Range extension and a further female specimen of the grinning izak (*Holohalaelurus grennian* Human 2006; Scyliorhinidae; Chondrichthyes).

Brett A. Human

Western Australia Fisheries and Marine Research Laboratory, PO Box 20,
North Beach WA 6920, Australia. E-mail: bretthuman@fish.wa.gov.au

ABSTRACT. A specimen of *Holohalaelurus* shark (Scyliorhinidae; Chondrichthyes) recently collected off southern Mozambique, represents a southward range extension of 2200km for the recently described, *H. grennian* Human 2006. This specimen presents not only a significant extension of its known distribution, but is also only the second female specimen known for this species. Moreover, the specimen exhibits morphological characters, particularly colouration, which are more typically attributed to congeners occurring in the southern part of its range. This paper is an account of the range extension for *H. grennian*, and compares the morphological and colouration differences in this specimen compared to the original species description. A shape analysis is conducted on the specimen, and a revised zoogeography of the genus *Holohalaelurus* is presented.

KEYWORDS: *Holohalaelurus*, Scyliorhinidae, Chondrichthyes, range extension, zoogeography, western Indian Ocean, conservation status.

INTRODUCTION

A recent review of the genus *Holohalaelurus* Fowler 1934 resolved the distribution of *Holohalaelurus* sharks in the western Indian Ocean (Human, 2006a). This resulted in the resurrection of *H. melanostigma* (Norman 1939), and the description of two new taxa, *H. favus* and *H. grennian*, from the western Indian Ocean.

Holohalaelurus sharks from the western Indian Ocean are poorly known and apparently rare, with the possible exception of *H. regani* in the southwest Indian Ocean (which is abundant in the southeast Atlantic), and their conservation status needs to be critically assessed. *Holohalaelurus favus* and *H. punctatus* from kwaZulu-Natal, South Africa, and southern Mozambique, were common by-catch species in trawl fisheries in the late 1960s and early 1970s (Human, 2006a). Since then both species have apparently suffered significant population declines and are possibly extinct there; no specimens of these species have been recorded since the 1970s, despite recent intensive biodiversity surveys as part of the African Coelacanth Ecosystem Programme.

Holohalaelurus punctatus has an apparently separate population distributed around Madagascar, although the current status of that population is unknown. The two species known from Kenya and Tanzania, *H. melanostigma* and *H. grennian*, are both known only from a handful of specimens, and females for *H. melanostigma* remain unknown.

Holohalaelurus grennian was described from four museum specimens consisting of three males and one female. The taxonomic history of this species was complicated by the placement of the female specimen in the *H. melanostigma* type series by Norman (1939), which he assumingly did on the grounds of supposed sexual dimorphism (Human, 2006a). The placement of the female in *H. melanostigma* was due to the lack of *bone fide* female specimens of *H. melanostigma* (which still holds true) and of male specimen conspecifics of the female specimen at the time. Male specimens readily identifiable as conspecific to Normans' female specimen have since been collected, validating the erection of the species *H. grennian*, and the assignment of the female specimen to that species (Human, 2006a). Additionally, shape variation analyses of the genus supported the validity of *H. grennian* and the specimens assigned to it (Human, 2007b).

The only other specimens reported in the literature, additional to the type series, were a female specimen that was not catalogued and discarded by Norman (1939), and an illustration by Igor Sidorenko from the Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO), USSR, of a presumed female specimen from an unknown locality (Human, 2006a). The type locality of *H. grennian* is off Ras Ngomeni, Kenya. Other specimens have been collected off Zanzibar Island and off Dar es Salaam, Tanzania, from depths ranging between 238–300m (Fig. 1; Human, 2006a). At the time *H. grennian* was described, it was thought to be sympatric with only one other species of *Holohalaelurus, H. melanostigma*.

Recently, a female specimen of *Holohalaelurus* (SAIAB 81902) was captured off Mozambique and was assigned to *H. punctatus*. However this specimen is identifiable as *H. grennian* and represents a significant range extension for the species, is the second female

specimen of *H. grennian* in a collection, and exhibits minor, but noteworthy, morphometric and colouration differences from the original species description.

