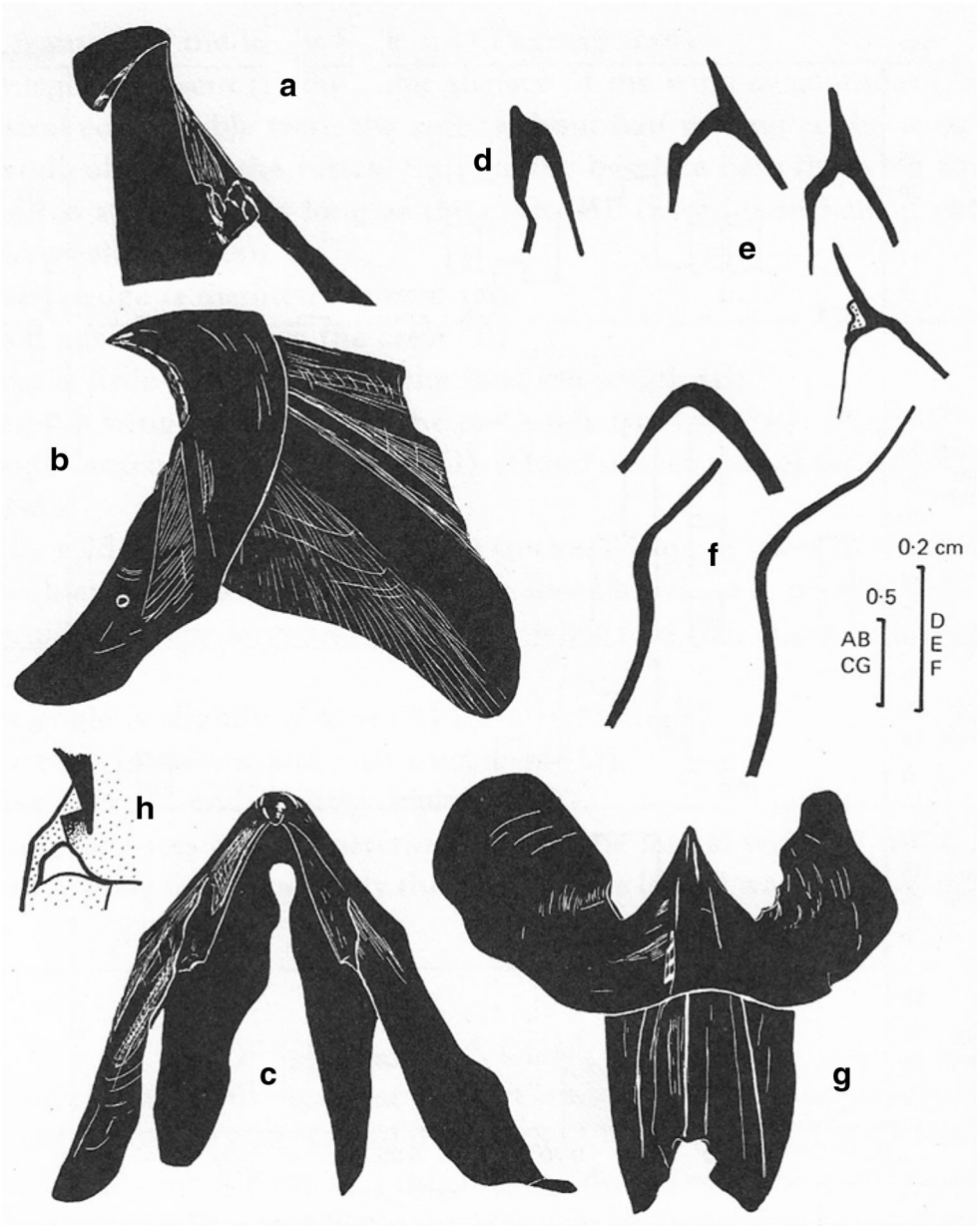

Fig. 1 Original drawings of ?*Mastigoteuthis* B beaks by Clarke (1980). The lower beak (LRL = 8.6 mm) was collected from a sperm whale caught offshore Durban, South Africa (Clarke 1986)

