Electrolux addisoni, a new genus and species of electric ray from the east coast of South Africa (Rajiformes: Torpedinoidei: Narkidae), with a review of torpedinoid taxonomy

Leonard J.V. Compagno[1] and Phillip C. Heemstra[2]

[1] Shark Research Centre, Iziko-South African Museum, Cape Town, South Africa,
e-mail lcompagno@iziko.org.za
[2] South African Institute for Aquatic Biodiversity, Grahamstown, South Africa,
e-mail p.heemstra@ru.ac.za

(Submitted 7 December 2006; accepted 23 February 2007)

ABSTRACT. A new genus and species of sleeper ray, *Electrolux addisoni* (Family Narkidae), with two dorsal fins is described from two adult males (total lengths 50 and 52 cm) caught on a shallow reef off the east coast of South Africa. *Electrolux* is distinguished from other genera of Narkidae by its prominent spiracular papillae, the morphology of its nostrils, nasal curtain, mouth, jaws, chondrocranium, basibranchial skeleton, pectoral and pelvic girdles, and unique and complex colour pattern. It has higher vertebral, pectoral radial, tooth and intestinal valve counts than other narkids and reaches a greater size than all species with the possibly exception of *Typhlonarke aysoni*. Taxonomic definitions are provided for the electric rays, for the family Narkidae, and for Electrolux, as well as keys to families of electric rays and to the genera of Narkidae. The systematics of the narkid genus Heteronarce is reviewed and the genus validated. Members of the Narkidae may include the smallest, or at least the shortest, living chondrichthyans (*Temera hardwickii* and an undescribed species of *Narke*). *Electrolux addisoni* is a reef-dweller that eats polychaete worms and small crustaceans, and has been photographed and videotaped by divers while actively feeding in the daytime. The conspicuous dorsal colour pattern may be aposematic, as the ray was seen to make a possible threat display when closely approached. *Electrolux addisoni* is recorded from four localities along an approximately 310 km. strip of coastline from Coffee Bay, Eastern Cape Province, to just north of Durban, kwaZulu-Natal inside the 50 m isobath. This conspicuous, active ray is known only from a few diver records from reefs reported over approximately two decades, and its conservation status needs to be critically assessed.

KEY WORDS: *Electrolux addisoni*, new genus and species, Narkidae, sleeper ray, Torpedinoidei, description, taxonomy, distribution, biology, conservation status.

The coastal fish fauna of the east coast of South Africa is a mixture of tropical and subtropical Indo-West Pacific fishes (mainly coral-reef species), many endemic warm temperate species, and several worldwide species. This South African fish diversity is not well known, and in the past 20 years, our cursory fish survey work has produced numerous range extensions, many new records and several new species. In addition to our own collecting efforts and those of fisheries biologists on South African research vessels (particularly RV *Africana*; see Compagno, 1999b) and fishing companies and observers on fishing vessels, our knowledge of the South African marine fish diversity is significantly enhanced by the specimens and photographs provided by various amateur ichthyologists (anglers, aquarists, divers and underwater photographers).

This paper describes a remarkable new genus and species of electric ray (Family Narkidae) from the east coast of South Africa. The species was first made known to us by diver-photographer Peter Chrystal (through Rudy van der Elst, *pers. comm.*), who photographed this spectacular ray on a patch of sand on Aliwal Shoal, kwaZulu-Natal, South Africa in 1984 (Figure 1). The ray was subsequently rediscovered on Protea Banks off Shelly Beach, kwaZulu-Natal in 1997 by underwater photographers Stephania and Peter Lamberti (*pers. comm.*) who sent us a video-clip of the ray (Figure 2). It has also been photographed underwater at the Tee Barge north of Durban by Dennis King. A live specimen was seen underwater by P. Heemstra at Coffee Bay, Eastern Cape in 2001, but the ray fled before he could net it.

From the 1984 photographs we immediately recognized an undescribed species of electric ray (Torpedinoidei or Torpediniformes) with a unique dorsal colour pattern that was far more elaborate and ornate than that of any electric ray known at the time, although Last & Stevens (1994) and de Carvalho (1999) subsequently described species of *Narcine* off Australia and in the Western Hemisphere with ornate but simpler colour patterns. The ray was tentatively considered as either a member of the family Narkidae or Narcinidae by Compagno (in Smith & Heemstra, 1995) but after video footage became available, Compagno (1999b) thought it to be an undescribed narkid most probably of the genus *Heteronarce* because of its general morphology and twin dorsal fins.

However, the ray frustrated us by eluding capture for nearly two decades despite efforts by colleagues to collect it. In September 2003 a specimen (**SAIAB** 78777) was collected by Mark Addison on a reef off Manaba Beach near Margate in southern KwaZulu-Natal. A second specimen was collected by Mark's father, Brent Addison at the same locality in October 2003. Both specimens (Figures 3-4) were presented by Mark Addison to the South African Institute of Aquatic Biodiversity and the second specimen was transferred to the fish collection of Iziko - South African Museum (**SAM** 36908).

Study (including radiography) of the two specimens and dissection of the paratype (**SAM** 36908) confirmed our hypothesis that they represented a new species of the Family Narkidae (sleeper rays), which in South African waters also includes the common onefin electric ray, *Narke capensis* and the rare Natal electric ray, *Heteronarce garmani* (Compagno in Smith & Heemstra, 1986, Compagno et al., 1989). However, this new electric ray proved sufficiently different from known narkid genera *Heteronarke, Narke, Temera* and *Typhlonarke* to warrant a new genus and species (Compagno, 2005). We also discuss the systematics of *Heteronarce* and the Family Narkidae, and the taxonomy of electric rays, and comment on the size of narkid rays and the biology, habitat and conservation status of the new ray.

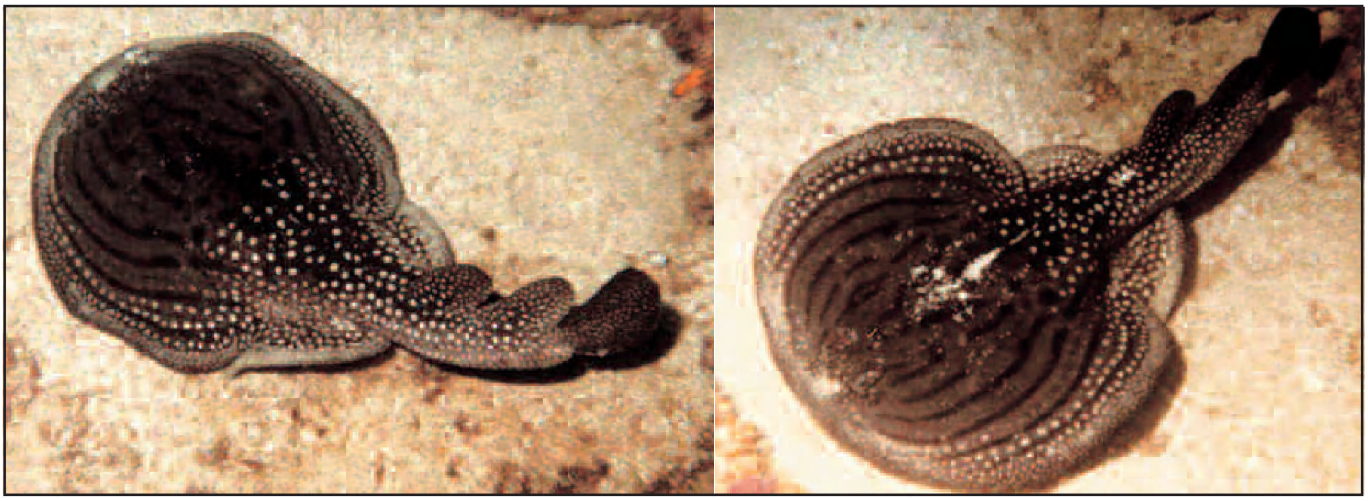

Figure 1. *Electrolux addisoni* photographed by Peter Chrystal at Aliwal Shoal, KwaZulu-Natal, South Africa in 1984. These two photographs were sent to the junior author by Rudy van der Elst and show the intricate concentric black stripe of the dorsal colour pattern on the disc of a live ray.

Figure 2. Two frames from a videotape of *Electrolux addisoni* taken by Stephania and Peter Lamberti in 1997 on Protea Banks off Shelly Beach, KwaZulu-Natal, South Africa. Left, ray vigorously feeding on substrate and moving towards the photographer, using its pelvic fins as legs. Right, ray stationary and giving a possible threat display, with disc curled and tail raised.

METHODS

External Morphology and Morphometrics: Terminology and abbreviations for torpedinoid external morphology and morphometrics are based on Bigelow and Schroeder (1953) for batoids, Compagno & Roberts (1982, 1984) for stingrays, and Compagno (1984, 1988, 2001) and Compagno *et al.* (2005) for sharks. Measurements and their abbreviations for electric rays are based on the system for sharks in Compagno (1984, 2001) with some modifications and additions. For the bases of precaudal fins the term **origin** is used for the anterior end of the fin base and **insertion for** the posterior end of the base. The morphometric abbreviations and definitions for torpedinoid measurements are presented below (Table 1). **Meristics**. Terminology and abbreviations for torpedinoid vertebral counts is derived from that for sharks in Compagno (1988) and for stingrays in Compagno & Roberts (1982, 1984) and are defined as follows: **SYN**, total synarcual vertebrae; sum of **SYC**, synarcual segments anterior to synarcual centra and determined by count of neural canals through lateral walls of synarcual, and **SYC**, synarcual centra in posterior end of synarcual. **MP**, monospondylous precaudal centra, between posterior end of synarcual and monospondylous-diplospondylous transition, sum of **MPN**, monospondylous precaudal centra without ribs, and **MPR**, monospondylous precaudal centra with ribs. **DP**, diplospondylous precaudal centra, between MP-DP transition and upper origin of caudal fin; sum of **DPN**, diplospondylous precaudal centra without ribs, and **DPR**, diplospondylous precaudal centra with ribs. **DC**, diplospondylous caudal centra from upper origin of caudal fin to end of vertebral column. **PC**, precaudal vertebrae, including **SYN**, **MP**, and **DP** vertebrae. **PCC**, precaudal centra, including **SYC**, **MP**, and **DP** centra. **TF**, total free centra from posterior end of synarcual to end of caudal centra; sum of **MP**, **DP**, and **DC** centra. **TC**, total free centra plus synarcual centra; sum of **SYC**, **MP**, **DP**, and **DC**. **TS**, total segments, all centra plus **SYS**. **SYN%**, total synarcual centra as percentage of total free centra, 100*(**SYN/TC**). **MP%**, monospondylous precaudal centra as percentage of total free centra, 100*(**MP/TC**). **DP%**, diplospondylous precaudal centra as percentage of total free centra, 100*(**DP/TC**). **DC%**, diplospondylous caudal centra as percentage of total free centra, 100*(**DC/TC**).

Tooth and intestinal valve terminology and count methodology is after Compagno (1988).

Terminology and information on torpedinoid anatomy including chondrocranial and hyobranchial morphology follows Henle (1834), Gill (1862), Haswell (1895), Garman (1913), Holmgren (1941), and Compagno (1973, 1977, 1988, 1999a). Clasper terminology for torpedinoids follows Leigh-Sharpe (1922, 1924, 1926) and Compagno (1988).

