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Giant squid beaks: implications for systematics

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The systematic position of the giant squid *Architeuthis* remains unresolved but comparison of beak morphometrics is an approach that has not been attempted before. Additional data for the relationship between mantle length (ML) and lower beak rostral length (LRL) suggest that *Architeuthis* sp. in the North Atlantic, South Africa and New Zealand are parts of the same asymptotic relationship. Comparison of beak dimensions of *Architeuthis* from the North Atlantic, South Africa and New Zealand with those of two distinct species of *Todarodes*, from the Mediterranean and southern Africa, indicate that there may be only one species of *Architeuthis* in these three regions. No consistent morphological evidence has yet been found to indicate more than one species of *Architeuthis* in the Atlantic or in the southern hemisphere.

The systematic position of the giant squid *Architeuthis* Steenstrup, 1857 (Cephalopoda: Architeuthidae), largest of all the invertebrates, is unresolved and there has been much speculation regarding the number of species worldwide. Twenty nominal species have been described on evidence ranging from complete animals to fragmentary remains such as beaks, suckers or an arm (Clarke, 1966; Voss, in Förch, 1998). Previous authors have considered that only seven or eight of these may be valid (Dell, 1970; Voss, in Förch, 1998). Nesis et al. (1985) found that the distribution range of *Architeuthis* may be divided into three regions (the northern Atlantic and Pacific Oceans and the southern hemisphere) and concluded that there are probably three species or subspecies worldwide.

The type material that exists for *Architeuthis* species is mostly in poor condition and not very informative (Förch, 1998). Direct comparison of *Architeuthis* specimens from different oceans is difficult because of their large size and many of the characters are either damaged or in a plesiomorphic state (Roeleveld & Lipinski, 1991). Comparison of *Architeuthis* beak morphometrics is a new approach to the systematic problem. However the use of beaks alone for specific identification cannot be relied upon any more than any other single organ (Clarke, 1986) and beaks are not equally useful for specific identification in all cephalopods (Ogden et al., 1999), although their measurements may be subjected to statistical analysis.

Previous data for the relationship between ML and LRL (see Appendix 1 for abbreviations) suggested that *Architeuthis* sp. (from sperm whale stomachs) in the South Atlantic is smaller, and grows more slowly, than in the North Atlantic (Clarke, 1980). Preliminary data on South Atlantic *Architeuthis* not from whale stomachs agreed better with large North Atlantic than smaller South Atlantic specimens (Roeleveld & Lipinski, 1991). Data from a further ten North Atlantic and 12 South Atlantic *Architeuthis* show that they are all part of the same asymptotic relationship ($y=10.6*\log_{10}x-17.7$). The addition of data for ten New Zealand *Architeuthis* (from Förch, 1998) altered the fitted function only slightly ($y=11.2*\log_{10}x-19.3$; Figure 1A). Further *Architeuthis* beak measurements were examined from three different regions to determine if there is any support for the existence of more than one species of *Architeuthis* worldwide. Measurements were taken from 12 South African and ten North Atlantic *Architeuthis* beaks, supplemented by data for three more North Atlantic beaks from Lordan et al. (1998) and for 13 New Zealand beaks from Förch (1998).

Locality, repository, catalogue number, sex, maturity stage and ML for *Architeuthis* beaks measured—from the North Atlantic, in the Zoological Institute, Bergen (UBZM) and the Science Museum, Trondheim (UTVM): NA-8, Valdersnes, Radøy, UBZM 63336, F II, 1620; NA-9, Sandane, Nordfjord, UBZM 45018, M III, 950; NA-11, Brandasund, UBZM 43688, head and arms; NA-12, Lerøy, Austreim, UBZM 43689, F I, head and viscera, 1310; NA-14, 55 n.m. WNW of Utsira, UBZM 60324, beaks only; NA-17, Ranheim 1954, UTVM 156, ?F, 1790; NA-18, Hemne, UTVM 110a, M; NA-19, Ranheim 1928, UTVM 108a, M, 1370; NA-22, no data, UTVM, F II, 1180; NA-23, no data, UTVM, F I, 935.

