

A giant squid (*Architeuthis dux*) off Reunion Island, western Indian Ocean: the greatest giant ever?

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A freshly dead individual of the giant squid Architeuthis dux, presumably mutilated by a predator of bigger or comparable size, is reported from the south-western Indian Ocean in proximity to Reunion Island. The species was identified from body and beak morphology and validated genetically. The dorsal mantle length (DML) estimated from beak measurements (lower rostral length, LRL) varied between 2153 and 3060 mm depending on the allometric equation used. The Architeuthis dux individual described here is the biggest giant squid ever reported for the region.

Keywords: Cephalopod habitat, distribution records, lower rostral length, dorsal mantle length, total length

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INTRODUCTION

The giant squid *Architeuthis dux* Steenstrup, 1857 is an enigmatic deep-water cephalopod inhabiting temperate oceans and adjacent subpolar and subtropical waters worldwide (Cherel, 2003; Nesis, 2003; Winkelmann *et al.*, 2013; Roper *et al.*, 2015; Wada *et al.*, 2015). Its biology and distribution remain obscure, despite recent technological advances, which allowed *in-situ* giant squid observations (Kubodera & Mori, 2005; Schroepe, 2013), and numerous records from all major oceans (Nesis *et al.*, 1985; Re *et al.*, 1998; Cherel, 2003; Martins & Alvarez Perez, 2009; Winkelmann *et al.*, 2013; Roper *et al.*, 2015).

Life history characteristics of the giant squid are largely unknown, despite the species probably being one of the largest marine animals. Anecdotal reports of total length (TL) often approach extreme values of several tens of metres (Heuvelmans, 1968; Paxton, 2016); however, scientific literature documents considerably smaller sizes. Even scientific records of *A. dux* that ranged within 15–20 m TL (Kirk, 1888; Berzin, 1971, 1972) are commonly challenged (Grist & Jackson, 2007; McClain *et al.*, 2015; Paxton, 2016). There is also disagreement on giant squid lifespan: estimates of longevity range from 2–3 years (Gauldie *et al.*, 1994; Lipiński, 1997; Lordan *et al.*, 1998; Grist & Jackson, 2007) to over 35 years (Landman *et al.*, 2004).

In the Indian Ocean, the first report of *A. dux* dates back to the 19th century (Vélain, 1877), while the number of occurrences currently exceeds 100 records (Yukhov, 1974, 2014; Clarke, 1980; Mikhalev *et al.*, 1981; Nesis *et al.*, 1985; Cherel, 2003; GBIF, 2016; OBIS, 2016). The majority of regional *A. dux* encounters originate from temperate and

sub-Antarctic waters, most of which correspond to remains recovered from predators' stomachs (usually from the sperm whale *Physeter macrocephalus* and various shark species), but some specimens were found floating at the surface or stranded (Vélain, 1877; Yukhov, 1974, 2014; Clarke, 1980; Mikhalev *et al.*, 1981; Cherel, 2003). To date, the largest reported Indian Ocean giant squids reached 2200–2300 mm in dorsal mantle length (DML) either measured or estimated from reference parts such as the lower beak (Cherel, 2003; Yukhov, 2014).

Only two giant squid occurrences have so far been documented in the tropical area of the Indian Ocean: around Mauritius (Staub, 1993) and Reunion Island (Cherel, 2003). Several giant squids from the Mozambique Channel, mentioned in Yukhov (2014), lack georeferencing data, corresponding measurements and other details. The global distribution of giant squid, reported in Roper & Boss (1982), also indicates a single record of the giant squid in the northern Indian Ocean; however no sampling details were provided. Here, we document the occurrence of the biggest giant squid ever discovered in the Indian Ocean, recovered in 2016 off Reunion Island.