ORDER RAJIFORMES, SUBORDER TORPEDINOIDEI - ELECTRIC RAYS

Definition (derived from Compagno (1973, 1977, 1999a). Rays (Rajiformes) with head broadly depressed and included with body and hypertrophied pectoral fins to form a thick, flattened, oval, circular or subquarate fleshy pectoral disc with broadly rounded apical margins. Trunk thick, broad, and depressed, not rising abruptly dorsal to pectoral bases. A pair of large, kidney-shaped electric organs in disc between propterygium, branchial region and pectoral girdle, generally visible through skin of ventral surface. Precaudal tail usually stout and muscular, more or less elongated, but diminutive in Hypnidae; tail with two, one or no dorsal fins, ventro-lateral folds (often present) but no median dorsal or ventral skin folds; tail without caudal electric organs or a sting. Preoral snout short to moderately long, 6-21% of total Total length, broadly rounded or truncated, front edge continuous with that of the pectoral disc and not angular, not formed into a tooth-studded rostral saw. Eyes small to moderate-sized in most taxa (eyes vestigial in some *Narke dipterygia* and absent externally in *Typhlonarke*) dorsal on the head, well medial to lateral margins of disc and anterior to spiracles; eyes with a velum on the cornea but no semilunar groove below them. Spiracles either contiguous with rear margins of eyes or separated from them by a space less than their width; spiracles with internal pseudobranchs. Nostrils moderately large, close together, just anterior to mouth; circum-narial flaps and grooves well developed on incurrent apertures of nostrils; anterior nasal flaps fused medially to form a broad nasal curtain, which is free posteriorly and usually reaches mouth; broad nasoral grooves present between excurrent apertures of nostrils and mouth. Mouth always subterminal on head although varying in position (close behind front edge of snout in *Electrolux*), small to moderate-sized, straight or arcuate. No gill sieves or rakers on internal gill slits. Teeth small and not fused into crushing plates; dental bands limited to medial half of jaws, not extending to mouth corners; teeth in 8-68 / 7-75 rows, total rows 15-141; tooth crowns carinate, monocuspidate or tricuspidate. Skin completely naked on all surfaces of disc, tail, fins, and claspers. Pectoral fins expanded, fused medially with head and trunk, usually not obviously distinct externally; pectoral fin bases very long, extending from nasal capsules to pelvic fin origins; pectoral axils much closer to vent than to first gill apertures. Propterygia of pectoral fin skeleton greatly elongated, longer than metapterygia, segmented anteriorly and forming a propterygial axis; propterygia reaching level of nasal capsules or ending behind them, radials extending in front of nostrils but not reaching snout tip. Mesopterygia large and expanded anterolaterally to opposite posterior quarter to half of basal segment of propterygial axis, and carrying its radials. Scapulocoracoids with a pair of lateral bars connecting coracoid bar with scapular processes on each side, separated by a large fenestra from lateral face of scapulocoracoid, which forms unique hollow tube, more or less elongated posterolaterally and terminating in a small, rounded-oval articular surface with a distinct procondyle for the propterygium, small anterodorsal and anteroventral foramina above and below a broad anterior bridge between the procondyle and a small mesocondyle for the mesopterygium, small postdorsal and postventral foramina, and a moderate-sized metacondyle for the metapterygium. Suprascapulae fused together above synarcual or behind it and above neural spines of free monospondylous vertebrae; suprascapulae without the complex attachment to vertebral column as in other batoids; distal ends of suprascapulae straight and not forked, articulating with scapular processes. Pelvic fins not divided into distinct anterior and posterior lobes (except in *Typhlonarke*, where the anterior lobes are fused with and protrude from the pectoral disc and the posterior lobes are fused to the posterior disc). Origins of pelvic fins anterior to pectoral free rear tips; pelvic fins with straight, convex, or concave posterior margins. Pelvic girdle with strong lateral prepelvic processes, short ischial and iliac processes, but without a medial prepubic process on puboischiadic bar; puboischiadic bar posteriorly arched or transverse, not anteriorly arched. Claspers short, stout, and protruding a short distance past pelvic free rear tips or not at all in adult males; clasper glans very simple, with small pseudosiphon and pseudopera but without clasper spines. Dorsal fins usually two (one in *Narke* and *Typhlonarke*, absent in *Temera*), moderately large (small in Hypnidae) and rounded-angular (not falcate). First dorsal fin when present with base over or just behind pelvic bases and over anterior half of precaudal tail. Caudal fin usually large to moderate-sized (small in Hypnidae); caudal fin vertebral axis horizontal to weakly diagonal and elevated, diphycercal or weakly heterocercal; dorsal and ventral caudal fin margins broadly rounded, terminal lobe mostly rounded or occasionally pointed, a low ventral caudal lobe present or absent; caudal fin without a differentiated postventral margin and without a discrete terminal lobe and subterminal notch. Vertebral column with cervicothoracic synarcual but no thoracolumbar synarcual; synarcual variable in length, ending before or behind suprascapulae; synarcual not formed anteriorly into a collar-like sheath around spinal cord but with a peg-like ventral projection fitting in foramen magnum and between occipital condyles. Cranium with rostrum variably developed, absent (Hypnidae), more or less reduced (Torpedinidae, Narkidae) or moderately large, wide, and trough-shaped (Narcinidae). Precerebral cavity more or less expanded into rostrum but not roofed dorsally, truncated anteriorly in Narkidae. Rostral nerves not enclosed in rostrum. Nasal capsules expanded laterally, ventrolaterally, ventrally or anteroventrally; internasal septum broad and depressed (Narcinidae) to more or less narrow and compressed (Hypnidae, Narkidae), broadly separating the nasal capsules or not. Antorbital condyles on anterior, lateral or posterior surfaces of nasal capsules; antorbital cartilages distally expanded, directed anteriorly or anterolaterally, fan-shaped or antler-shaped and branched; antorbital cartilages not articulating with propterygia. Preorbital processes rudimentary or absent, no supraorbital crests, no postorbital processes and no low suborbital shelves. Anterior fontanelle not delimited anteriorly by a transverse ridge. Cranial roof with frontoparietal fenestra absent or very small to huge; separated from anterior fontanelle by an epiphysial bar or not. Basal plate flat or arched and without basal angle; basal plate with a single internal carotid foramen or two narrowly separated carotid foramina at its midline. Occipital condyles small, ventral, and not covering occiput. Dorsal and ventral labial cartilages present in Narcinidae and Narkidae; absent and presumably lost in *Hypnos* and *Torpedo*. Hyobranchial skeleton without basihyoid element; hypobranchials discrete, parasagittal, not fused to form a midventral plate and not fused to well-developed basibranchial copula. Branchial rays expanded distally as broad circular plates. Mode of reproduction ovoviviparous as far as is known, with prenatal young nourished primarily by their yolk sacs.

ELECTROLUX COMPAGNO & HEEMSTRA, *genus novum.*

TYPE SPECIES: *Electrolux addisoni* Compagno & Heemstra *sp nov.* described below.

GENERIC DIAGNOSIS: Narkid electric rays with subcircular disc, length 51% TL; snout short, broadly rounded and nearly straight (Figs 1- 4). Eyes well-developed, close to front edge of disc, but mostly hidden by loose skin. Spiracles (Fig. 5) contiguous with eyeballs, rim a low, rounded, ridge with 5 or 6 long, slender stiff papillae and 2 or 3 short, soft papillae, including one minute papilla on eye; spiracle diameter ~ 1.1-1.3 times eye diameter. Incurrent apertures of nostrils nearly circular, flaps of incurrent apertures (circumnarial flaps) broad, large, flattened, trumpet-like and elongated, their length 2/3-3/4 length of anterior nasal flaps; posterior margin of nasal curtain deeply incised, with prominent lateral lobes and a small medial lobe; ventral surface of curtain with a shallow medial groove; length of anterior nasal flap about 1.1 in outer internarial width; lateral margins of curtain nearly parallel. Mouth and nostrils projecting ventrally from disc as a prominent nasoral turret (Figs 6A & 7) near front edge of disc. Lips between labial folds and dental bands thin and with small transverse pleats of skin; lower lip narrow and thin, no mental

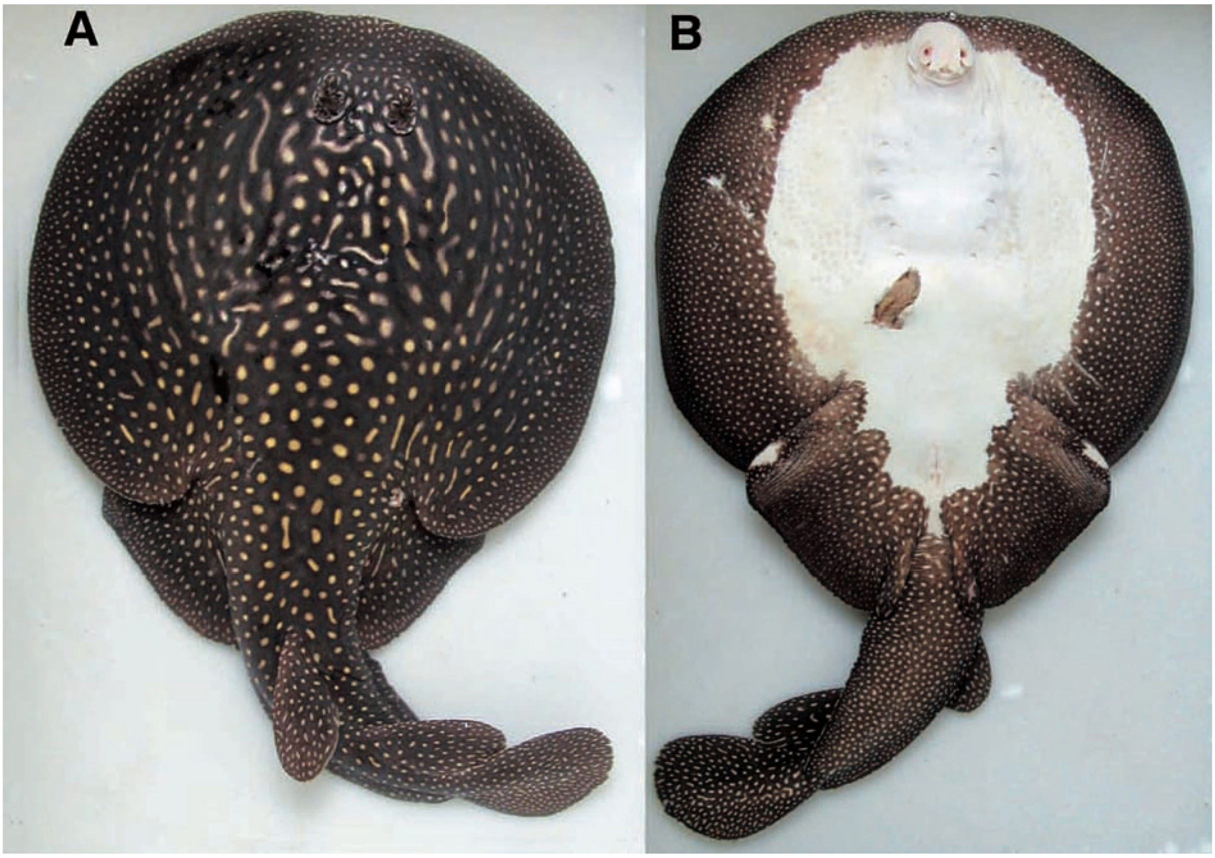

Figure 3. Holotype of *Electrolux addisoni,* 515 mm TL adult male, in A, dorsal and B, ventral views. Note differences in dorsal disc colour pattern compared with live animals (Figs. 1 & 2).