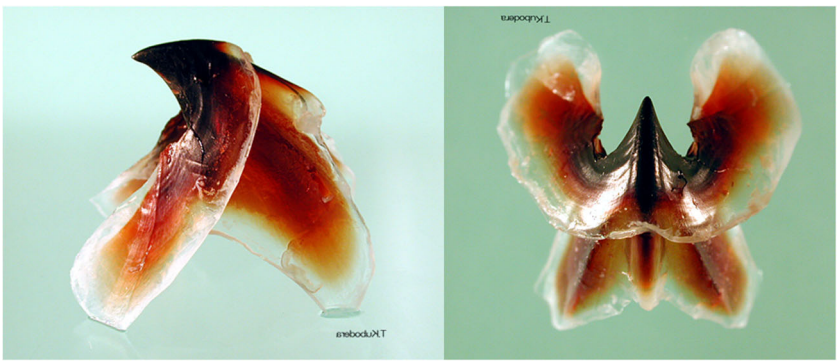

Fig. 2 Photos of an *Asperoteuthis acanthoderma* beak by T Kubodera (Okutani et al. 2005). The lower beak (LRL = 7.5 mm) was collected from a sperm whale caught by JARPN-II in the North Pacific

I identified two ?*Mastigoteuthis* B lower beaks from stomach contents of the wandering albatross *Diomedea exulans* Linnaeus, 1758, which were collected in 1992. They were smaller but identical to a large beak from the M Clarke's sperm whale collection (Table 1). Then, two pairs of beaks from stomach contents of a silky shark *Carcharhinus falciformis* (Müller and Henle, 1839) and a swordfish *Xiphias gladius* Linnaeus, 1758, were identified as being ?*Mastigoteuthis* B, with lower beaks looking similar to those of *A. acanthoderma* on photos from the web site of the National Science Museum, Tokyo, Japan (Okutani et al. 2005). The link between ?*Mastigoteuthis* B beaks and the genus *Asperoteuthis* was reinforced in 2006 when I examined five beaks identified as *Asperoteuthis* sp. by Gomez-Villota (2007). At that time, the systematics of the genus *Acanthoderma* was still confused, thus precluding identifying beaks to the species level with confidence. More recently, examination of two *A. acanthoderma* lower beaks from a stranded sperm whale in Singapore (Chua et al. 2019) and beaks from two *A. acanthoderma* specimens from the Indian Ocean that were visually identified (Braid personal communication) definitively synonymized ?*Mastigoteuthis* B with *A. acanthoderma*.

A review of the existing literature on *A. acanthoderma* listed 22 specimens (Table 2). Many of them were damaged, thus precluding accurate body measurements. The largest specimen is a mature female with a mantle length of 163 cm (342 cm total length), which was found floating dead at the surface off Florida; unfortunately, there was no information on her beak size (Judkins et al. 2009). Dietary informations added 307 records of *A. acanthoderma*, mainly as ?*Mastigoteuthis* B beaks (Table 1). Most of the lower beaks were fully darkened, thus indicating adult squids. The largest measured beak had a ~ 13.3 mm LRL (estimated from Text-Fig. 159 in Clarke 1980). A very large beak with a 20.8 mm LRL is an outlier, thus possibly indicating another species (Clarke and MacLeod 1982). Remarkably, almost all the beaks ($n = 302$, 98.4%) were collected from sperm whales, with few of them having been found in stomach contents from two shark species, one bony fish and one seabird (Table 1).

Pooling the data from both specimens and beaks (a total of 329 individuals) indicates that *A. acanthoderma* has a circumglobal distribution. The species was recorded in tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans (Tables 1 and 2). Its presence in subantarctic waters needs confirmation from whole specimens and/or lower beaks, because only two upper beaks were provisionally identified as *A. acanthoderma* from stomach contents of a southern sleeper shark *Somniosus antarcticus* Whitley, 1939, and of a Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898 (as *Mastigoteuthis* B and ?*Mastigoteuthis* B, respectively) caught in the southern Indian Ocean (Cherel and Duhamel 2004; Cherel et al. 2004, 2011).