METHODS AND MATERIALS

VOYAGE DETAILS
The specimen was collected by P.C. and E. Heemstra aboard the R/V Dr Fridtjof Nansen, and deposited in the ichthyological collection of the South African Institute for Aquatic Biodiversity as SAIAB 81902. The research cruise was a joint venture involving SAIAB, the Instituto Nacional de Investigacao Pesqueira of Mozambique, FAO, and the Institute for Marine Research, Bergen, Norway. The specimen was collected in a bottom trawl approximately 285km eastnortheast of Maputo, and about 140km south of Inhambane, Mozambique (Fig. 1). The start position of the trawl was 25° 05.5' S, 35° 18.4' E, and finished at 25° 07.2' S, 35°17.6' E, with a bottom depth of 347–353m.
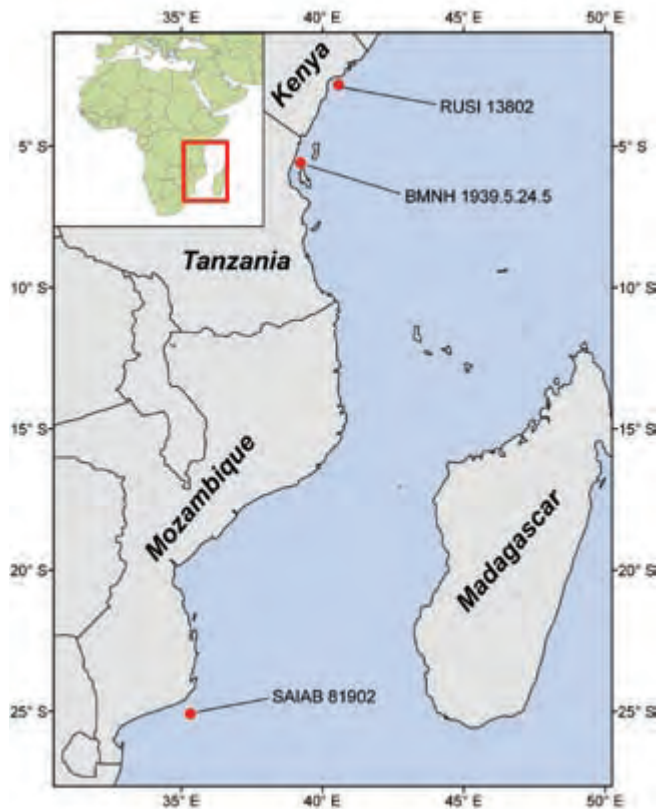
MORPHOMETRICS AND MERISTICS

Fig. 1. The known distribution of *Holohalaelurus grennian*. The new female specimen (SAIAB 81902) represents a southward range extension of 2,200km. Other specimens (not shown on this chart) have been collected off Dar es Salaam, Tanzania, without further details.

Morphometric and meristic measures were taken according to Compagno (2001), with modifications

(Human, 2006b) suited for scyliorhinid sharks. The new specimen was compared to *Holohalaelurus* specimens recorded in Human (2006a, 2007b; Appendix 1).

SHAPE ANALYSES
Human (2006b, 2007a, b) introduced a methodology for whole body shape analysis of congeneric species, using a wholly multivariate approach that is followed here. Briefly, a size corrected and classification analysis is made to examine whether specimens cluster into *a priori* assigned species groups. The morphometrics of the current specimen were combined with the *Holohalaelurus* dataset used by Human (2007b) to determine if the current specimen clustered with other *H. grennian* specimens, based on shape.

RESULTS

MORPHOMETRICS AND MERISTICS
The morphometric and meristic measures of the female *H. grennian* specimen described here, are compared to the morphometric and meristic measures of other *H. grennian* specimens (from Human, 2006a) in Table 1; the abbreviations used are listed in Appendix 2.

Overall, the morphometric and meristic measures of the specimen were within the range of those recorded for previous *H. grennian* specimens (Table 1), but differed slightly from other specimens in having a proportionately smaller, less depressed head, i.e. a shorter PP1, HDL, PG1, PSP, and longer DPI. The head is proportionately narrower with a longer snout (longer PRN), narrower mouth width (shorter MOW), eyes positioned closer together and positioned more posteriorly to the mouth (shorter INO, and longer EMA), and narrower spacing between the nares (shorter INW and IOW). The speciman also has proportionately smaller 1st and 3rd gill slits (shorter GS1, GS3). In common with the head, the trunk is less depressed and the anterior body was generally stouter and longer than other *H. grennian* specimens (larger HDH2, HDW2, HDH, HDW, TRH, TRW, GIR, ABH, ABW, longer TRL and PPS). The caudal peduncle is more compressed (larger TAH, smaller CPW), seemingly to accommodate a proportionately longer caudal fin (shorter PCL, ACS, and longer CDM). The specimen also has a slightly higher vertebral count due to a larger number of caudal diplospondylous vertebrae.

This specimen of *H. grennian* also has enlarged denticles on the dorsal midline between the pectoral fin and the origin of the first dorsal fin, visible only under close inspection. It has no enlarged denticles on the dorsal surfaces of the pectoral fins. Human (2006a) noted slightly enlarged denticles on the dorsal midline for this species, but denticles were enlarged more so in those specimens compared to this specimen. The only *Holohalaelurus* species that lacks enlarged denticles on the dorsal midline is *H. punctatus* (Human, 2006a). The inconspicuous buccal papillae is in agreement with the original species description of *H. grennian*, in contrast

to *H. punctatus*, which has obvious buccal papillae.

This specimen's pectoral fin radials (P1R) were undetectable through manual manipulation of the fin, as were those of the female paratype, whereas the pectoral fin radials of the male specimens could be detected and were measurable, despite male specimens being smaller than the female specimens. This apparent difference in the pectoral fin radial flexibility may represent a sexual dimorphic character state for this species.