MATERIALS AND METHODS

Squid collection

A squid specimen of several metres long (Figure 1A, B), lacking the distal part of the mantle (including the fin), was found floating at the surface waters off Saint Gilles, Reunion Island by the game fishing vessel 'Maeva 4' (12 m length overall) on 4 March 2016. The precise GPS position was not recorded, but coordinates were estimated to be 21°03'S 55°08'E from eyewitness statements of '5–6 nautical miles off Saint-Gilles'. Digital photographs were taken by fishermen and used for

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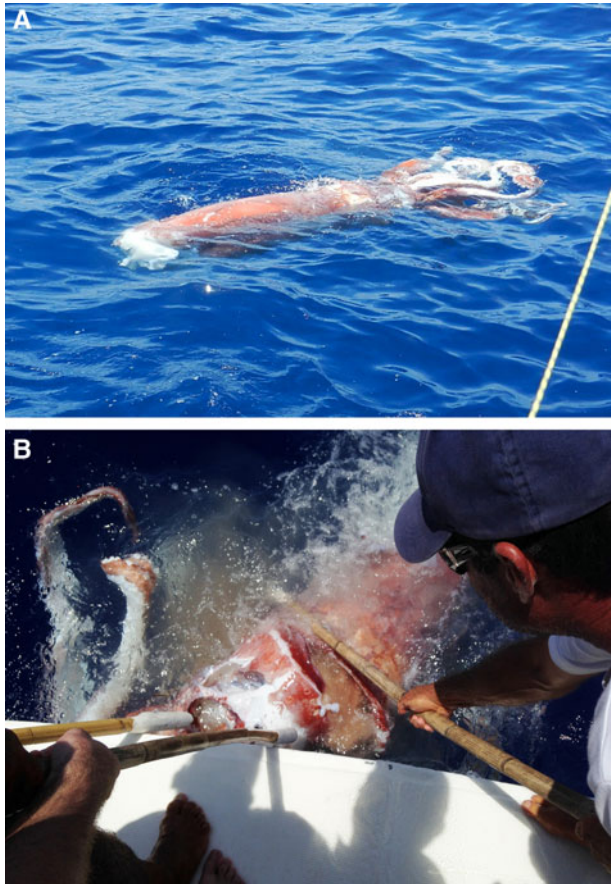


Fig. 1. The giant squid *Architeuthis dux* specimen at the surface, off Saint Gilles, Reunion Island on 4 March 2016. (A) Free-floating squid; (B) Attempts to pull the specimen on board by the crew of FV 'Maeva 4'.

morphological examination. Although dead, the squid did not manifest any signs of decomposition and possessed natural skin pigmentation. Due to the size and weight of the specimen and lack of suitable equipment, the vessel's crew and fishermen were unable to pull the squid onboard undamaged. Only the head with tentacles were recovered using regular fishing gaffs. Squid remains were transported to shore, where it was stored in the freezer at -18°C . The squid was donated by the fishermen to University of Reunion Island for further examination.

Sampling

Frozen remains of the specimen were stored for 102 days in the freezer before examination. The squid was thawed for 24 h at ambient temperature before sampling and measurements. Intact parts were measured with a calliper or measuring tape. The buccal mass, together with the beak, was removed from the mollusc's head prior to beak extraction. Before its preservation in 70% alcohol, the beak lower rostral length (LRL) was measured with a digital Vernier calliper with an accuracy of 0.01 mm. Muscle tissues were sampled from the individual once thawed and stored in 96% alcohol for genetic sequencing and species identification.

Genetic analysis

Genomic DNA was extracted from 20 mg of muscle tissue, after an overnight digest, using the automated KingFisher Duo

Prime Purification System by ThermoScientific following the manufacturer's protocol (Thermo Fisher Scientific, USA). A 313 bp region of the mitochondrial cytochrome c oxidase I gene (COI) was amplified using the forward mICOIntF- [5' GGWACWGGWTGAACWGTWTAYCCYCC 3'] (Leray *et al.*, 2013) and reverse jgHCO2198- [5' TAIACYTCIGGRT GICCRAARAAYCA 3'] (Geller *et al.*, 2013) primer combination (see online Electronic Supplement 2 for laboratory specifications).

Sequence similarity searches on the query DNA sequence were done using the BLASTn search implemented on the NCBI nucleotide database (Madden, 2013) and the Hidden Markov Model (HMM) alignment tool implemented on the BOLD reference database (Ratnasingham & Hebert, 2007).