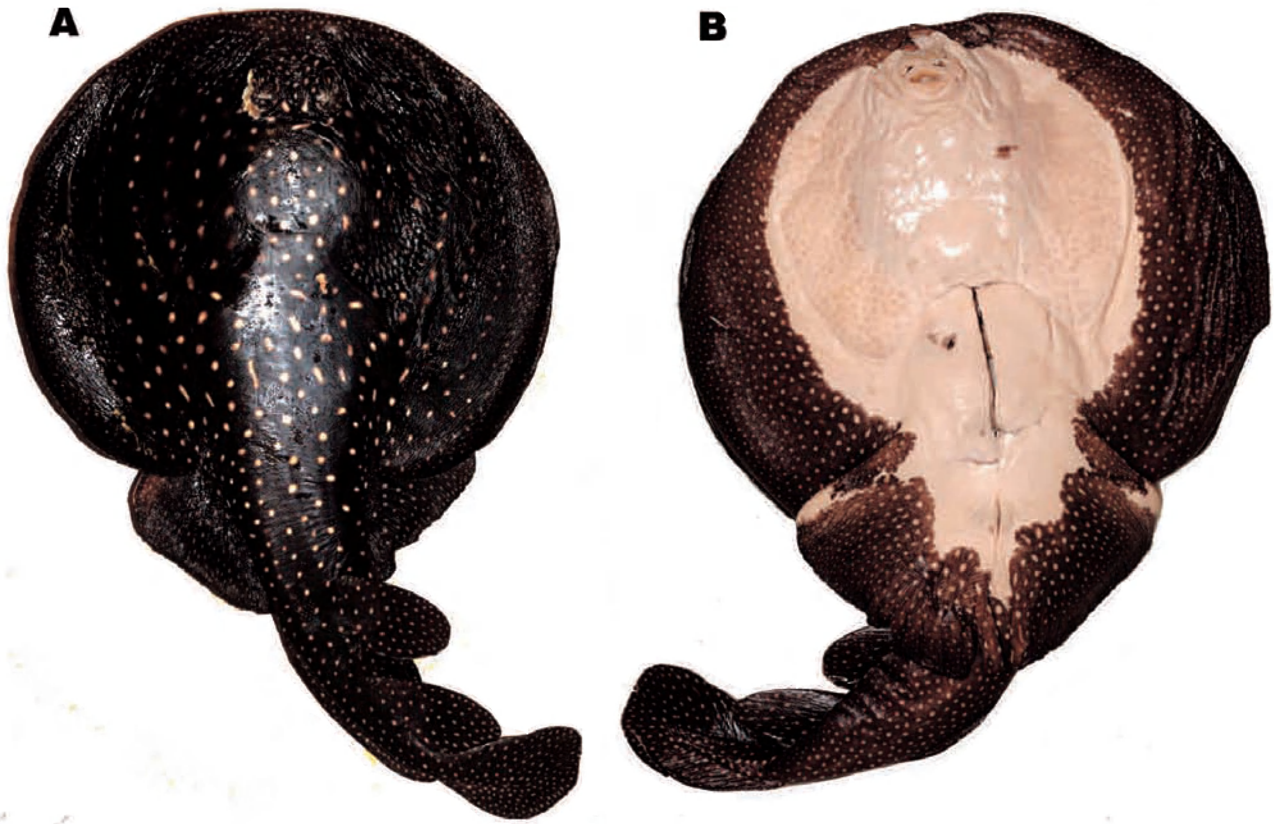

Figure 4. Paratype of *Electrolux addisoni*, 502 mm TL, adult male, in A, dorsal and B, ventral views.

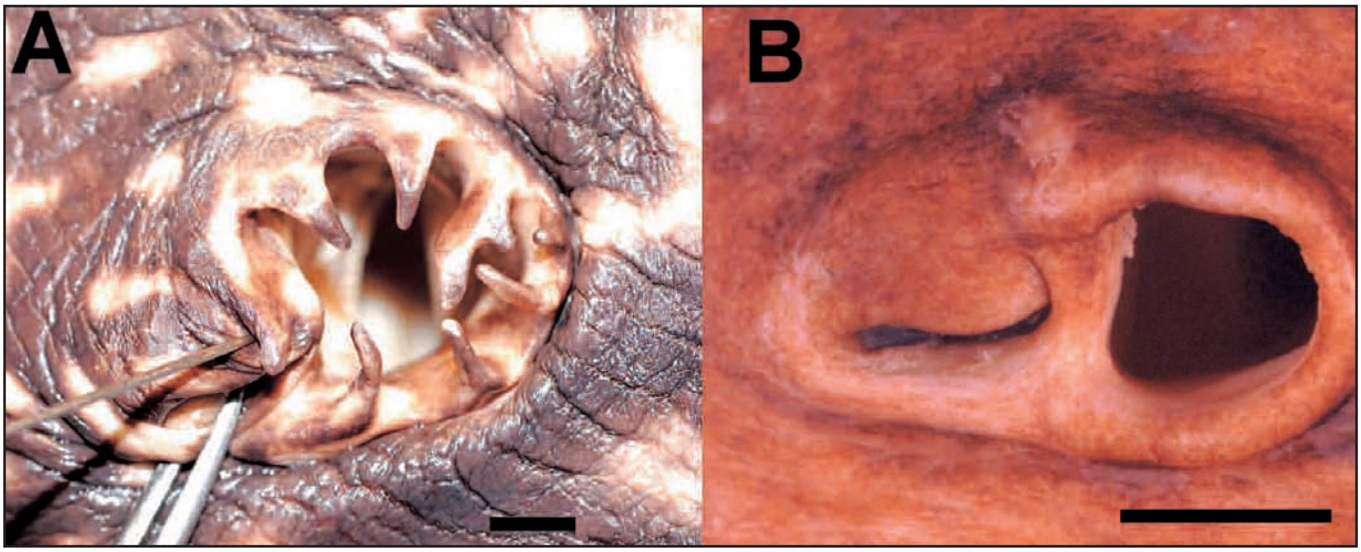

Figure 5. Photos of left eye and spiracle (anterior to left) of: A. *Electrolux addisoni*, holotype, with papillose depressed spiracular rim. Pin penetrates skin at base of ocular papilla, forceps are clamped on fleshy lower eyelid. B. *Heteronarce garmani*, SAM 34813, 289 mm TL adult male, with smooth elevated spiracular rim. Photographs by authors. Scale bars = 5 mm

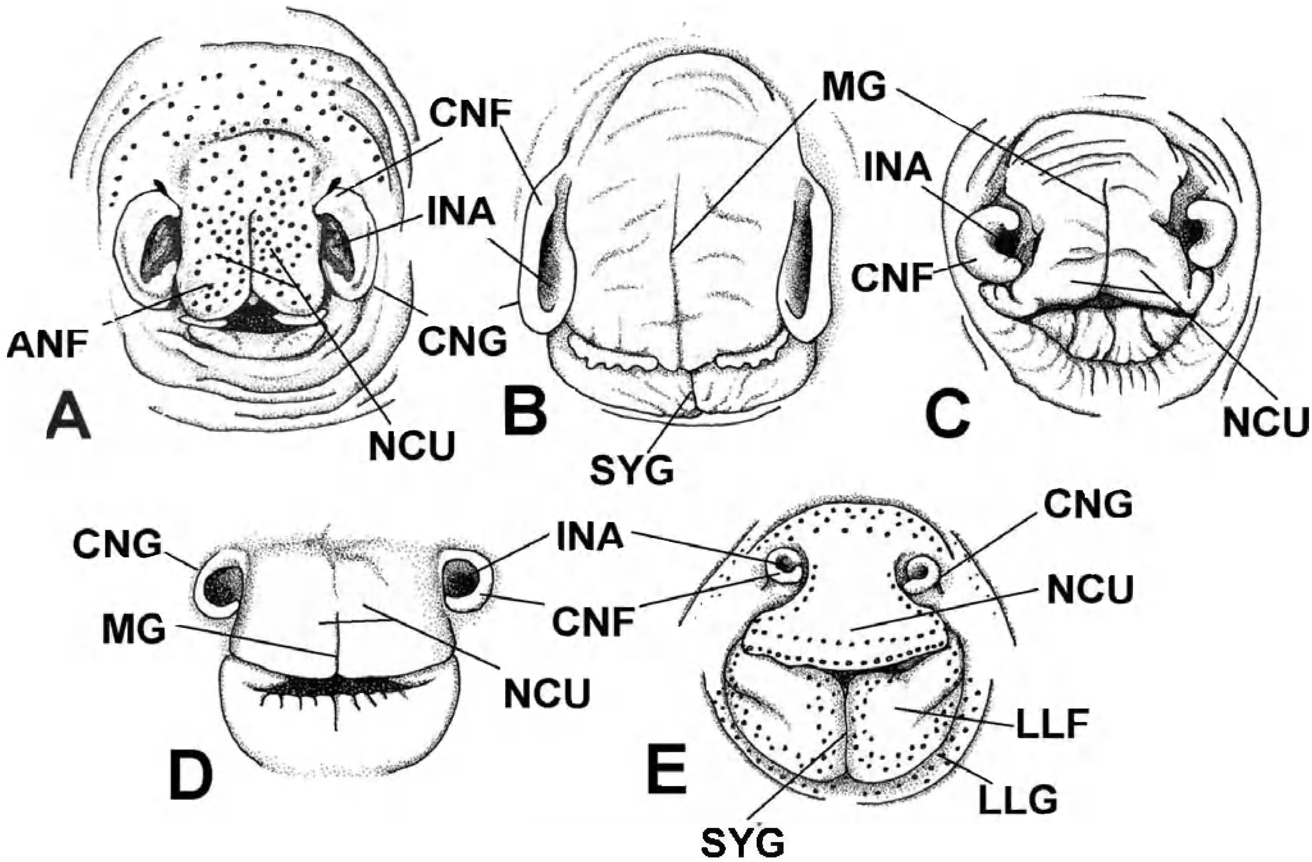

Figure 6. Mouth and nostril drawings of A. *Electrolux addisoni,* holotype. B. *Heteronarce garmani*, RV *Benguela* G13531 88N 30-08, 125 mm TL female. C. *Narke capensis*, SAM uncataloged, 265 mm TL adult male. D. *Temera hardwickii*, SU-35728, 104 mm TL adolescent male. E. *Typhlonarke aysoni* from SIO 61-149-6A and Garrick (1951). Drawings by Elaine Heemstra based on specimens and sketches or photographs by LJVC . Abbreviations: ANF, anterior nasal flap; CNF, circumnarial fold; CNG, circumnarial groove; INA, incurrent aperture; LLF, lower labial fold; LLG, lower labial groove; MG, medial groove on nasal curtain; NCU, nasal curtain; SYG, symphysial groove.