SHAPE ANALYSES

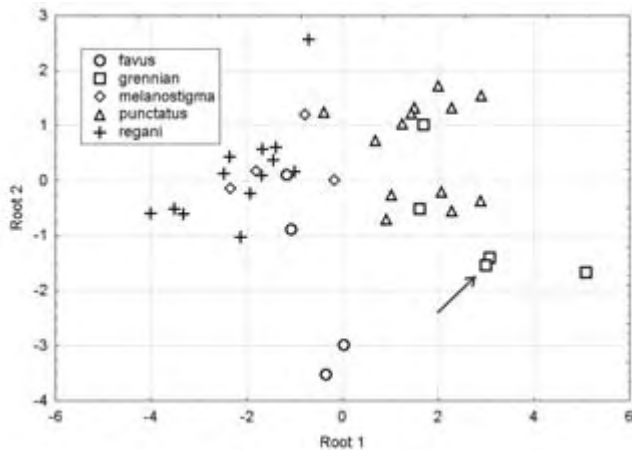*Holohalaelurus* specimens used in shape analysis are

Fig. 2. Projection of the canonical scores for each *Holohalaelurus* specimen against the first and second discriminant roots. The arrow points to the *H. grennian* specimen collected from Mozambique.

given in Appendix 1. The results were very similar to those recorded by Human (2007b), the first nine eigenvectors accounting for 75% of the overall variance in the dataset, and the first seventeen eigenvectors accounting for 90% of the overall variance (Table 2). From the MPCA analysis, seven size corrected morphometric measures had 25% or more of their variance accounted for by the first and second eigenvectors, and six of these were incorporated into the DFA model, with only MOL, GS5, and D1P contributing significantly to the model (Table 3). Four roots resulted from the canonical analysis, although only the first and second roots contributed significantly to the discriminating power of the model (Table 4). The first root accounted for ~80%, and the second root ~13%, of the discriminatory power of the model.

There was little evidence of species separation in the canonical analysis (Fig. 2), although species clustering was evident, particularly for *H. regani*; and the recent *H. grennian* specimen clustered within that species group. The *H. punctatus*, *H. favus*, and *H. melanostigma* species groups are less resolved compared to previous analyses (Human, 2007b). Consequently, the classification analysis was not as successful in discriminating species (82.1% correct overall; Table 5), compared to the results previously achieved (89.7% correct overall; 2007b). Table 5 shows that all of the *H. regani* specimens were correctly identified and only one *H. melanostigma*

specimen was incorrectly classified. However, two specimens of *H. grennian* and *H. punctatus* had been misidentified.

COLOURATION

The current specimen (Fig. 3) agrees in colouration with the description for *H. grennian* in most respects (Human, 2006a), with many small dark brown spots on a yellow-brown background dorsally, the spots becoming larger along the lateral midline and on the dorsal surface of the pectoral fins, but not developing into the small stripes observed on some other *H. grennian* specimens; there are few white spots on the dorsum, with a white spot at the second dorsal-fin origin, and a large white spot above the pectoral-fin insertion, about level with the gill slits; characteristic stripe present on both dorsal fins, stripe narrow and bordered by a pale margin; caudal fin with dusky patches on the hypaxial fin web and on the terminal lobe; ventrum uniformly off-white, with no markings or spots, although sensory pores are noticeably black, confirming that black ventral sensory pores appear to be a character common to all *Holohalaelurus* sharks when alive or freshly preserved.

The notable exception to the colouration and patterning given in the original description of the species is the presence of some dorsal fin markings that are superficially similar to those seen in congenerics. This female specimen has V-shaped markings on both dorsal fins, which are absent in other known *H. grennian* specimens (Fig. 4). Similar patterning has only been described for *H. punctatus*, although these markings had faded on the specimens by the time they were examined by Human (2006a), and were recorded accordingly, although the distinguishing black stripes surrounded by a pale margin are present on this specimen, they are situated much lower, closer to the inner margins, and not reaching to the posterior margins of the dorsal fins, compared to other *H. grennian* specimens in which the stripe is positioned midway along the posterior margin of the fin (Human, 2006a).

DISCUSSION

The known distribution of *H. grennian* spans more than 22 degrees of latitude (Fig. 1), and is apparently restricted to the African upper continental slope. The specimen described here represents a southward range extension of 2,200km, which significantly extends its distribution.