Size reconstruction

Reconstruction of animal size from reference parts is a common approach used for damaged or digested specimens (Clarke, 1980, 1986; Hansel *et al.*, 1988; Cherel, 2003; Staudinger *et al.*, 2009; Potier *et al.*, 2011). We used the giant squid beak as a reference part for further size reconstruction of the entire individual based on published allometric equations. We focused on the DML and the TL reconstruction since the former is a 'reference' length for cephalopod measurements (Roper & Voss, 1983) while TL is commonly used for demonstration of extreme size of the giant squid among cephalopods (e.g. McClain *et al.*, 2015; Paxton, 2016). The most robust allometric equations were selected from the literature based on the following three criteria: statistical significance (if provided by the authors), large sample size, and the *A. dux* size range covering extreme sizes of reference parts and entire squid.

The lower rostral length was used as a predictor of the DML based on Roeleveld (2000) (1) and Paxton (2016) (2) equations:

$$\text{LRL} = 11.2 \times \log_{10}\text{DML} - 19.3 \text{ (values are in mm)} \quad (1)$$

$$\text{DML} = e^{(-1.168+98.031 \times \text{LRL})} \text{ (values are in m)} \quad (2)$$

The total length was extrapolated from the DML based on the following relationships: Paxton (2016) (3) and McClain *et al.* (2015) (4):

$$\text{TL} = 0.006 + 5.117 \text{ DML} \text{ (values are in m)} \quad (3)$$

$$\text{TL} = 1.59 \times \text{DML}^{1.98} \text{ (values are in m)} \quad (4)$$

Records of Indian Ocean occurrences of *A. dux* from GBIF (GBIF, 2016), OBIS (OBIS, 2016) and other published records (Vélain, 1877; Yukhov, 1974; Roper & Boss, 1982; Staub, 1993; Cherel, 2003) were used for mapping regional giant squid distribution. The Indian Ocean area is considered here following the official description of the International Hydrographic Organization: from the Asian Continent to Antarctica, with its western and eastern borders positioned at 20°E off South Africa and $146^{\circ}55'\text{E}$ off Southern Australia respectively (IHO, 1953).

Table 1. Details of the measurements of *Architeuthis dux* found off Reunion Island and comparisons with other large Indian Ocean giant squid individuals. LRL is lower rostral length, DML is dorsal mantle length, and TL is total length. Estimates marked by 'P' are based on Paxton (2016) equations, estimates marked by 'R' are derived using Roeleveld (2000) regression, and 'MC' corresponds to McClain *et al.* (2015) equation.

Sample	Date	Geographic position	State	LRL, mm	Length, mm	
					DML	TL
This study	4.3.2016	21°03'S 55°09'E ^a	Dead, floated at the surface	19.74	2153 (99% PI: 1500–2950) (P) 3060 (R)	7262 (MC), 11,025 (P) 14,558 (MC), 15,664 (P)
Vélain (1877)	2.11.1874	Saint Paul Island	Stranded	–	–	7150
Berzin (1971)	Before 1970	Between 35°S and 45°S	From sperm whale stomach	–	–	19,000 ([sic] 9000)
Staub (1993)	14.5.1993	Off Morne Brabant, Mauritius Island	Dead, floated at the surface	–	–	4500 ^b
Norman & Lu (1997)	Before 1998	Off Tasmania	Commercial fishing trawl	–	2400 ^c	–
Cherel (2003)	18.4.1998	Off Saint-Paul, Reunion Island	Dead, floated at the surface	17.0–17.5	1740–1930 (R)	–
		Kerguelen Archipelago	Beak recovered from sleeper shark stomach	18.13	2200 (R)	–
Yukhov (2014)	14.4.1969	37°10'S 65°56'E	From sperm whale stomach	–	2300 ^d	–

^aEstimated, see paper text for details.

^bApparently standard length.

^cNo exact geographic position presented in the source. Specimen cannot be attributed either to Pacific or Indian Ocean.

^dNot an Indian Ocean record (Yukhov, 2016 personal communication).