groove, but ventral dental band bisecting it medially; lower labial folds and grooves short, ending far lateral to midline of mouth (Figure 7); labial cartilages very small, their bases well lateral to symphyses. Total tooth row counts 32-34 or 15-16 / 17-18. Superscapulae C-shaped (Fig. 13A), situated anterior to coracoid bar. Total pectoral radials 47-53; metapterygial axis not greatly reduced in length, with equal numbers of radials to propterygium (17-19 each); no neopterygial radials on scapulocoracoid. Pelvic fins not divided into discrete anterior and posterior lobes. Puboischiadic bar with stout angular iliac processes (Fig. 14A). Total basipterygial pelvic radials 17-19, Claspers short and extremely flat in adult males (Figure 15), not extending past pelvic free rear tips. Two dorsal fins, subequal in area, second dorsal slightly smaller than first, first dorsal origin over pelvic free rear tips and well behind pelvic insertions. Lateral tail folds broad. Total synarcual segments 14-16, monospondylous precaudal centra 30, diplospondylous precaudal centra, 61- 62, precaudal centra 96-97, precaudal total segments 105-108, total free centra 118-120, total centra 123-125, total segments 132-136. Neurocranium with a narrow, large, erect, flattened medial rostral cartilage, and two lateral rostral cartilages below it forming a large ventrally-directed yoke-like structure (Fig. 9); antorbital cartilages with narrow anterior branched ends (Figs 11 and 12); ethmoid region of chondrocranium laterally compressed, strongly bent and expanded ventrally; no frontoparietal fenestra; otic capsules small and not expanded laterally. Jaws antero-ventro-medially expanded, palatine processes of palatoquadrates nearly straight. Second hyobranchial cartilages large, Intestinal valve count 17 (paratype). Mature males 50-52 cm. TL. Elaborate colour pattern of pale spots on dark brown background present on most of body; dorsal surface of disc of living rays with concentric black lines and pale spots.

Derivation of generic name: The name alludes to the well-developed electrogenic properties of this ray (collectors and photographers have experienced the shocking personality of this bold, active and brightly patterned electric ray first-hand), the discovery of which sheds light (Latin, *lux*) on the rich and poorly-known fish diversity of the Western Indian Ocean. And the vigorous sucking action displayed on the videotape of the feeding ray that was taken by Stephania and Peter Lamberti may rival a well-known electrical device used to suck the detritus from carpets, furniture, and other dust-gathering surfaces in modern homes. The gender of the name *Electrolux* is feminine.

Comparison with other genera: *Electrolux* differs from all other narkids including *Heteronarce* in having large spiracular papillae (Fig. 5); very broad, elongated and flattened circumnarial flaps (Figure 6; flaps narrower and usually shorter in other narkids); prominent anterior nasoral turret; narrow thin lower lips without a mental groove (lower lips large and with a mental groove in other genera); small labial cartilages and labial folds ending well lateral to midline of mouth (Fig. 7) labial folds enlarged and meeting at midline of mouth in other genera); broad lateral tail folds (tail folds narrow in other narkids and obsolete in *Typhlonarke*); pectoral radials more numerous (47-53 versus 40-43 radials in other narkids); metapterygia not reduced and radials equal to propterygial radials (metapterygia shorter and their radials fewer than propterygial radials in other genera); claspers not extending past pelvic fin free rear tips (extending past pelvic fin tips in most narkids except *Typhlonarke aysoni* and some *Narke capensis*); higher vertebral counts for most vertebral count groups (Table 6); chondrocranium with enlarged medial rostral cartilage and enlarged yoke-shaped lateral rostral cartilages (Fig. 9); rostral cartilages small and slender in other genera (as in Fig. 10); compressed, ventrally bent and expanded ethmoid region (laterally expanded in other taxa); antorbital cartilages with very narrow branched anterior section (broadly branched in most narkids); palatine processes of palatoquadrates straight, not curved medially; higher intestinal valve counts (17 in *Electrolux* vs. 8-10 in other genera); greater size (see discussion below); and unique coloration.

Electrolux and *Heteronarce* are the only narkid genera with two dorsal fins. Two dorsals are primitive for torpedinoids and for batoids, but *Narke* and *Typhlonarke* have one dorsal fin in the position of the first dorsal fin of *Electrolux* and *Heteronarce* and presumably have lost their second dorsal fins, while *Temera* has no dorsal fins. *Electrolux* and *Heteronarce* also agree in their nearly parallel-edged anterior nasal flaps (nasal flaps more divergent in other narkids, particularly *Typhlonarke* and *Narke*), long and thinner circumnarial flaps (short and thick in other narkids), larger rounded-angular basibranchial copula (copula reduced and tack-shaped in *Narke* and *Temera*), and the lack of a frontoparietal fenestra (*Narke, Temera,* and *Typhlonarke* with prominent fenestra). nostrils with circular rather than elongate-oval incurrent apertures; a V - shaped posterior margin on its nasal curtain (nearly straight in *Heteronarce*); short, stout iliac processes on the pelvic girdle (Fig. 14A, iliac processes slender, long, curved and attenuated at least in *H. bentuvai, H. garmani* and *H. mollis*); and more tooth rows (Table 4; total 32-34 vs 20-24 in *Heteronarce*).

Electrolux additionally differs from *Typhlonarke* in having well-developed eyes (rudimentary in the latter genus and absent externally), a medial groove on its nasal curtain (absent in *Typhlonarke*), a trilobate V-shaped posterior edge on its nasal curtain (transverse and undivided in *Typhlonarke*), more tooth rows and smaller teeth (32-34, vs. 15-24 total in *Typhlonarke*), a stouter precaudal tail, undivided pelvic fins without leg-like anterior lobes, and longer more slender jaws (jaws short and very stout in *Typhlonarke*). *Electrolux* differs from *Narke* in having shorter iliac processes on its pelvic girdle.

Species: A single known species, *Electrolux addisoni* Compagno & Heemstra, described below.

***Electrolux addisoni* sp. nov.**
Ornate sleeper-ray
Figures 1-4, 5A, 6A, 7A, 8, 9A, 11A, 12A, 13A, 14A, 15, 16A, 17A, 18.

Heteronarce? sp. nov. Compagno, 1999b: 116.
Undescribed genus and species. Compagno, 2005: 529.

Holotype: SAIAB 78777, adult male, 515 mm TL, 305 mm disc width, Indian Ocean on reef off Manaba Beach near Margate, southern KwaZulu-Natal, 30°51.4′ S, 30°23.1′ E; depth 6-12 m; collected by Mark Addison, September 2003.

Paratype: SAM 36908, adult male, 502 mm TL, 291 mm DW, locality the same as in holotype but collected by Brent Addison, October 2003.

DESCRIPTION. Measurements in millimetres and proportions as percentages of total length (TL) are presented in Table 2 for the types of *Electrolux addisoni.* Disc subcircular, thick and fleshy; greatest width slightly more (1.1-1.2 times) than its length. Edge of disc a continuous curve, anterior edge nearly straight but broadly curving to sides of disc, with snout, pectoral anterior margins, pectoral apices, and the posterior and inner pectoral margins not distinct but continuously curving rearwards, mesially, and recurving anteriorly to form broad but discrete free rear tips before merging with the sides of tail base. Snout short, preorbital length 6.4-8.2 % TL, preoral length 6.2-8.4 % TL. Prespiracular head length 2.4-2.7 times interspiracular width, preoral length about 1.8-2.6 times as great as outer internarial width. A pair of small endolymphatic foramina on nuchal region of head about eye-length behind spiracles and about on anterior-posterior line tangent to their inner margins. Electric C- or narrowly kidney-shaped and about three times as long as wide; organs not obvious through skin of dorsal surface but prominent on white medial area of ventral surface; electric organ cells rounded-oval to hexagonal, count of cells for right organ approximately 289 on paratype. Vent anterior to pelvic inner margins and free from them, vent long and with broad lateral folds and conspicuous abdominal pores on the folds of the posterior third of vent. Tail stout, depressed, horizontally oval in cross section, with cutaneous lateral folds (about 7 mm wide) along lower part of tail from above rear end of pelvic fins and below midbase of first dorsal fin to base of caudal fin; tail moderately flattened below folds but broadly convex above; tail from vent to caudal tip about 1.3 times as long as snout-vent length; caudal peduncle nearly flat below folds, narrowly convex above them. Interdorsal space 75-106 % of first dorsal fin base; dorsal-caudal space 70 to 71 % of second dorsal fin base.

Eyes well-developed, protruding above surface of disc, posterior to a transverse vertical plane at mouth; upper eyelids thickened, lower eyelids enlarged and apparently mobile, capable of covering palpebral apertures. Eyeball included in anterior edge of spiracle; dorsal rim of spiracle with 8 slender papillae (Fig. 5), their configurations symmetrical between right and left spiracles and arranged as follows: measurements of left spiracle papillae of holotype, followed by lengths of paratype's papillae in parentheses, first (anterior-most) papilla short, soft, recumbent on top of fleshy orbit, 2.5 mm (2.8 mm); second and third papillae (proceeding clockwise around spiracle rim) cuneate, flattened and stiff, lengths 4.4 (4.5) and 4.7 (3.8) mm respectively; fourth papilla stiff, flattened, resembling a forefinger and short thumb, lengths 6.1 (6.1) and 1.6 (2.0) mm respectively; fifth papilla short, simple, sausage-shaped, 2.6 (1.7) mm; sixth, seventh and eighth papillae long, slender, stiff, and finger-like, lengths 4.8 (4.1), 4.2 (3.5) and 8.0 (4.8) mm respectively. The spiracle papillae are bilaterally symmetrical for the left and right spiracles, with the three long, slender papillae on the lateral margins, short fleshy papilla on top of eyes, finger and thumb papilla on posterior rims and two cuneate papillae on medial edges of spiracles.

Nostrils undivided, incurrent apertures with trough- or trumpet-shaped circum-narial folds (Fig. 6A), resembling a funnel cut in half vertically and separate from mouth; circumnarial folds somewhat expanded ventrally. Nasal curtain fleshy, elongated, with numerous small pores and a median longitudinal groove or sulcus on its ventral surface; distal (posterior) edge of curtain emarginate and trilobate, with a short, bifid fleshy barbel-like anterior nasal flap at each lateral corner with broadly rounded posterior ends, and a short barbel-like lobe on midline of inner surface ; with mouth closed, the nasal curtain extends over front of lower jaw. Each anterior nasal flap has a strong mesonarial flap above (dorsal to) its posterior tip. Excurrent apertures moderately large, hidden ventrally by nasal curtain and circumnarial folds but open broadly above them to posterior surface of snout in front of mouth, internarial space between inner ends of excurrent apertures hidden, internarial space about 3.7-4.0 in mouth width when jaws are retracted and mouth closed.

Gill openings small, width of fifth 0.4-0.8 times width of first gill opening and 1.9-2.8 in spiracular length; distance between inner ends of first pair of gill openings about 2.9-3.0 times interspiracular width and about 1.5-1.9 times distance between fifth pair.