The species has previously been recorded from depths of 238–300 m, and at 234–353 m depth, this specimen represents the deepest record for the species. Despite this, the depth range for the species is restricted to just over 100m, possibly indicating a close affinity for a particular habitat. It is not known if the apparent depth range difference between the Mozambique specimen and the Kenyan/Tanzanian specimens represents regional differences in habitat preferences,
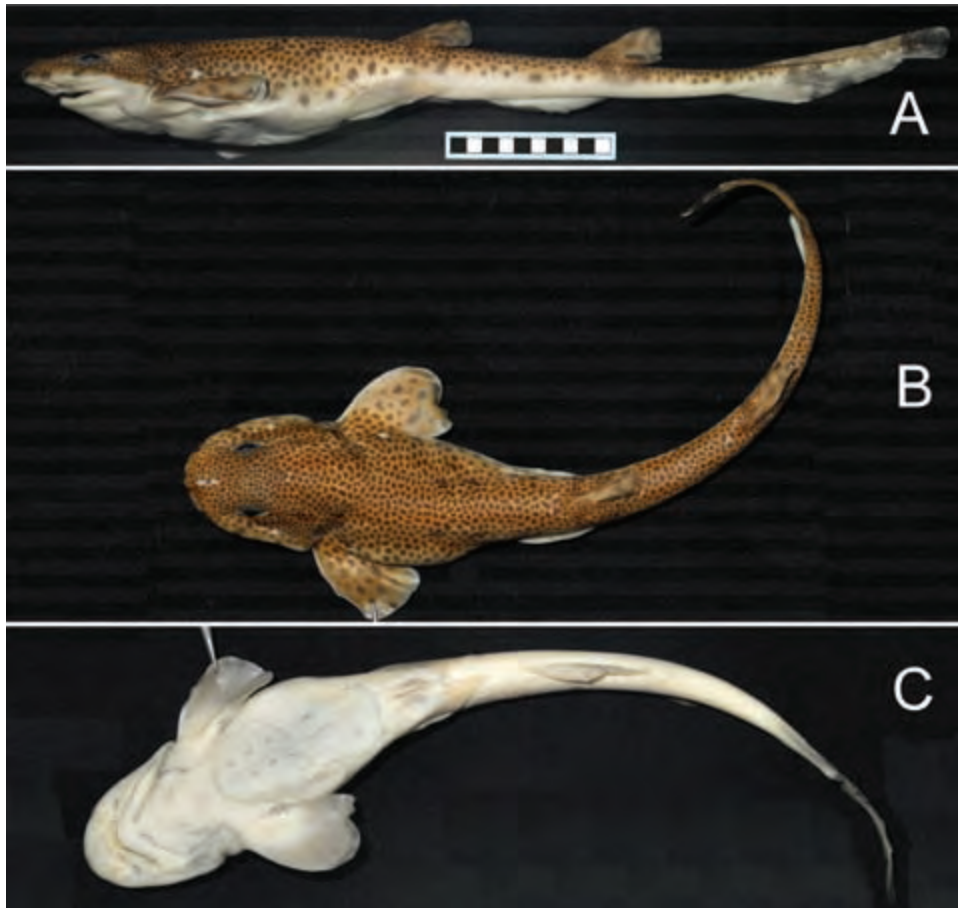
Fig. 3. Lateral (A), dorsal (B), and ventral (C) photographs of the female *H. grennian* specimen (SAIAB 81902) collected off Mozambique. Note the V-shaped markings present on both dorsal fins, and the black ventral sensory pores.

Fig. 4. Comparison of dorsal fin markings of *H. grennian* specimens illustrating the differences between those specimens collected off Tanzania and Kenya (A, B), compared to the specimen collected off Mozambique (C). Holotype RUSI 13802, male (A); Paratype BMNH 1939.5.24.5, female (B); and SAIAB 81902, female(C).

or an artefact of small sample size.

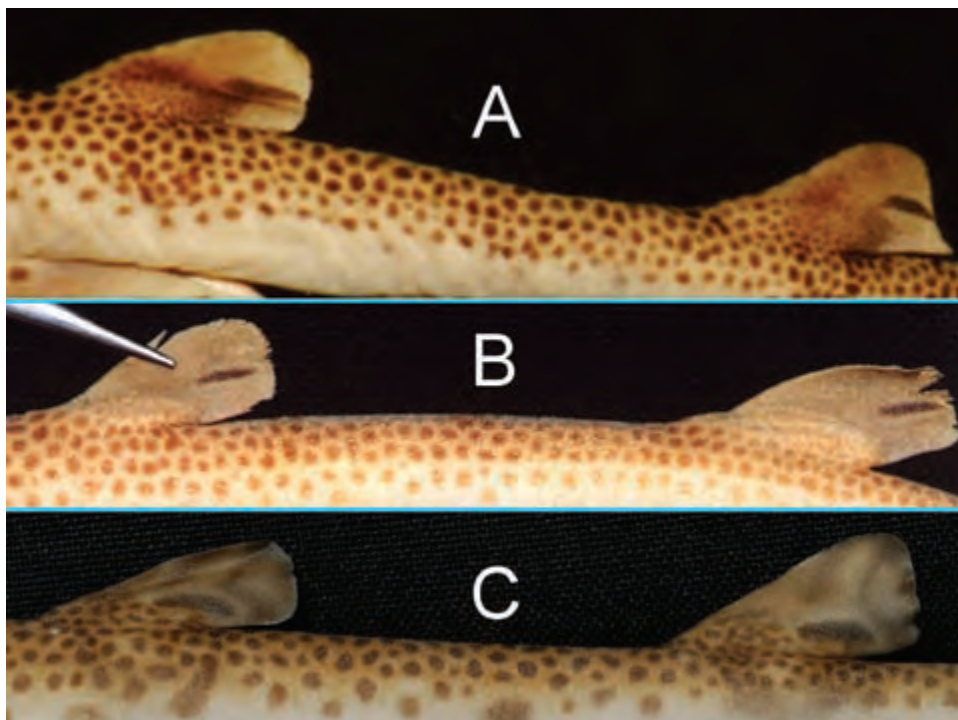This specimen of *H. grennian* is interesting because it exhibits characters that are more typically associated with *H. punctatus*, which has a restricted southwestern Indian Ocean distribution. The reduced dorsal midline denticles and the presence of the V-shaped markings on this *H. grennian* specimen is more typical of *H. punctatus*, representing possible regional differences and potential population sub-structuring within *H. grennian*. Furthermore, these differences may also speculatively be attributed to hybridisation between *H. grennian* and *H. punctatus* in the southern Mozambique region at some time, or are remnants of a speciation event, and that these characters were lost as the species dispersed northwards.