RESULTS

Remains description and identification

The mantle, tentacles and tips of six out of eight arms were missing from the preserved remains. The head was split in two parts at the level of the eyes at the moment of squid recovery (Figure 1A, B). Measurements used for length estimates (i.e. LRL) are presented in Table 1; other measurements taken from intact parts are summarized in the Electronic Supplement 1, Table E-1. Based on the external morphology of the individual (examined from photographs and preserved remains) and on the beak morphology (Clarke, 1986; Xavier & Cherel, 2009), the specimen was identified as the giant squid *Architeuthis dux*. Injuries visible on squid remains, while drifting at the surface (Figure 1A), clearly reflected an external impact: the tail and fin were missing, and the terminal part of the mantle showed naked muscles without skin.

Genetics

A 313 bp region of the mtDNA COI gene was isolated in the specimen and the sequence was deposited in the NCBI database (accession number: KY614519). The squid query sequence returned 100% sequence similarity to the mtDNA COI region of the whole mitochondrial reference genomes and partial mtDNA COI reference sequences of *Architeuthis dux* stored in GenBank (Winkelmann *et al.*, 2013; Benson *et al.*, 2014; Kameda *et al.*, 2015).

Occurrences

The present record of a giant squid complements previous records off the Mascarene Islands and is the third georeferenced occurrence of this species in the tropical Indian Ocean (north of the tropic of Capricorn: 23°26'13.6"S) (Staub, 1993; Cherel, 2003) (Figure 2).

Size

The estimated DML of the present *A. dux* specimen varied from 2153 mm (99% prediction interval, PI 1500–2950 mm) to 3060 mm, depending on the equation used (Table 1). Extrapolations from DML into TL estimates suggest a specimen length ranging between 11,025 and 15,664 mm (Table 1).

DISCUSSION

The dorsal mantle length of *A. dux* reported here (3060 mm, estimated from equation (1)) exceeds the DML of the other Mascarene Islands specimens (Staub, 1993; Cherel, 2003) (Table 1). Cherel (2003) also estimated DML from Roeleveld's (2000) equation (1); however, direct size comparisons are less reliable with the specimen from Staub (1993) due to the ambiguous information on how measurements were taken. Comparisons of the giant squid proportions with human personages, depicted next to the specimen in photographs, suggest that Staub (1993) probably measured standard length (i.e. the length from the posterior end of the mantle to the tip of the arms) which was referred to as a 'body measurement' ('son corps mesurait') in the original paper.

In this study, the *A. dux* DML is 28% longer than the longest one reported by Cherel (2003) from the Kerguelen Archipelago (Table 1). On a global scale, our DML estimates based on Roeleveld's (2000) equation exceeds 'longest reliably measured' DML (2794 mm) (Kirk, 1880 in Paxton, 2016) reported to date, and may represent the largest giant squid ever discovered. However, Paxton (2016) suggested that Roeleveld's (2000) equation overestimates DML, at least for large individuals. Based on Paxton's (2016) regression formula, the DML estimate for our *A. dux* is 2153 mm (99% PI 1500–2950 mm), which makes it the largest specimen ever reported in the Indian Ocean (Table 1) and place it among the 12 largest giant squids (DML above 2000 mm)