South Atlantic, in the South African Museum (SAM): SA-2, off Green Point light house, SAM-S1868, F II-III?, 1700; SA-3, 27°52′S 14°40′E, SAM-S1681, F II, 1680; SA-4, Soetwater, Kommetjie, SAM-S2486, F III, 1850; SA-5, 34°47′S 18°14′E, SAM-S2546, F II, 1400; SA-6, Kommetjie, SAM-S2556, head only, est. 1600; SA-7, W of Cape Columbine, 32°53′S, SAM-S2562, F ?II-III, 1770; SA-8, 34°22′S 17°45′E, SAM-S3354, M III, 1030; SA-9, 33°10′S 16°40′E, SAM-S3352, F II, 1380; SA-10, 32°50′S 16°40′E, SAM-S3353, M III, 1180; SA-11, 33°45′S 17°30′E, SAM-S3386, M III, 1280+; SA-12, 33°43′S 17°29′E, SAM-S3410, F, ~1890; SA-13, W of Hout Bay, SAM uncatalogued, ?F II, 1790.

Comparative beak measurements were taken from *Todarodes sagittatus* (Lamarck, 1798) and *T. angolensis* Adam, 1962–Mediterranean *T. sagittatus*: TS3–40, 36°54′N 13°43′E, SAM-S2907, M III, 295; TS3–41, 38°11′N 11°18′E, SAM-S2905, M III, 250; TS3–42, 38°09′N 11°12′E, SAM-S2902, M II, 224; TS3–45, 38°11′N 11°18′E, SAM-S2905, F III, 363; TS3–46, 38°24′N 11°43′E, SAM-S2898, M III, 344; TS3–47, 38°51′N 15°52′E, SAM-S2903, F I, 258; S2899, 40°43.6′N 13°31.8′E, SAM-S2899, F I, 312; S2900, 39°57.5′N 14°59.5′E, SAM-S2900, F I, 282; S2901, 37°57.1′N 11°18.1′E, SAM-S2901, F III, 338.

Southern African *T. angolensis*, in the Port Elizabeth Museum (PEM): TA-i, 24°04.1′S 13°20.6′E, PEM 1116, M, 269; TA-iii, 33°27.1′S 17°32.1′E, PEM 835, F, 380; TA-iv, 33°27.1′S 17°32.1′E, PEM 830, M, 310; TA-v, 33°27.1′S 17°32.1′E, PEM 842, M, 308; TA-vi, 32°52′S 17°34′E, PEM 730, F, 315; TA-vii, 24°04′S 13°20′E, PEM 1119, F, 238; TA-viii, 24°09′S 13°37′E, PEM 1117, M, 290; TA-ix, 24°09′S 13°37′E, PEM 1122, F, 350; TA-x, 32°52′S 17°34′E, PEM 727, M, 317; TA-xi, 32°52′S 17°34′E, PEM 732, F, 307.

Beak measurements for *T. angolensis* and *T. sagittatus* (also relatively large squids) were included in the analysis in order to gain a measure of possible differences between beak morphometrics of congeneric species. In the absence of a clearly defined sister group (the supposedly related neoteuthids are rare, and the animals very small), the most suitable comparison was considered to be two undeniably distinct congeneric species, preferably of large animals, to reduce differences due to size. Though beaks may not be equally distinguishable between species in different families of squid, *Todarodes* may be the more suitable to evaluate any differences found between the *Architeuthis* groups because the beaks of *T. sagittatus*, *T. pacificus* and *T. filippovae* have been considered indistinguishable by conventional beak characters (Clarke, 1986).

Beak measurements for *Architeuthis* and *Todarodes* are presented in Appendix 1. To minimize differences due to size, indices were calculated by dividing each beak measurement by the respective lower rostral length. Indices of eight beak dimensions were available for standard discriminant functions analysis with ©Statistica software (F to enter 1.00, F to remove 0.00). Missing data were substituted by means because of the small data matrix.