Given the total length of the specimen, it is assumed that it is either adolescent or mature. The specimen was, however, not gravid and was not dissected to ascertain maturity. Egg cases and reproductive traits of *H. grennian* remain unknown.

Despite the differences in morphometric statistics, dorsal midline denticles (enlarged, but easily overlooked) and colouration described for this specimen, the key for *Holohalaelurus* of Human (2006a) remains effective for discriminating species in the genus, even though the morphometric differences were sufficient to reduce the resolution of the shape analyses of the genus compared to Human (2007b). It is hypothesised that the reduced performance of the DFA and classification analyses is a result of this female introducing stronger signals of sexual dimorphism into the analyses. Additional female specimens of all *Holohalaeurus* species are required in order to test this hypothesis.

ZOOGEOGRAPHY OF *HOLOHALAELURUS*

Holohalaelurus sharks are distributed on the African continental shelf and upper to mid-slopes from Namibia, in the southeast Atlantic Ocean, around South Africa and northwards to at least Kenya, and probably Somalia, in the western Indian Ocean. The exception to this distribution is a population, possibly disjunct from the African shelf population, of *H. punctatus*, that occurs around Madagascar. *Holohalaelurus punctatus* is also found from kwaZulu-Natal, South Africa, to southern Mozambique (although possibly extinct there now) and is sympatric with *H. favus* with a similar distribution, although also possibly extinct there now. *Holohalaelurus regani* is also sympatric in this region, although it is more commonly found south and west of kwaZulu-Natal, around South Africa and to southern Namibia, and is the only representative of *Holohalaelurus* south and west of kwaZulu-Natal.

Holohalaelurus grennian is (was) sympatric with *H. punctatus* and *H. favus* in the southern part of its range, but may be the only species occurring in northern Mozambique and southern Tanzania. In northern Tanzania and Kenya *H. grennian* is sympatric with *H. melanostigma*. However, while *H. grennian* inhabits the upper continental slope, there is apparent niche partitioning between the two species with *H. melanostigma* inhabiting the mid-slope at depths of 607–658m. It is possible that both *H. grennian* and *H. melanostigma* occur north of Kenya, as there are anecdotal reports of *Holohalaelurus* sharks occurring off Somalia which may be either or both of these species (Human, 2006a).

Although it is likely that *Holohalaelurus* sharks occur in Somalia, they probably do not occur north of there, as they have not been recorded from the Red Sea (a relatively well known ichthyofauna), and are unlikely to leave the African continental shelf to inhabit the Arabian shelf as the Somali upwelling represents a significant ecological barrier. The range extension described here suggests that further deep water trawling of the lower continental shelf, and upper and mid continental slopes in the western Indian Ocean will lead to further range extensions of the genus *Holohalaelurus*.

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Table 1. Comparison of the morphometric and meristic measurements of the female *H. grennian* specimen (SAIAB 81902) compared to other *H. grennian* specimens (3 male, 1 female, from Human 2006a). WT is measured in grams, TL in millimeters, and all other measurements are expressed as percentage of TL. See Appendix 2 for abbreviations.