Mouth protrusile but scarcely distensible; mouth and jaw tips apparently forming a short tube when protracted and opened; lips thin, transversely-pleated, projecting (Fig. 7A) and surrounded by a shallow groove; lips pleated between lateral edges of dental bands and small labial folds; no prominent groove between labial folds, which include labial cartilages at

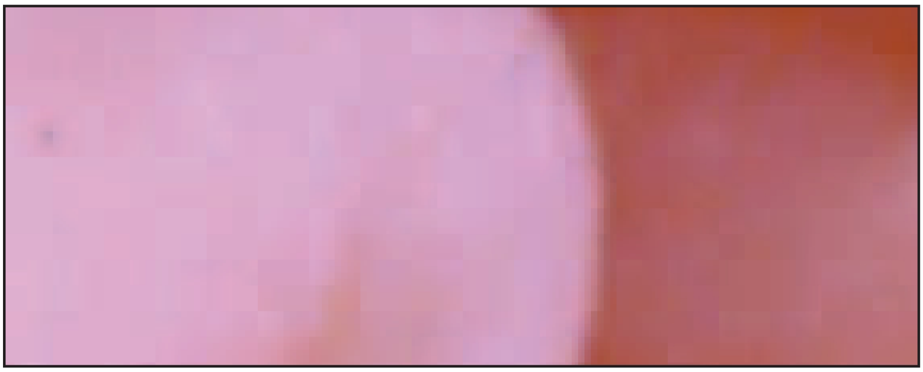

Figure 7. Mouth with nasal curtain lifted of A. *Electrolux addisoni*, paratype, mouth opened. B. *Heteronarce garmani*, SAM 34813, 256 mm TL adult male, mouth closed, upper dental band partly obscured by debrisScale bars = 5 mm Abbreviations: EXA, excurrent aperture; LDB, lower dental band; LLF, lower labial fold; LLG, lower labial groove; LLP, lower labial pleats; NOG, nasoral groove; SYG, symphysial groove; UDB, upper dental band; ULG, upper labial groove; ULF, upper labial fold; ULP, upper labial pleats.

corners of mouth; mouth width 3.7-4.0 times in interspiracular distance and 1.5-1.6 times spiracle length.

Tooth bands occupy about half of mouth width, firmly connected to jaw cartilages by connective tissue, band widths greater than inner internarial distance. Teeth in quincunx arrangement, forming a tessellated pavement. Tooth formula 7-8~1~7 / 8~1~8-9, tooth row counts 15-16 / 17-18 rows or 32-34 total rows; ca. 6 - 8 series functional, as indicated by wear on crowns. Teeth very small, similar in both jaws and similar from symphysis to mouth corners, teeth in midline of mouth about 1 mm wide across crown foot and lateral teeth slightly smaller; labial surface of crown obliquely flattened, extending lingually as a single small stout cusp (Fig. 8) worn-off on most functional teeth); prominent basal ledge and groove on crown; roots small and lingually projecting, divided ventrally by a transverse groove; no teeth exposed on ventral surfaces of jaws when mouth is closed, but dental bands visible along anterior edge of jaws.

Pectoral girdle crescentic in dorso-ventral view (Fig 13A). Anterior margin of coracoid cartilage concave medially but convex laterally. Propterygium a narrow segmented axis, articulates with procondyle of lateral face of scapulocoracoid, curves anteriorly, and is divided into 6 axial segments, the distal-most segment poorly calcified; mesopterygium elongated and unsegmented, articulating with the mesocondyle on lateral scapulocoracoid face and runs parallel to proximal segment of propterygium; metapterygium forming an axis of 4 segments, the proximal segment articulates with metacondyle on posterior corner of lateral face of scapulocoracoid and the distal segments extend rearwards into the pectoral base and free rear tip. 17 or 20 pectoral radials on propterygium, 12 or 13 on mesopterygium and 17 or 20 on metapterygium, total radials 46 or 53; no neopterygial radials articulating on lateral face of scapulo-coracoid; distal 2-4 segments of pectoral radials are bifid.

Pelvic fins separate, deltoid-rounded anterior corner rounded, posterior (lateral) edge slightly convex, fairly thick and fleshy, pelvic fin origins well anterior to pectoral fin insertions; anterior edge stiff and thick, supported by the densely calcified anterior radial, apices broadly rounded, posterior (lateral) edge nearly straight or slightly convex when fins are fully spread; free rear tips well-developed, narrow, rounded-subangular, inner margin of pelvics distinct, not attached to sides of tail at free rear tips; no frenum between pelvic inner margins; pelvic fin length ~ 40-43 % disc width. In live animals the pelvics are often broadly spread and appear rounded rather than angular. Pelvic girdle (puboischiadic bar) broad (Fig. 14A), its median antero-posterior width equals one sixth of girdle's transverse length; prepelvic process at each lateral end of girdle thin and weakly calcified extending anteriorly for the lengths of 7 centra. Iliac

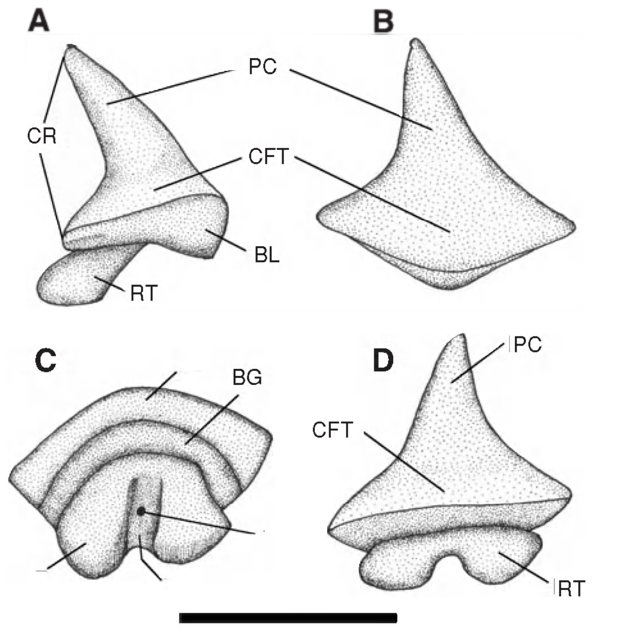

Figure 8. Lower replacement tooth (cusp unworn) from symphysis, removed from lingual end of dental band in the paratype of *Electrolux addisoni*, A. Lateral view. B. Labial view. C. Basal view. D. Lingual view. Abbreviations: BG, basal groove; BL, basal ledge; CF, central foramen; CFT, crown foot; CR, crown; PC, primary cusp; RT, root; TG, transverse groove.

processes well-developed on pelvic girdle, expanded dorsally from lateral node, these short, stout, nearly straight, and angular; large basal condyle present on postero-lateral surface of each lateral node for articulation of long pelvic basipterygium, a short but prominent, blunt ischial process present on lateral node medio-posteriorly to basal condyle and mesial to basipterygium. 17 or 19 radials articulating with pelvic basipterygium, plus anterior enlarged radial (apparently a fused double radial) articulating with lateral node of pelvic girdle; the enlarged anterior radial projects postero-laterally and supports the leading edge of the pelvic fin.

Claspers broad, flat and short (Fig. 15), nearly reaching free rear tips of pelvics ; clasper depth at base about 2.7 in base width and with a depressed elliptical cross-section; in dorso-ventral view claspers with parallel sides and a broad, bluntly rounded tip; in lateral view, dorsal and ventral surfaces nearly parallel along their lengths but with a short tapering posterior tip. Dorsal clasper groove open, with apopyle dorsolateral on base of clasper and hypopyle dorsal on glans; clasper glans with a long, low flap or cover rhipidion on the mesial edge of groove, a long slit-like pseudosiphon (*slot* of Leigh-Sharpe, 1922) mesial to cover rhipidion and near rear tip of clasper, and a long pseudopera (*slit* of Leigh-Sharpe, 1922) on postero-lateral tip of clasper.

Dorsal and caudal fins compressed, flexible and close together; first dorsal fin origin above axil between inner edge of pelvic fin and clasper, or about opposite pelvic insertions; apex of first dorsal fin reaches past level of second dorsal fin origin; apex of second dorsal fin reaches well past caudal fin origin; dorsal fins similar in shape, but first dorsal fin slightly larger than second, second dorsal fin height 81- 86 % of first dorsal height, and second dorsal base 86-97 % of first dorsal base; anterior margin of dorsal fins strongly sloping and broadly convex, apices broadly rounded; posterior and inner margins weakly differentiated and convex; first dorsal base about 41-47 % of anterior margin; second dorsal fin base about 41% of anterior margin. First dorsal fin with 6 radials, second dorsal fin with 7; dorsal-fin radials divided into 3 or 4 segments.

Caudal fin fairly high, short, and oval, its lower rear edge forming a continuous broad convex curve to tip of fin, upper margin slightly less convex, tip broadly rounded; vertebral column axis slightly raised; hypaxial lobe narrower than epaxial lobe; fin height 70-78 % of dorsal caudal margin, which is 1.5-1.6 times in distance from first dorsal origin to upper caudal origin. Caudal fin with 25 dorsal radials (radials 21 & 22 fused at the base) and 31 ventral radials, plus a V-shaped terminal radial.

Antorbital cartilages short, directed anteriorly, with expanded posterior condyle for articulating with sockets on nasal capsules, with narrow shaft and moderately expanded, weakly branched anterior end, separated from anterior extensions of proterygia by ~ 4 cm; rear surface of chondrocranium with two prominent occipital condyles fitting two lateral sockets on anterior surface of synarcual.

Hyomandibula large (Figs 11A & 12A), articulating directly to lateral edge of lower jaw (Meckel's cartilage). On radiographs (Fig. 12A; also in *Heteronarce*, Fig. 12B), the synarcual seemed to be divided into anterior and posterior segments above the fourth gill arch, but detailed investigation of radiographs and dissection of the paratype revealed that the 'joint' between the two sections was the superimposed anterior edge of the basibranchial copula; a lateral strut on each side that seems to extend from the synarcual to the scapulocoracoid is the fifth ceratobranchial, which extends from the basibranchial to the scapulocoracoid. Vertebral counts are listed in Table 6. Spiral intestinal valve with 17 turns in the paratype (Table 7).