Overall discrimination of the three *Architeuthis* plus two *Todarodes* groups was highly significant ($P<0.001$). The chi-square test for significance of roots (or discriminant functions) showed that the first root was highly significant ($P<0.001$), explained 90% of the variation and was weighted most heavily by LWL index. The second root was significant but not highly so ($0.01>P>0.001$) and explained a further 8% of the variation.

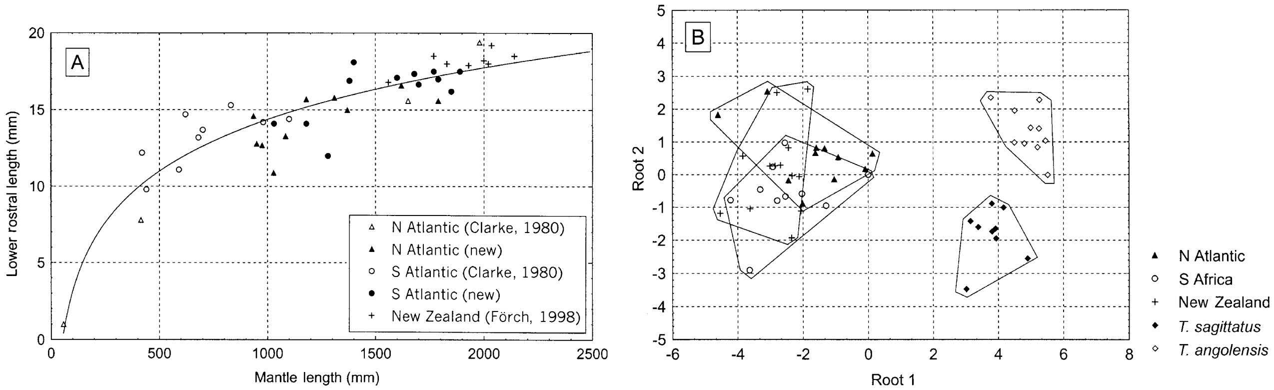

Figure 1. (A) Regressions of mantle length vs lower rostral length for *Architeuthis* sp. from the North Atlantic (triangles) and from sperm whales captured off Donkergat, South Africa (circles); after Clarke (1980; open symbols), with additional data for the North and South Atlantic (filled symbols) and New Zealand (from Förch, 1998; crosses) and with the axes reversed. (B) Discriminant functions analysis for beaks of three *Architeuthis* groups plus two *Todarodes* spp. Scatterplot of individual scores for the first two discriminant functions (roots 1 and 2).

The scatterplot of the individual scores for the first two discriminant functions (roots 1 and 2, Figure 1B) shows considerable overlap between the three *Architeuthis* groups whereas the two *Todarodes* species are clearly separated. Only 81% of the North Atlantic, 58% of the South African and 62% of the New Zealand *Architeuthis* cases were correctly classified, in contrast to 100% of both *Todarodes* spp.

For the five indices that were not available for New Zealand *Architeuthis*, means were compared with ©Statistica by *t*-test for independent samples and the non-parametric Mann–Whitney U-test (because some variances were found to differ significantly). The results were very similar for both tests: North Atlantic and South African *Architeuthis* differed significantly only in LRC index, whereas for the two *Todarodes* spp. three of the five indices, of LRC, URW, and UWW, were significantly different.

The inclusion of North and South Atlantic and New Zealand *Architeuthis* in a single asymptotic relationship (Figure 1A) suggests that there may be only one species of *Architeuthis* in the Atlantic Ocean and New Zealand waters. Furthermore, discriminant functions analysis shows that the South African *Architeuthis* overlap as much with the New Zealand group as with that of the North Atlantic (Figure 1B). This does not support the suggestion of Clarke (1980) that North and South Atlantic *Architeuthis* differ, nor that of Nesis et al. (1985) that there may be separate species or subspecies of *Architeuthis* in the North Atlantic and the southern hemisphere. Tests for differences between means of other beak measurements also show less difference between beaks of *Architeuthis* from the North Atlantic and South Africa than between the two species of *Todarodes*. These results suggest that the three *Architeuthis* groups may be variants within a single species.