	SAIAB 81902	Average	Range		SAIAB 81902	Average	Range
WT	51.8	34.8	10.5 - 61.9	D1L	8.4	7.2	6.1 - 8.2
TL	257	227.8	165 - 273	D1A	8.0	7.0	5.5 - 8.2
PCL	75.9	78.8	76.9 - 80.1	D1B	5.6	4.6	3.6 - 5.5
PD2	58.4	59.9	56.7 - 62.9	D1H	3.9	3.9	3.0 - 4.9
PD1	39.3	39.4	38.2 - 41.2	D1I	2.7	2.8	2.4 - 3.4
BDL	62.6	60.6	59.4 - 63.1	D1P	3.9	3.3	2.9 - 3.5
IDS	14.8	16.0	15.2 - 16.7	P2L	10.9	12.5	11.5 - 13.9
D2C	34.4	33.5	31.5 - 35.8	P2A	5.1	5.5	4.0 - 6.7
DCS	13.0	13.5	12.0 - 14.6	P2B	7.0	7.7	7.1 - 8.3
PAL	48.6	48.6	45.8 - 53.2	P2H	2.3	2.6	2.2 - 3.2
PP2	33.9	31.9	29.1 - 34.8	P2I	5.1	5.5	4.1 - 7.3
PP1	15.2	17.6	16.7 - 18.1	P2P	5.8	6.8	5.8 - 7.7
SVL	36.6	34.3	32.7 - 37.1	CLO	-	5.2	2.1 - 10.3
TRL	20.2	16.8	15.8 - 18.0	CLI	-	6.9	4.8 - 11.7
PPS	13.6	9.9	8.6 - 11.5	CLB	-	0.8	0.6 - 1.5
PAS	9.3	9.9	8.0 - 11.6	D2L	9.7	9.4	9.1 - 9.7
VCL	64.2	64.0	62.6 - 65.9	D2A	9.1	9.3	8.7 - 9.7
PCA	35.4	37.4	36.7 - 37.9	D2B	6.2	6.2	6.0 - 6.4
ACS	15.6	16.7	14.6 - 17.9	D2H	4.1	3.9	3.0 - 4.3
HDH2	7.8	5.7	5.3 - 6.4	D2I	2.9	3.4	2.9 - 3.9
HDW2	12.5	14.0	13.3 - 14.5	D2P	3.9	3.8	3.4 - 4.2
INO	5.8	6.7	6.4 - 7.0	ANL	13.6	13.5	12.1 - 15.2
HDH	8.8	6.9	6.3 - 8.1	ANA	6.8	6.9	5.9 - 7.3
HDW	13.2	13.4	12.6 - 14.3	ANB	11.3	11.0	10.0 - 12.0
TRH	9.1	7.7	7.0 - 8.6	ANH	2.9	2.6	2.4 - 3.0
TRW	13.2	10.2	7.9 - 12.1	ANI	2.7	2.7	2.1 - 3.1
GIR	37.0	28.3	26.7 - 31.1	ANP	7.2	7.4	5.5 - 8.8
ABH	10.3	8.6	7.9 - 9.7	CDM	21.8	21.0	19.9 - 21.5
ABW	12.8	8.1	7.5 - 9.5	CPV	7.0	7.4	5.8 - 8.4
TAH	5.6	4.4	3.6 - 4.9	CPU	9.9	10.3	9.5 - 10.9
TAW	5.4	5.0	4.7 - 5.3	CST	4.7	6.1	4.8 - 7.9
CPH	2.7	2.4	2.2 - 2.6	CSW	2.3	2.6	2.4 - 3.0
CPW	1.4	1.8	1.7 - 1.9	CTR	3.1	3.5	2.4 - 4.0
HDL	15.6	18.1	17.0 - 19.2	CTL	5.8	7.2	5.9 - 8.5
PG1	13.8	15.6	14.6 - 16.7	DPI	24.9	19.8	17.0 - 22.5
PSP	9.3	10.8	10.4 - 11	DPO	8.9	11.0	8.8 - 14.4
POB	6.2	6.8	6.2 - 7.3	PDI	6.2	6.1	4.9 - 7.5
EYL	3.5	3.5	2.9 - 4.1	PDO	21.6	22.2	19.7 - 24.5
EYH	1.4	1.6	1.2 - 2.2	DAO	10.9	10.2	9.4 - 11.0
SPL	0.8	0.8	0.6 - 1.0	DAI	5.4	5.7	4.8 - 7.0
ESL	0.6	0.6	0.5 - 0.7	P2 fused	0.0	0.5	0.0 - 0.9
EMA	1.9	0.6	0.4 - 0.9	P2 free	5.4	4.2	3.6 - 5.1
ING	1.6	2.3	1.6 - 2.7				
GS1	1.6	2.3	2.1 - 2.6	VERT	112	102.0	90 - 108
GS2	1.6	1.9	1.5 - 2.4	mono	27	26.5	24 - 28
GS3	1.2	1.8	1.5 - 2.0	predip	52	50.3	49 - 52
GS4	0.8	1.3	0.9 - 1.6	caudaldip	33	25.3	17 - 30
GS5	0.4	0.6	0.3 - 1.1				

Table 1 continued.

					DENT			
POR	3.7	3.7	2.8 - 4.4		DENT			
PRN	3.9	2.7	1.9 - 3.3		UL	21	20.0	19 - 21
MOL	2.7	3.8	2.7 - 5.3		US	0	1.5	0 - 3
MOW	7.4	9.5	8.7 - 10.1		UR	22	20.0	19 - 21
NOW	2.7	2.4	2.1 - 2.7		U tot	43	41.5	40 - 43
INW	3.1	3.7	3.2 - 4.2		LL	19	18.0	17 - 19
IOW	7.8	8.4	8.2 - 8.5		LS	0	2.5	0 - 4
ANF	1.2	1.0	0.7 - 1.2		LR	18	18.5	17 - 22
P1L	12.3	12.0	11.2 - 13.7		L tot	37	39.0	38 - 41
P1A	11.3	11.9	10.0 - 13.9					
P1B	7.0	7.4	7.1 - 8.0					
P1H	8.2	7.9	6.7 - 9.4					
P1I	6.2	5.6	4.4 - 7.1					
P1P	7.8	7.8	6.1 - 9.3					
P1R	0.0	5.0	0.0 - 7.5					

Table 2. The first nine eigenvectors from the multigroup principal component analysis that account for 75% of the variance in the dataset.

Eigenvector	Eigenvalue	%	Cumulative	Cumulative %
1	0.141319	29.3	0.141319	29.3
2	0.083411	17.3	0.224730	46.5
3	0.039191	8.1	0.263921	54.7
4	0.023374	4.8	0.287296	59.5
5	0.022920	4.7	0.310216	64.2
6	0.019582	4.1	0.329798	68.3
7	0.015453	3.2	0.345251	71.5
8	0.013648	2.8	0.358899	74.3
9	0.012924	2.7	0.371823	77.0

Table 3. Summary of the stepwise discriminant function analysis. Wilks' Lambda approx. 0.08264, F (24,102) 4.4515 p<0.0000. *denotes variables that contributed significantly to the model.