Live colour: The spectacular and elaborate dorsal colour pattern of live *Electrolux addisoni* is shown in Figures 1 and 2. The dorsal surface and most of the ventral surface of the disc and pelvic fins, the claspers, the tail and median fins are dark brown covered with dense small pale spots which are white in the preserved types (Figs 3 and 4) but pale yellow in life. The pale spots are larger on middle of dorsal disc, where there are several scattered, short, pale streaks; also light streaks irregularly present in dark ventrolateral surfaces of disc and anteroventral surfaces of pelvic fins near apices. In life the ray is covered with mucus, and there are several curved,

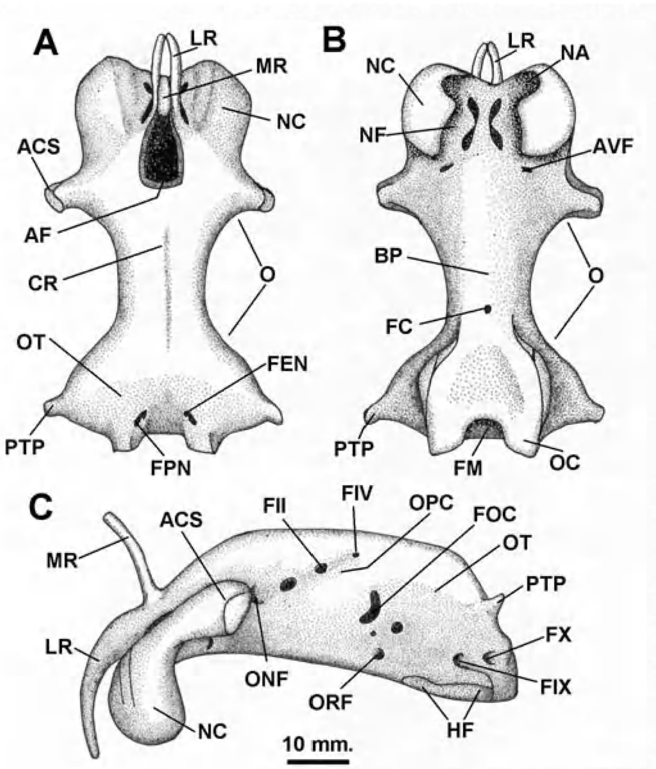

Figure 9. Chondrocranium of *Electrolux addisoni*, paratype, in **A.** dorsal, **B.** ventral, **C.** lateral views. Abbreviations: ACS, articular socket for antorbital cartilage; AF, anterior fontanelle; AVF, foramen for orbitonasal vein draining nasal sinus; BP, basal plate; CR, cranial roof; FII, fenestra for optic nerve; FIV, foramen for trochlear nerve; FIX, foramen for glossopharyngial nerve; FX, foramen for vagus nerve; FC, carotid foramina; FEN, foramen for endolymphatic duct; FM, foramen magnum; FOC, fenestra for superficial ophthalmic nerve; FPF, frontoparietal fenestra; FPN, fenestra for perilymphatic space; HF, hyomandibular facet (double); LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; NC, nasal capsule; NF, nasal fenestra; O, orbit; OC, occipital condyle; ONF, orbitonarial foramina; OPC, socket for optic pedicel; ORF, orbital fissure; OT, otic capsule; PTP, pterotic process.

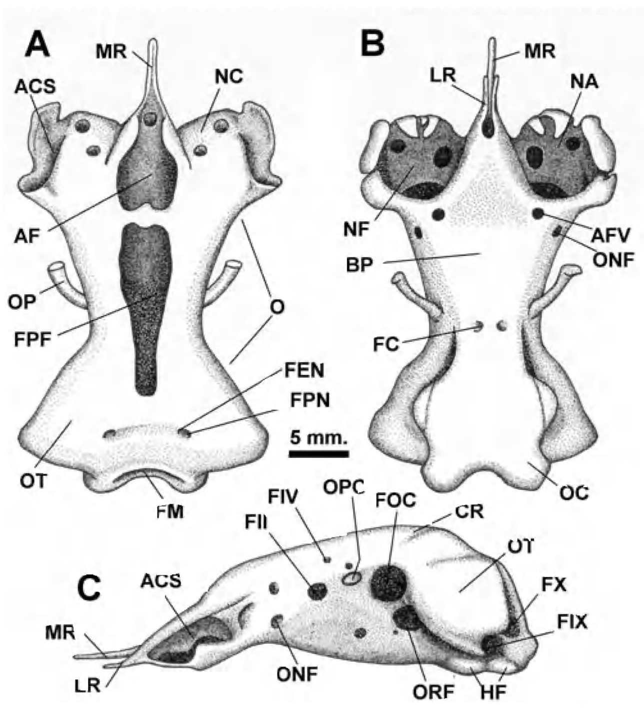

Figure 10. Chondrocranium of Narke capensis, Africana A12093 095 040 1035, 231 mm adult female, in A. dorsal, B. ventral, C. lateral views. Abbreviations as in Fig. 9.

(some concentric) black stripes on the dorsal disc which disappear when the mucus is rinsed off; the light spots and streaks are often obscured by sediment when the ray is at rest. Ventral surface of disc and pelvic bases abruptly white in center, forming a pear-shaped symmetrical blotch from the nasoral turret to the vent and pelvic insertions and including the gill slits and most of the electric organs (Figs 3B, 4B).

Etymology. The species is named for Mark Addison, Managing Director of Blue Wilderness dive charters of Widenham, KwaZulu-Natal. Mr Addison collected the holotype and instigated the capture of the paratype. He has an extensive knowledge of the marine fish fauna of South Africa and has provided much valued assistance in our fish survey research.

Size: The holotype (515 mm TL adult male) weighed 1.8 kg., and the paratype (502 mm TL adult male) weighed 1.9 kg. *Electrolux addisoni* is apparently one of the largest members of the Narkidae, although females have yet to be examined, and the size range for maturation is unknown for males. Compagno & Last (1999a) noted that the Narkidae includes species that are adult at 9-46 cm TL and possibly reached a greater length, but *Electrolux* extends this to 52 cm, or possibly greater. Whitley (1940) stated that *Typhlonarke aysoni* reaches a far greater size than what is known for *E. addisoni*, with a maximum DW of about. 91 cm. and estimated TL over 122 cm. However, adult male specimens of *T. aysoni* examined by Whitley (1940), Garrick (1951) and by ourselves were only 21-38 cm. TL, and Garrick (1951: 5) repeated Whitley's comments but indicated that "most specimens taken are under 400 mm in total length". We wonder if Whitley's maximum DW figure (not his direct observation but based on the comment that "Graham records a maximum width of 36 inches") might be based on mistaken identity of the much larger *Torpedo fairchildi* for *T. aysoni*, although it is extremely difficult to mistake the two. The family Narkidae includes the smallest living batoids (Compagno *et al.*, 1999) and perhaps the smallest or at least the shortest, of the living chondrichthyans (Fig. 16). Males of *Temera hardwickii* examined by us are fully mature at 82-109

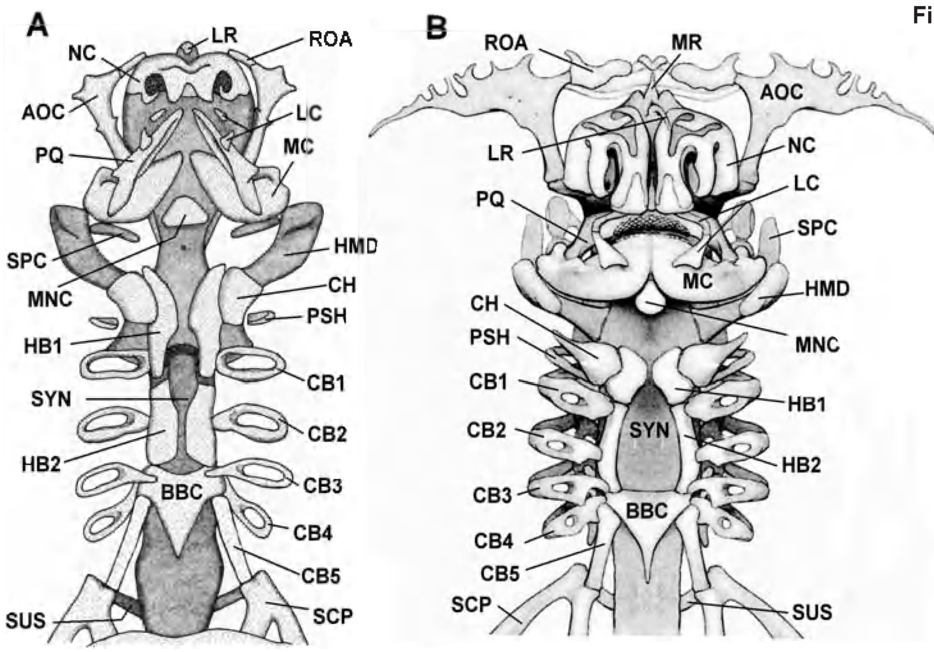

Figure 11. Narkid hyobranchial skeleton in ventral view. **A**. *Electrolux addisoni*, composite of SAIAB 78777 and SAM 36908, derived from radiograph of holotype and dissection of paratype. **B**, *Narke japonica*, drawing modified and simplified from Garman (1913: pl. 67, fig. 3) in ventral view. Abbreviations: AOC, antorbital cartilage; BBC, basibranchial copula; CB1-5, ceratobranchials 1-5; CH, ceratohyal; HB1-2, hyobranchials 1 and 2; HMD, hyomandibula; LC, labial cartilages: LR, lateral rostral cartilages; MC, Meckel's cartilage (lower jaw); MNC, mental or symphysial cartilage; MR, medial rostral cartilage; NC, nasal capsules; PQ, palatoquadrate (upper jaw); PSH, pseudohyoids; ROA, rostral appendix; SCP, scapular process of scapulocoracoid (shoulder girdle); SPC, spiracular cartilage; SUS, suprascapulae of scapulocoracoid; SYN, synarcual.

mm TL and females at 105-148 mm TL; the species has been reported as reaching 458 mm TL. Adult males of a dwarf species of *Narke* from the Taiwan Straits are 99-109 mm TL and possibly reach 149 mm (see study material). In comparison to these tiny narkids, *Electrolux addisoni* is a giant, with the holotype 6.3 times longer and 139 times heavier than the smallest adult male *T. hardwickii* examined by us (82 mm TL and 13 grams).

Available data for the smallest living sharks suggest that they may be almost twice as long as the smallest narkids. Compagno (1988: 24) discussed the minimum size of sharks and noted that although the diminutive dalatiid shark *Squaliolus laticaudus* is popularly considered the smallest living shark at a minimum adult length of 150 mm (Figure 16), it has several rivals of similar size. The proscylliid catshark *Eridacnis radcliffei* matures at 166-242 mm TL, with a 186 mm adult male weighing 14 gm, and a 242 mm pregnant female 37 gm. The etmopterid lantern shark *Etmopterus carteri* is adult at 186-212 mm, *E. perryi* is adult at 160-200 mm, *E. polli* is adult at 229-241 cm and probably smaller (a recently examined adult male is 195 mm long), and *E. virens* is adult at 181-257 mm. The dalatiid kitefin shark *Euprotomicrus bispinatus* is mature at 200-266 mm while the two *Squaliolus* spp. (*S. aliae* and *S. laticaudus*) are mature at 15 or 20-25 cm

BIOLOGICAL NOTES. *Electrolux addisoni* belongs to the sleeper ray family Narkidae, based on the genus *Narke* and Greek *narke*, numbness, torpor, that alludes to the sluggish nature of these sedentary rays and the numbing effects of their electric organs. *Electrolux addisoni* however, is far from torpid while feeding on the substrate (Fig. 2A), and vigorously thrusts its mouth into loose sand or gravel while walking actively on its spread pelvic fins. It may lie motionless on the substrate, but when approached can arch its back, curl its disc, and raise its tail to perform a possible threat-display directed at the photographer (Fig. 2B). The stomach contents of the paratype included the semi-digested and fragmentary remains of approximately eight polychaete worms (including a tube-worm) and at least one small shrimp-like crustacean. Stomach contents weighed 5.6 grams. *Electrolux* as an infauna or meiofauna feeder agrees with the South African narkids *Narke capensis*, which mostly eats polychaetes (Compagno *et al.* 1989), and *Heteronarce garmani* (one specimen examined, Benguela G13531 88N 30-08, 127 mm immature female), which had a stomach filled with mud-balls.