The beak morphometrics add to the growing accumulation of data that seems to support the possibility that there may be only one species of *Architeuthis*. No consistent morphological evidence has yet been found to indicate more than one species of *Architeuthis* in the Atlantic or New Zealand (Förch, 1998). It is interesting that morphometrics of *Architeuthis* beaks show as much variation as of the soft parts, in contrast to conventional wisdom that measurements of structurally hard characters (e.g. chitin vs muscular tissue) should be more reliable.

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Appendix 1. Architeuthis *and* Todarodes *beak measurements, in mm, after Clarke (1986) and Wolff (1984).*

	Spec.	ML	LRL	LWL	LJW	LHL	LCL	LRC	LRW	URL	UJW	UHL	UCL	URW	UWCL	UWW
North Atlantic *Architeuthis*	NA-8	1620	16.6	—	—	—	—	—	—	—	—	—	—	—	—	—
	NA-9	950	12.8	—	—	—	—	—	—	—	—	—	—	—	—	—
	NA-11	—	15.4	43.5	14.7	29.4	47.6	60.9	53.1	15.5	12.9	64.5	90.0	35.4	78.1	20.5
	NA-12	1310	15.8	—	13.3	20.5	39.0	59.0	—	15.9	13.3	—	—	33.4	—	19.5
	NA-14	—	13.6	38.4	11.6	17.8	39.6	57.2	47.8	12.5	11.0	52.4	77.7	28.2	65.4	17.4
	NA-17	1790	15.6	49.5	12.2	—	—	—	62.7	—	—	—	—	—	—	—
	NA-18	—	17.9	65.4	16.4	27.3	58.4	81.9	78.7	16.2	15.1	84.7	118.1	41.6	107.2	25.0
	NA-19	1370	15.0	43.6	11.3	—	—	63.9	3.8	13.7	12.2	60.5	85.4	30.8	74.8	17.5
	NA-22	1180	15.7	44.0	12.8	25.7	52.3	68.0	57.0	14.9	12.9	—	97.8	33.7	85.9	21.5
	NA-23	935	14.6	42.4	10.9	22.8	42.7	59.4	53.3	13.1	10.9	58.0	83.9	31.0	72.7	21.0
South Atlantic *Architeuthis*	SA-2	1700	16.7	48.4	13.2	28.4	47.5	71.3	61.6	17.0	14.8	70.4	103.2	36.3	84.5	22.4
	SA-3	1680	17.4	51.6	13.9	31.7	54.3	75.4	62.9	17.1	14.3	75.3	103.5	37.0	85.0	21.8
	SA-4	1850	est. 16.2	57.4	13.6	27.8	52.0	79.0	67.5	16.5	14.3	73.8	110.8	37.7	98.1	22.4
	SA-5	1400	18.1	58.4	14.8	26.4	57.2	80.6	68.4	17.6	14.8	79.7	113.7	38.0	100.1	25.0
	SA-6	est. 1600	17.1	59.6	13.8	26.9	56.1	76.0	69.9	17.3	14.8	78.0	114.0	40.7	99.9	25.6
	SA-7	1770	17.5	52.4	12.8	34.9	51.6	76.0	63.1	18.8	16.2	71.0	104.5	36.4	90.8	20.1
	SA-8	1030	14.1	38.4	11.5	18.9	40.5	59.1	46.0	15.1	12.5	59.1	86.5	30.6	75.5	16.5
	SA-9	1380	16.9	51.7	14.0	25.5	53.3	73.2	61.3	17.2	14.6	72.3	101.9	38.4	89.9	22.5
	SA-10	1180	14.1	42.9	12.6	22.1	46.0	59.8	53.7	15.4	12.8	61.9	90.3	34.0	78.4	19.2