Discussion

The present work resolved the long-standing taxonomic problem associated to the enigmatic ?*Mastigoteuthis* B beaks by demonstrating that they are not those of a new species but, instead, that they correspond to lower beaks of the large chiroteuthid *A. acanthoderma*. Drawings and photos of both ?*Mastigoteuthis* B and *A. acanthoderma* beaks were available independently of each other, but no one realized their synonymy until a close comparative examination showed they are identical. Hence, lower beaks originally described as ?*Mastigoteuthis* A and ?*Mastigoteuthis* B by Clarke (1980) correspond to two species of the genus *Asperoteuthis*, *A. lui* (Braid 2017) and *A. acanthoderma* (this study), respectively, thus shifting the two taxa from the family Mastigoteuthidae to the closely related family Chiroteuthidae.

Synonymizing ?*Mastigoteuthis* B with *A. acanthoderma* increased 14 times the species records worldwide. *A. acanthoderma* has a circumglobal distribution in the tropics and subtropics, and it does not occur in polar waters. Molecular analysis confirmed this wide, multi-ocean distribution, since low genetic variation was found between one specimen from Japan and another one from the Caribbean Sea (Braid and Bolstad 2017). The presence of *A. acanthoderma* in subantarctic waters is questionable, because the finding of accumulated beaks in the diet of the wide-ranging (from Antarctica to the subtropics; Weimerskirch et al. 2014) wandering albatross from the Crozet Islands does not necessarily prove that the squids were caught in the Southern Ocean. Within that context, it is important to note that the distribution of the Southern Ocean *A. lui* was included in maps referring to *A. acanthoderma*, thus erroneously extending southwards the distribution of *A. acanthoderma* (Jereb and Roper 2010; Okutani 2015; Reid 2016). Overall, the genus *Asperoteuthis* include one small (*A. mangoldae*), one medium-sized (*A. lui*) and one large (*A. acanthoderma*) species, each having a distinct biogeography, with overlaps between the cosmopolitan *A. acanthoderma* and the two other species. *A. mangoldae* is known from the equatorial Pacific Ocean (off the Hawaiian Islands and off Jarvis Island), where it is more abundant than *A. acanthoderma* (Young et al. 2019), and the circumpolar Southern Ocean *A. lui* occurs rarely in southern subtropical waters, where *A. acanthoderma* dominates (Table 1, Braid 2017).

The synonymization also highlights trophic relationships of the species as a prey of top marine predators. To the best of my knowledge, a single specimen of *A. acanthoderma* was previously found in the stomach of a sperm whale that was caught in the northern Pacific (Table 2), while several hundred beaks were sorted from stomach contents of various predators caught elsewhere (Table 1). The occurrence of *A. acanthoderma* in the diet of the deep-diving sperm whale and in nets conducted at 200–1500 m (Table 2) is in agreement with *Asperoteuthis* species being considered meso- and bathypelagic squids (Young et al.

2007; Arkhipkin and Laptikhovsky 2008). The presence of *A. acanthoderma* in the diet of the surface-feeder wandering albatross can be easily explained by its likely positive buoyancy, as several specimens were collected floating dead at the surface (Table 2).

The present study illustrates the usefulness of using different means (specimens' morphology and anatomy, DNA analysis, beak morphology) that complement each other to disentangle and clarify taxonomic issues. In many cases, predators are relevant bio-sampling organisms that provide significant biological information on their prey (Cherel and Weimerskirch 1999, Cherel 2020). For example, the synonymy between *A. lui* and ?*Mastigoteuthis* A was established by comparing DNA sequences from whole specimens with those of buccal masses that were identified from their beaks and found in stomachs of the Antarctic toothfish *Dissostichus mawsoni* Norman, 1937 (Braid 2017). Finally, the present work also exemplifies why beaks have to be well illustrated and photographed when describing new species to science or when "unknown" beaks are recovered from stomach contents of marine predators.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability All data generated or analysed during this study are included in this published article.

Author contribution Not applicable.

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