The conspicuous dorsal colour pattern of *Electrolux addisoni* combined with the ray's boldness and activeness near divers, and its possible threat display (Figure 2B) may be aposematic and indicates that the ray is well-armed with electric organs and should be avoided. On the shallow, well-lit reefs where *E. addisoni* has been found, its main potential predators may be large carcharhinoid sharks (requiem sharks, Carcharhinidae, and hammerheads, Sphyrnidae) and lamnoid sharks (ragged-tooth sharks and white sharks). Ebert (1990) found that two species of electric rays successfully defended themselves from much larger sixgill sharks (*Hexanchus*), which are apex predators with a broad prey spectrum. The small blind narcinid *Benthobatis yangi* from Taiwan was observed to repel a *Hexanchus nakamurai*. And two individuals of the larger torpedinid *Torpedo* cf. *nobiliana* from South Africa that were examined showed bite patterns of *Hexanchus griseus*, indicating that the sharks grabbed the rays but were repelled (probably with a shock) before they could inflict a strong and lethal bite. These

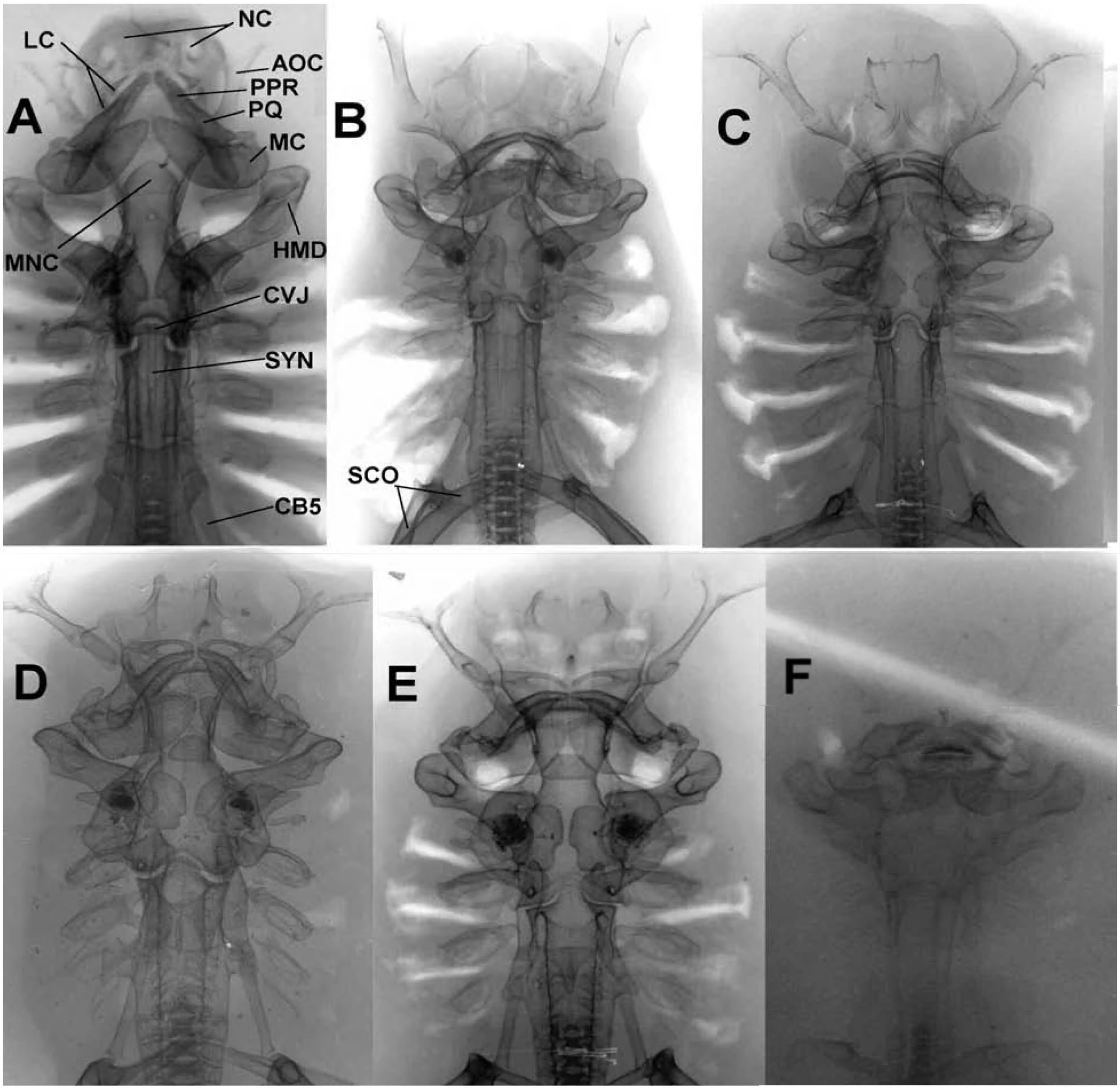

Figure 12. Narkid syncranium (neurocranium and splanchnocranium) and associated structures, monochrome inverted photographs from radiographs. A. *Electrolux addisoni*, holotype. B. *Heteronarce garmani*, **BMNH** 1921.3.1.3, 169 mm adult male holotype. C. *Heteronarce mollis*, **CAS** 58351, 218 mm TL female. D. *Narke dipterygia*, **SU**-41717, female ca. 135 mm TL. E. *Temera hardwickii*, **CAS** 58369, 108 mm TL female. F. *Typhlonarke aysoni*, **SIO** 61-149-6A, 92 mm TL immature female. Abbreviations: AOC, antorbital cartilage; CB5, 5th ceratobranchial (attaching basibranchial copula to scapulocoracoid; CVJ, occipito-cervical joint of chondrocranium and synarcual; HMD, hyomandibula; LC, labial cartilages; MC, Meckel's cartilage; MNC, mental (symphysial) cartilage; NC, nasal capsules; PPR, palatine process of palatoquadrate; PQ, palatoquadrate; SCO, scapulocoracoid (shoulder girdle); SYN, cervicothoracic synarcual.

incidents probably occurred in deep water where the sixgill sharks may have been using non-visual senses to locate their potential prey. Neither of these deep-water electric rays has a prominent colour pattern, and aposematic coloration and threat displays might be of little use to them in a visually limited environment. However, a quick defensive shock apparently can minimize damage by aborting a predator's attack. For the inshore *Electrolux addisoni*, aposematic coloration and a threat display might prevent a shark attack if the visual warnings are reinforced by a shock. There are other conspicuously marked inshore narcinids and torpedinids as well as the boldly marked narkid *Heteronarce bentuviai*, but their behaviour is for the most part poorly known.

Distribution and Habitat: As presently known, *Electrolux addisoni* is endemic to the east coast of South Africa in warm-temperate or subtropical waters along approximately 310 km of coastline with a very narrow continental shelf (10-36 km wide to the 200 m isobath) but the few sightings were all inside the 50 m isobath. It could be more wide-ranging elsewhere in warm waters of southern Africa and even off East Africa. Known localities (Fig. 17, map) are mostly from dive sites off south-central kwaZulu-Natal (depth and

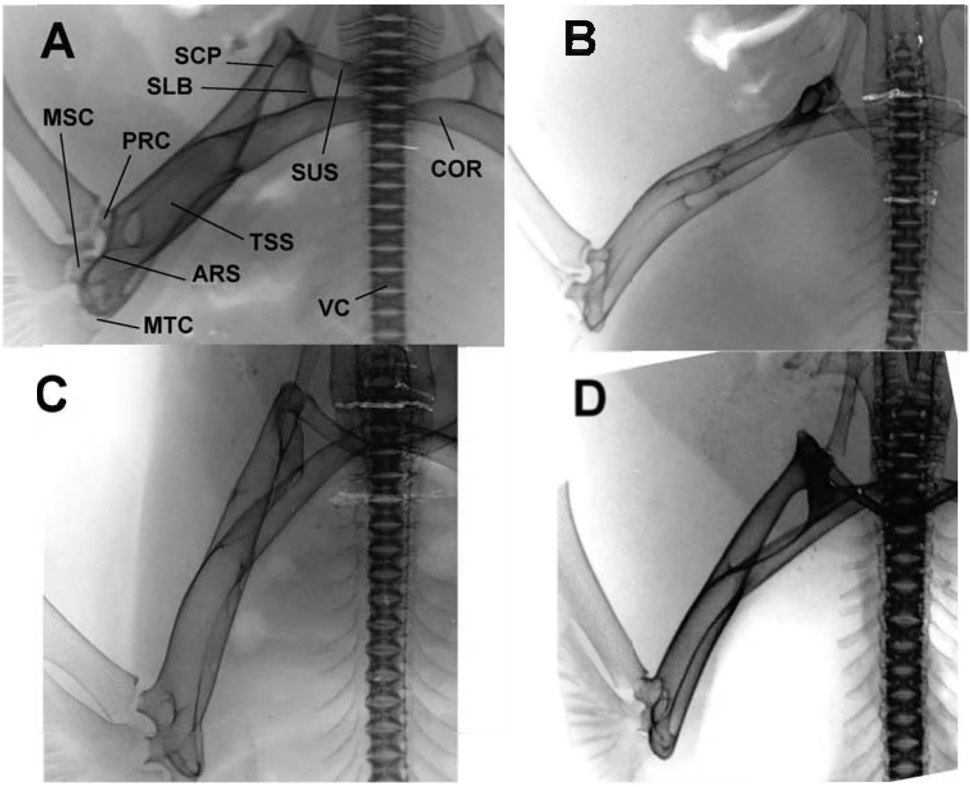

Figure 13. Narkid pectoral girdles (scapulocoracoids), radiographs showing left side in ventral view. **A**, *Electrolux addisoni*, holotype. **B**. *Heteronarce mollis*, CAS 58351, 218 mm TL female. **C**, *Narke japonica*, SU 61723, ca. 215 mm TL, female. **D**, *Temera hardwickii*, SU 35736, 105 mm TL, female. Abbreviations: ARS, articular surface; MSC, mesocondyle or mesopterygial condyle; MTC, metacondyle or metapterygial condyle; PRC, procondyle or propterygial condyle; SCP, scapular process; SLB, lateral bar; SUS, suprascapulae; TSS, tubular section; VC, vertebral column.