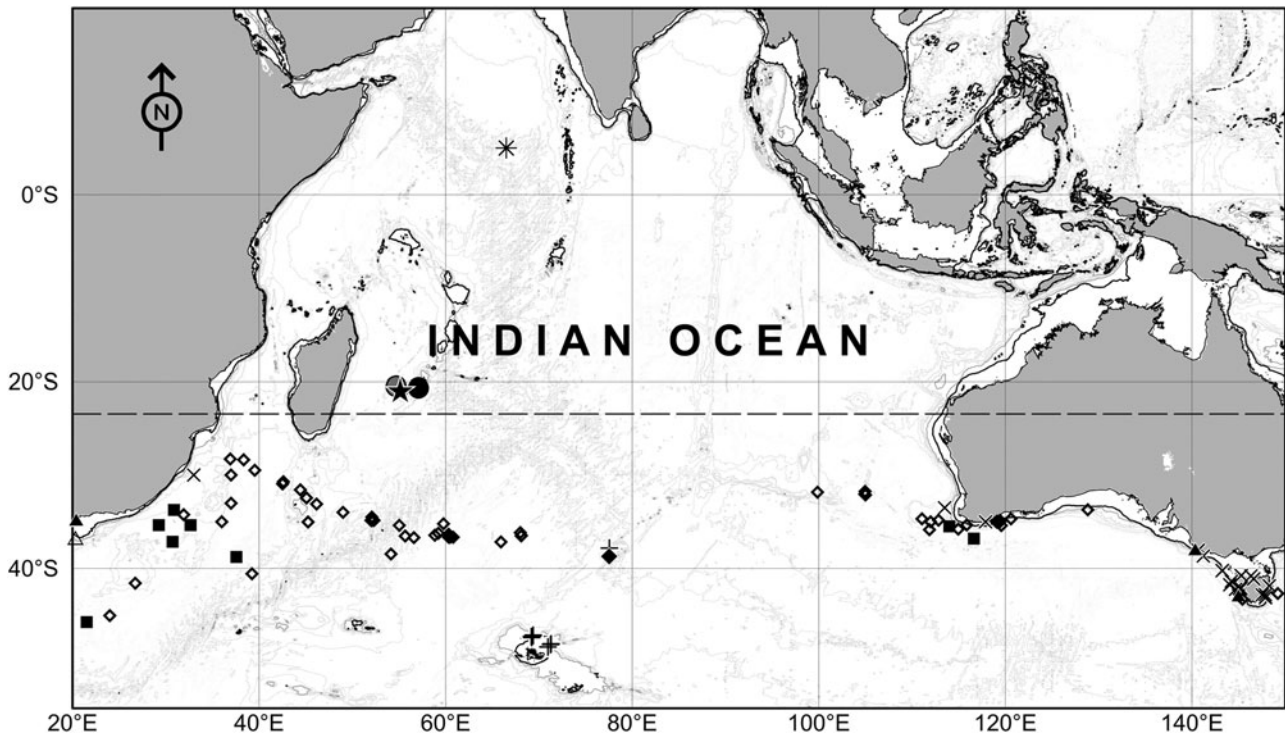


Fig. 2. The geographic positions of *Architeuthis dux* Steenstrup, 1857 records from the Indian Ocean. This study's record is the star; Published records: the Reunion Island record from Chérel (2003)* is the grey dot, the Staub' (1993)* record off Mauritius Island is the black dot, the black squares and snowflake are from Roper & Boss (1982)**. The snowflake represents a single northern Indian Ocean record. The oblique crosses are data from GBIF (2016), full triangles are OBIS (2016), and crosses are from Chérel (2003). The full diamond is from the Vélain (1877)*** record of a stranded giant squid; the empty triangle is from Wendy West, unpublished data; the empty diamonds are from Yuhkov (2016, personal communication, earlier presented as a map in Yuhkov, 1974). For references marked with *, the positions of the observations were estimated from the description published in the original paper. For references marked with **, positions were estimated from the original map presented in the paper. For references marked with ***, positions mark the central position of the island where stranding occurs. The 200 m isobath (dark line) and bathymetry from 1000 to 5000 m (in 1000 m steps, light lines) are shown. Coastline and bathymetry data are from GEBCO (2016).

reported globally (Kirk, 1880, 1882; Frost, 1936 in Sweeney & Roper, 2001; Keil, 1963 in Sweeney & Roper, 2001; Gauldie *et al.*, 1994; Norman & Lu, 1997).

The extrapolation of TL based on DML estimates is highly uncertain; therefore we present TL estimates only for comparison purposes with other published giant squid size records and as an indicator of a potential extreme upper range of TL. The extrapolated TL (11,025–15,664 mm) of the giant squid reported here (Table 1) exceeds the TL of an individual stranded on Saint Paul Island (7150 mm) (Vélain, 1877) and the biggest known Indian Ocean giant squid (9000 mm) reported by Berzin (1971) (originally incorrectly stated as having a TL of 19 m). Paxton's (2016) challenge of the 19 m TL size was validated by Dr Valentin Yuhkov¹ (2016, personal communication) who participated in the discovery of the Berzin' (1971) individual in the stomach of a sperm whale. This 19 m total length instead of 9 m appeared to be a misprint in Berzin (1971) (Yuhkov, 2016, personal communication), later reproduced in the English translation (Berzin, 1972) and referenced in several papers on giant squid biology (Sweeney & Roper, 2001; Paxton, 2016). Taking these considerations into account, size estimates of the recovered specimen described here rank at the higher end of the TL range, with the largest giant squid ever measured to be the specimen

stranded on the New Zealand coast in 1887 (Kirk, 1888)², with 684 inches (17,374 mm) in TL.