	SA-11	1280+	est. 12.0	44.5	—	19.3	42.3	61.6	52.4	16.1	13.8	60.1	89.2	32.5	78.2	17.2
	SA-12	~1890	17.5	51.0	14.5	25.3	50.9	71.1	61.2	17.3	15.4	74.4	102.9	38.4	90.2	21.8
	SA-13	1790	17.0	52.7	15.5	23.3	50.0	72.7	63.5	16.9	14.3	69.6	98.4	36.4	85.8	21.7
Mediterranean *Todarodes sagittatus*	TS3-40	295	7.6	12.3	5.6	7.5	13.6	21.3	17.2	8.6	6.2	23.8	30.1	14.1	23.4	5.2
	TS3-41	250	6.5	10.7	5.1	6.4	12.5	17.6	13.9	7.2	5.2	20.8	25.3	12.3	19.3	5.0
	TS3-42	224	6.3	10.6	4.5	5.9	11.7	16.6	13.7	6.3	4.8	19.4	23.7	9.6	18.3	5.5
	TS3-45	363	10.7	17.5	7.3	11.7	22.4	30.2	24.0	11.2	8.1	32.9	40.7	16.8	31.9	7.7
	TS3-46	344	11.0	16.6	7.7	9.7	17.4	28.1	23.9	12.2	8.5	31.7	29.5	14.8	29.3	5.4
	TS3-47	258	6.6	12.8	4.7	6.2	13.3	18.9	15.5	6.4	5.1	20.7	26.8	13.8	21.2	6.9
	S2899	312	8.1	14.8	5.1	7.6	15.1	23.5	20.8	7.3	6.2	25.6	32.7	13.5	26.0	7.5
	S2900	282	7.4	13.6	5.2	7.6	14.2	21.9	18.0	7.2	6.0	24.7	29.2	14.7	22.9	6.9
	S2901	338	9.9	16.0	6.8	11.7	—	26.2	21.3	10.8	7.8	30.6	37.8	19.2	28.5	8.7
Southern African *Todarodes angolensis*	TA-i	269	6.7	9.4	5.5	5.7	11.5	16.7	13.2	6.8	4.5	18.1	23.4	8.4	17.2	3.7
	TA-iii	380	8.9	12.6	6.8	7.9	16.0	22.4	18.5	—	—	—	—	—	—	—
	TA-iv	310	7.2	10.3	5.2	5.5	12.2	18.7	15.6	7.7	5.1	21.4	27.1	10.0	20.7	4.1
	TA-v	308	6.8	10.8	5.2	5.4	11.6	18.0	15.4	7.2	4.7	19.6	25.3	9.5	20.0	4.2
	TA-vi	315	6.7	11.8	4.8	5.8	11.2	18.2	14.7	6.3	4.6	20.1	25.8	8.8	20.5	4.5
	TA-vii	238	6.0	8.8	4.1	5.7	10.2	14.2	12.6	5.3	4.0	16.8	21.4	8.2	16.4	4.0
	TA-viii	290	6.7	9.4	5.3	5.4	12.6	17.4	13.4	6.9	4.6	19.2	25.0	9.3	19.3	3.9
	TA-ix	350	7.7	12.6	6.6	7.8	16.1	21.9	18.3	8.2	5.4	24.3	31.2	11.8	24.6	5.0
	TA-x	317	7.5	11.4	6.2	5.3	11.6	19.6	16.2	7.9	5.1	21.4	17.6	10.0	21.6	4.5
	TA-xi	307	6.8	11.2	5.3	6.2	12.3	18.4	15.2	6.3	4.6	19.8	25.3	9.6	20.1	4.4

LRL, lower rostral length; LWL, lower wing length; LJW, lower jaw angle width; LHL, lower hood length; LCL, lower crest length; LRC, lower rostral tip to corner of lateral wall; LRW, lower rostral tip to inner margin of wing; URL, upper rostral length; UJW, upper jaw angle width; UHL, upper hood length; UCL, upper crest length; URW, upper rostral tip to inner margin of wing; UWCL, upper wing to crest length; UWW, upper wing width.

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