	Wilks' lambda	Partial lambda	F – remove (4, 29)	p level	Tolerance	1 – tolerance (r^2)
*MOL	0.182	0.455	8.687	0.000	0.503	0.497
*GS5	0.114	0.727	2.719	0.049	0.412	0.588
*D1P	0.114	0.724	2.760	0.047	0.409	0.591
P2H	0.104	0.792	1.909	0.136	0.250	0.750
GS4	0.106	0.779	2.057	0.112	0.487	0.513
P2I	0.097	0.851	1.273	0.303	0.321	0.679

Table 4. Chi squared test of significance from the successive removal of canonical roots to examine which roots contribute significantly to the discriminating power of the model.

Roots removed	Eigenvalue	Canonical R	Wilks' lambda	Chi-square	d.f.	p level
0	4.190	0.899	0.083	81.03005	24	0.000
1	0.660	0.630	0.429	27.50822	15	0.025
2	0.290	0.474	0.712	11.04145	8	0.199
3	0.089	0.285	0.919	2.75787	3	0.430

Table 5. Percentage and numbers of specimens correctly classified into their putative species of *Holohalaelurus*. The first column shows the observed species classification, and the following columns the species classification of specimens predicted from the discriminatory functions model.

	% correct	favus	grennian	melanostigma	punctatus	regani
favus	50	2	0	0	0	2
grennian	60	0	3	0	2	0
melanostigma	75	0	0	3	0	1
punctatus	85	0	1	0	11	1
regani	100	0	0	0	0	13
Total	82.1	2	4	3	13	17

APPENDICES

APPENDIX 1. *Holohalaelurus* comparative material.
Those lots highlighted with an asterisk were used in the shape variation analyses and includes all specimens within the lot. Abbreviations: BAH - Brett Human field number; BMNH - British Museum Natural History; LJVC - Leonard Compagno field number; MNHN - Muséum National d'Histoire Naturelle; RUSI - SAIAB (previously Rhodes University/ J.L.B. Smith Institute of Ichthyology); SAIAB - South African Institute for Aquatic Biodiversity; and SAM - South African Museum.

Holohalaelurus favus Human 2006 - RUSI 6139*, holotype, mature male 515mm TL; RUSI 6138*, paratype, mature female 423mm TL; RUSI 6140*, adolescent female 291mm TL; and RUSI 6271*, immature male 193mm TL.

Holohalaelurus grennian Human 2006 - RUSI 13082*, holotype, mature male 267mm TL; BMNH 1939.5.24.5*, paratype, also paratype of *Scyliorhinus* (*Halaelurus*) *melanostigma* Norman 1939, juvenile female 206mm TL; SAM 36077*, mature male 273mm TL; SAM 36078*, juvenile male 165mm TL; and SAIAB 81902*, immature female 257mm TL.

Holohalaelurus melanostigma (Norman 1939) - BMNH 1939.5.24.2*, holotype, adolescent male 335mm TL; BMNH 1939.5.24.3*, paratype, adolescent male 330mm TL; BMNH 1939.5.24.4*, paratype, juvenile male 267mm TL; and RUSI 14114*, mature male 384mm TL.

Holohalaelurus punctatus (Gilchrist 1914) - RUSI 6128*, neotype, mature male 298mm TL; MNHN 1987-1291, male 348mm TL; MNHN 1987-1292, male 321mm TL; MNHN 1987-1293, female 277mm TL; MNHN 1987-1294, male 335mm TL; MNHN 1988-0356, male 355mm TL; MNHN 1991-0410, female 272mm TL; MNHN 1991-0411, female 220mm TL; MNHN 1991-0412, male, 330mm TL; RUSI 6129*, adolescent male 235mm TL; RUSI 6131*, immature female 181mm TL; RUSI 6132*, immature female 227mm TL; RUSI 6133*, immature female 196mm TL; RUSI 6134*, immature male 176mm

TL; RUSI 6136*, adolescent female 236mm TL; RUSI 6137*, immature female 218mm TL; RUSI 40829*, 4 specimens, all mature males 303mm TL, 310mm TL, 323mm TL, and 326mm TL; and BMNH 1921.3.1.1*, holotype of *H. polystigma* (Regan 1921), mature male 316mm TL.