Together with individuals reported by Staub (1993) and Chérel (2003), our record is the third northernmost occurrence of giant squid observed to date in the Indian Ocean. Besides an *A. dux* global occurrences map that appeared in Roper & Boss (1982) (which was missing sampling details), giant squid have never been reported from equatorial waters nor from the northern hemisphere of the Indian Ocean. The presence of a giant squid off India as mentioned by Coro *et al.* (2015) and based on Silas (1968, 1985) is obviously erroneous: the original Silas (1968, 1985) papers did not show any record of *A. dux* encounters in Indian waters in their ocean-wide accounts of various squid species.

Global ocean records of the giant squid in the tropics are only known from the eastern tropical Atlantic (Nigmatullin, 1976; Nesis *et al.*, 1985), demonstrating apparently the capacity of errant individuals to penetrate into tropical waters via deep, cold-water currents. The principal area of the Indian Ocean giant squid distribution seems to correspond with subtropical and temperate waters of the southern hemisphere (Figure 2) (Vélain, 1877; Yuhkov, 1974, 2016, personal

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²It should be noted some ambiguity exists in Kirk (1888). A length measurement of 684 inches was given in the table, while in the text he referred to a length of 55 feet 2 inches (662 inches, or 16815 mm) for the same individual.

communication; Clarke, 1980; Cherel, 2003; GBIF, 2016; OBIS, 2016) lying between the North Subtropical Front and the Polar Front (Kostianoy *et al.*, 2003, 2004). Our findings suggest that the distribution of *A. dux* is much wider than the 'bi-subtropical distribution' described by Nesis (2003). The nutrient-poor waters of the Indian Ocean Subtropical Gyre province, characterized by high heat content, deep propagation of warm waters and oligotrophic conditions (Jayne & Marotzke, 2002; Gouretski & Koltermann, 2004; Longhurst, 2007), likely represent the northern border of the giant squid habitat in the Indian Ocean.

The majority of Indian Ocean *A. dux* have been described from squid remains discovered in predators' stomachs, mainly sperm whales (Clarke, 1980; Mikhalev *et al.*, 1981; Nesis *et al.*, 1985; Yukhov, 2014) and to a lesser extent sleeper sharks *Somniosus* sp. (Cherel, 2003), swordfish *Xiphias gladius* (Wendy West³, unpublished data) and several albatross species *Diomedea* spp. (Cherel *et al.*, 2002; Cherel, 2003). Similarly, two *A. dux* remains found floating at the surface (Cherel, 2003) also showed signs of predation by sperm whales and an unknown predator. We suggest that the giant squid described here was severely mutilated due to predation. The whole tail of the specimen was most likely severed by a predator, rather than other means of injury (e.g. propeller of a vessel), given the preferences of giant squid to deep-water habitats (Kubodera & Mori, 2005) and visible patterns of tissue damage (Figure 1A). Injuries at the mantle tip (Figure 1A) suggest predation by a large animal, probably a sperm whale, as they are known to prey on giant squid and regularly occur within the region (Clarke, 1980; Jefferson *et al.*, 1993; Mannocci *et al.*, 2014), or possibly a great white shark (*Carcharodon carcharias*), which occasionally visit Reunion Island waters (Zuffa *et al.*, 2002; Jaquemet, unpublished data). Smaller predators such as squid or fish leave predation marks that differ in size and shape from the ones observed here (Chapman *et al.*, 2006; Lowry *et al.*, 2009; Papastamatiou *et al.*, 2010).

The present record complements the current knowledge on *A. dux* distribution and biology on regional and global scales. We document a rare occurrence of giant squid in tropical waters of the Indian Ocean and one of the largest individuals ever reported worldwide. *Architeuthis dux* remains an enigmatic species requiring more scientific efforts to address the current challenges in the understanding of its natural history, its role in ocean ecosystems and the potential threats to its conservation, especially those due to human activities (Guerra *et al.*, 2011; Leite *et al.*, 2016).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315417001588>.

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