Holohalaelurus regani (Gilchrist 1922) - SAM 32448*, neotype, mature male 628mm TL; BAH 20020110.01*, mature male 630mm TL; BAH 20020414.06*, mature male 598mm TL; BAH 20020414.07*, mature female 460mm TL; BAH 20020414.08*, mature female 483mm TL; BAH 20020414.09*, gravid female 455mm TL; BAH 20020414.10*, mature female 428mm TL; BAH 20020414.11, gravid female 431mm TL; BAH 20020414.12*, mature male 598mm TL; BAH 20020419.02*, mature male 600mm TL; BAH 20020419.03, mature female 515mm TL; BAH 20020419.04*, gravid female 466mm TL; LJVC 860111, juvenile female 140mm TL; RUSI 952, 2 specimens, both juvenile females, 254mm TL and 205mm TL; RUSI 2800*, juvenile female 349mm TL; RUSI 25726*, mature male 598mm TL; RUSI 38280, adolescent female 351mm TL; RUSI 48813, immature female 224mm TL; RUSI 53725*, mature male 604mm TL; SAM 12986, adolescent male; SAM 12987, 3 specimens, juvenile males, 270mm TL and 420mm TL, immature male, 270mm TL; SAM 12988, gravid female 425mm TL; SAM 12989, juvenile male 270mm TL; SAM 12990, 5 specimens, 4 juvenile females, 176mm TL, 200mm TL, 230mm TL, and 254mm TL, and one juvenile male, 232mm TL; SAM 12991, adolescent female; SAM24408, 2 specimens, one adolescent female, one mature male; SAM 27027; SAM 31695; SAM 32619, mature female; SAM 32995; SAM 33287; SAM 34500; and SAM 34648.

APPENDIX 2. Morphometric and meristic abbreviations based on Compagno (2001) and Human (2006b).

WT, weight; TL, total length; PCL, precaudal length; PD2, pre-second dorsal fin length; PD1, prefirst dorsal fin length; BDL, body length; IDS, inter-dorsal space; D2C, second dorsal - caudal length; DCS, dorsal - caudal space; PAL, pre-anal length; PP2, pre-pelvic length; PP1, pre-pectoral length; SVL, snout - vent length; TRL, trunk length; PPS, pectoral - pelvic space; PAS,

pelvic - anal space; VCL, vent - caudal length; PCA, pelvic - caudal space; ACS, anal - caudal space; HDH2, head height 2; HDW2, head width 2; INO, inter-orbital width; HDH, head height; HDW, head width; TRH, trunk height; TRW, trunk width; GIR, girth; ABH, abdomen height; ABW, abdomen width; TAH, tail height; TAW, tail width; CPH, caudal peduncle height; CPW, caudal peduncle width; HDL, head length; PG1, pre-first gillslit length; PSP, pre-spiracular length; POB, pre-orbital length; EYL, eye length; EYH, eye height; SOD, subocular pocket depth; SPL, spiracle length; ESL eye spiracle length; EMA, anterior eye mouth length; ING, inter-gill length; GS1-GS5, gill slit height; POR, pre-oral length; PRN, pre-narial length; MOL, mouth length; ULA, upper labial furrow length; ULH, upper labial furrow height; LLA, lower labial furrow length; NOW, nostril width; INW, internarial width; IOW, internarial outer width; ANF, anterior nasal flap length; P1L, pectoral fin length; P1A, pectoral fin anterior margin length; P1B, pectoral fin base length; P1H, pectoral fin height; P1I, pectoral fin inner margin length; P1P, pectoral fin posterior margin length; P1R, pectoral fin anterior most radial length; DIL, first dorsal fin length; D1A, first dorsal fin anterior margin length; D1B, first dorsal fin base length; D1H, first dorsal fin height; D1I, first dorsal fin inner margin length; D1P, first dorsal fin posterior margin length; P2L, pelvic fin length; P2A, pelvic fin anterior margin length; P2B, pelvic fin base length; P2H, pelvic fin height; P2I, pelvic fin inner margin length; P2P, pelvic fin posterior margin length; P2fused, pelvic fin fused inner margin length; P2free, pelvic fin free inner margin length; CLO, clasper outer length; CLI, clasper inner length; CLB, clasper base length; D2L, second dorsal fin length; D2A, second dorsal fin anterior margin length; D2B, second dorsal fin base length; D2H, second dorsal fin height; D2I, second dorsal fin inner margin length; D2P, second dorsal fin posterior margin length; ANL, anal fin length; ANA, anal fin anterior margin length; ANB, anal fin base length; ANH, anal fin height; ANI, anal fin inner margin length; ANP, anal fin posterior margin length; CDM, dorsal caudal margin length; CPV, pre-ventral caudal margin length; CPU, upper post-ventral caudal margin length; CST, subterminal caudal lobe length; CSW, subterminal caudal lobe width; CTR, terminal caudal fin margin height; CTL, terminal caudal fin lobe length; DPI, first dorsal fin midpoint to pectoral fin insertion length; DPO, first dorsal fin midpoint to pelvic fin origin length; PDI, pelvic fin midpoint to first dorsal fin insertion; PDO, pelvic fin midpoint to second dorsal fin origin; DAO, second dorsal fin origin to anal fin origin length; DAI, second dorsal fin insertion to anal fin insertion length; VERT, total vertebral count; mono, monospondylous vertebral count; predip, precaudal diplospondylous vertebral count; caudaldip, caudal diplospondylous vertebral count; DENT, dentition; UL, upper jaw left tooth count; US, upper jaw symphysial tooth count; UR, upper jaw right tooth count; U tot, upper jaw total tooth count; LL, lower jaw left tooth count; LS, lower jaw symphysial tooth count; LR, lower jaw right tooth count; L tot, lower jaw total tooth count.