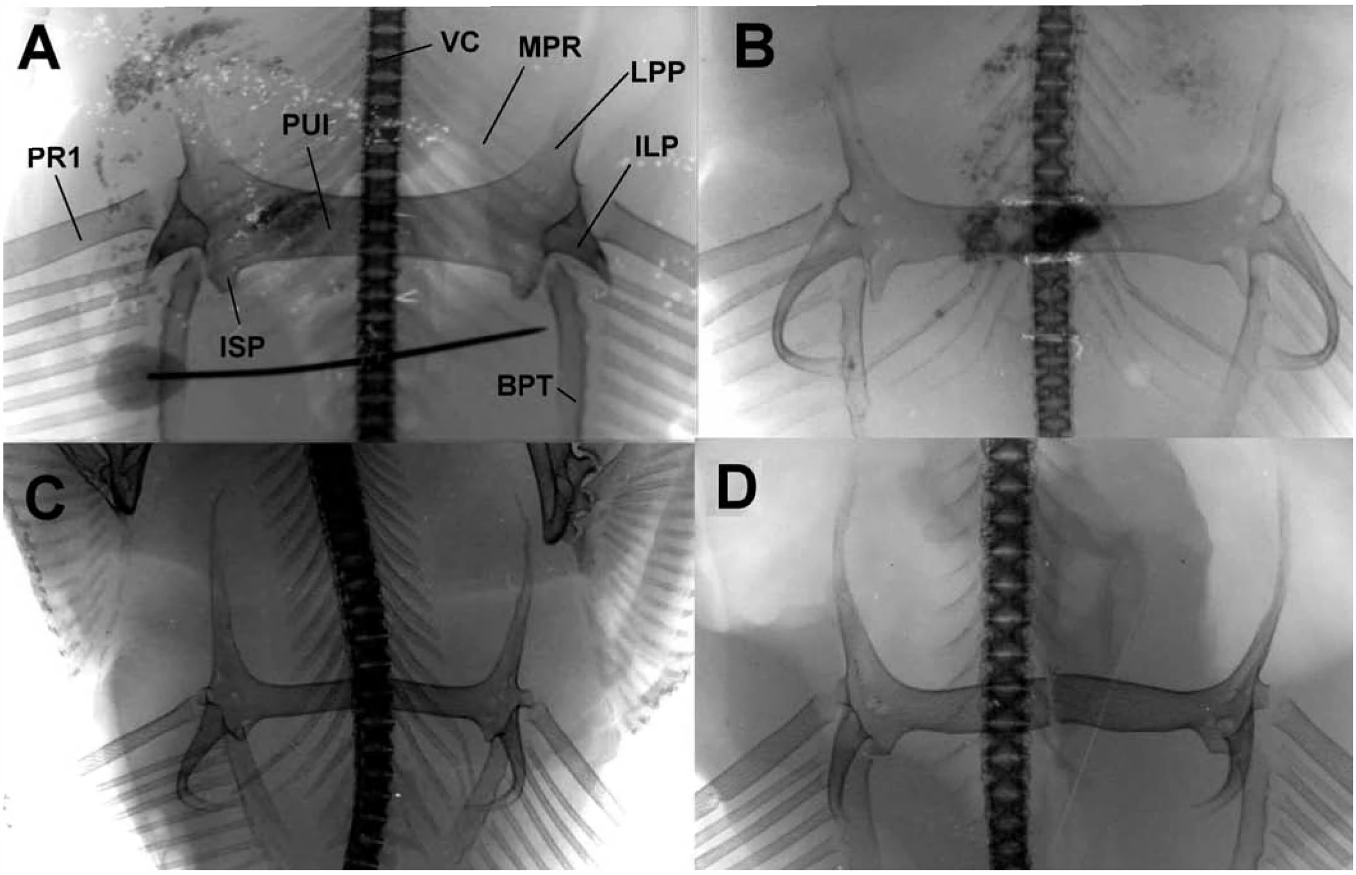

Figure 14. Narkid pelvic girdles (puboischiadic bars). **A**, *Electrolux addisoni,* holotype (note pin posterior to pelvic girdle). **B**, *Heteronarce mollis,* CAS 58351, 218 mm TL female. **C**, *Narke dipterygia*, SU-41717, female ~ 135 mm TL. **D**, *Temera hardwickii*, SU 35736, 119 mm TL, female. Abbreviations: BPT, basipterygium; ILP, iliac process; ISP, ischial process; LPP, lateral prepelvic process; MPR, ribs on monospondylous precaudal vertebrae; PR1, first pelvic fin radial; PUI, puboischiadic bar; VC, vertebral column.

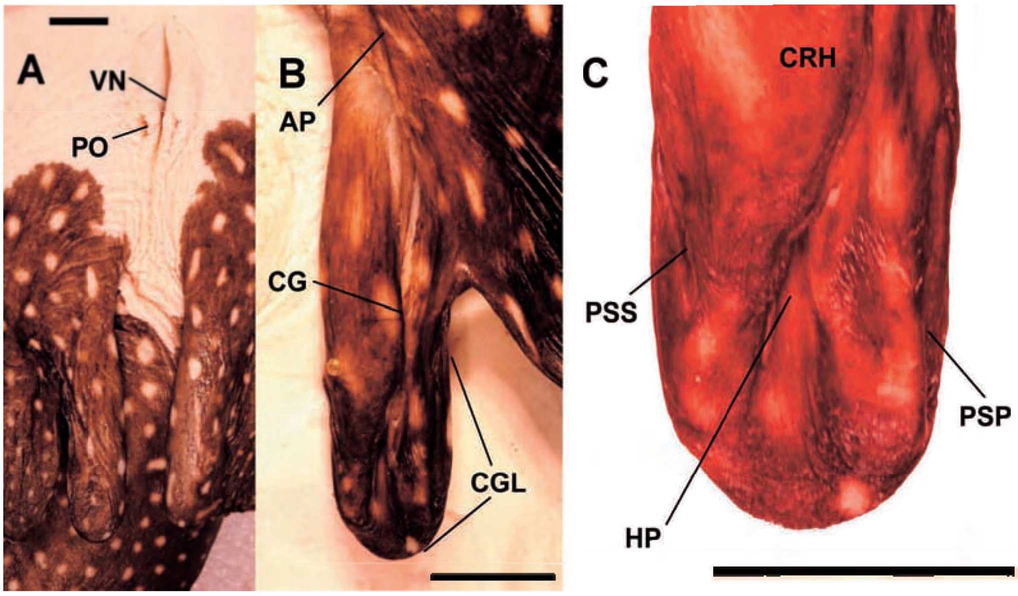

Figure 15. Claspers of *Electrolux addisoni*, paratype: **A**, claspers and vent, ventral view; **B**, right clasper in dorsal view; C, clasper glans in dorsal view. Abbre-viations: AP, apopyle; CG, clasper groove; CGL, clasper glans; CRH, cover rhipidion; HP, hypopyle; PO, abdominal pores; PSP, pseudopera; PSS, pseudo-siphon; VN, vent. Scale bars = 10 mm.

locality data in part from Koornhof, 1995). These include from southwest to northeast (Fig. 17, numbered 1-5): 1, Coffee Bay, Eastern Cape (ca. 31°58′S, 29°9′E; depth ~ 10 m); 2, Manaba Beach, the type locality near Margate (30°51.4′S, 30°23.1′E, depth 6-12 m); 3, Protea Banks, about 8 km off Shelly Beach near Margate (ca. 30°49.8′S, 30°28.8′E, depths ~ 28-35 m); 4, Aliwal Shoal, 4.8 km. off Park Rynie (ca. 30° 19.2′S, 30°48′E, depths ~ 14-30 m.); 5, Tee (or T-) Barge north of Durban and about 3 km off Virginia Beach (an artificial reef habitat at ca. 29°47′S, 31°05′E, depths ~ 20-27 m.).

Wallace's (1967) survey of electric rays from the east coast of southern Africa did not report this species. To our knowledge, this ray has not been seen south of Coffee Bay or along the south coast to False Bay. *Electrolux addisoni* was not taken by the South African Marine and Coastal Management's (MCM) research vessel *Algoa* during Cruise 014 off Mozambique in 1994 with 28 stations on soft bottom at 37-500 m depth. The *Algoa* collected torpedinoids in small numbers including *Heteronarce garmani, Narcine rierai*, and a second species of Narcine similar to the Malagasy *N. insolita* (Compagno *in* Smith & Heemstra, 1995, Compagno, 1999b, de Carvalho et al., 2002). The MCM research vessel *Africana* did not collect either *E. addisoni* or *H. garmani* in thousands of inshore and offshore bottom trawl stations at 17-200 m. during two decades of fisheries survey (ongoing) on the east coast of South Africa from Cape Agulhas to Port Alfred. However, *Narke capensis* were commonly caught by the *Africana* in this area at 27- 90 m depths (average depth 55 m) and apparently also occur in shallow inshore waters. M. Marks (*pers. comm.*) caught *N. capensis* by hand while diving at 4.5 m in False Bay in the Western Cape Province.

Electrolux addisoni occurs on the continental shelf on reefs with sandy or gravelly areas from close inshore to less than 50 m depth and including patches of appropriate habitat on inshore and offshore rocky banks and reefs. We wonder if this conspicuous ray is largely restricted to soft bottom patches on reefs off subtropical South Africa because of its having not been seen or collected elsewhere in southern Africa, including dive sites south of Coffee Bay and off Mozambique.

Conservation Status: The conservation status of this ray is uncertain but worrisome, because it is only known from a few records to date on a heavily utilized narrow strip of habitat with extensive and intensive recreational diving and sport and commercial fishing, along with runaway coastal housing development. Its known habitat and geographic distribution suggest that *Electrolux addisoni* could be at risk from human activities including harassment and disturbance by divers, as well as fisheries, pollution, and habitat degradation. There are no known fisheries that target this species or include it as bycatch, although it might become of some interest in the aquarium fish trade, and it would make a spectacular aquarium exhibit provided one could collect live specimens and keep them successfully in captivity. In terms of its known range and area 'footprint' (perhaps not more than a few square kilometers), rarity, and exposure to human activities, this species might rank high on the IUCN Red List criteria for threatened species, possibly Critically Endangered (IUCN, 2006), although there are problems with ranking it with IUCN criteria, because data on trends in abundance are non-existent. The senior author suggests that species of electric rays with limited ranges in the tropical-subtropical southwestern Indian Ocean, particularly species of insular *Torpedo* and quite possibly narkids and

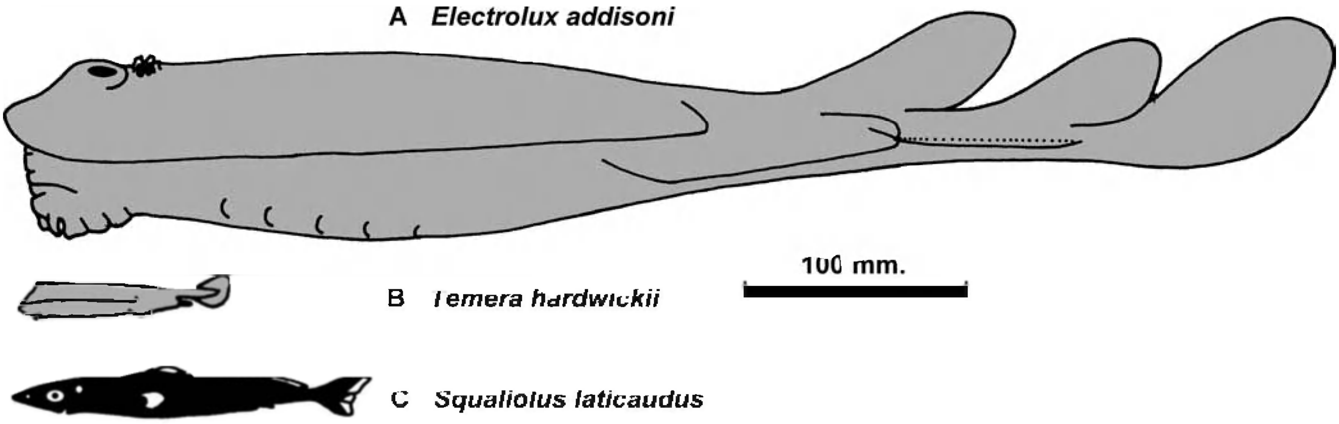

Figure 16. Size comparisons of the possibly largest narkid. A, *Electrolux addisoni* (holotype at 515 mm TL) with B, the smallest adult male examined of the diminutive narkid *Temera hardwickii* (ZRC no number, 82 mm TL) and C, the adult male holotype of the dalatiid shark *Squaliolus laticaudus* (USNM 70259, ca. 150 mm long, after Smith 1912).

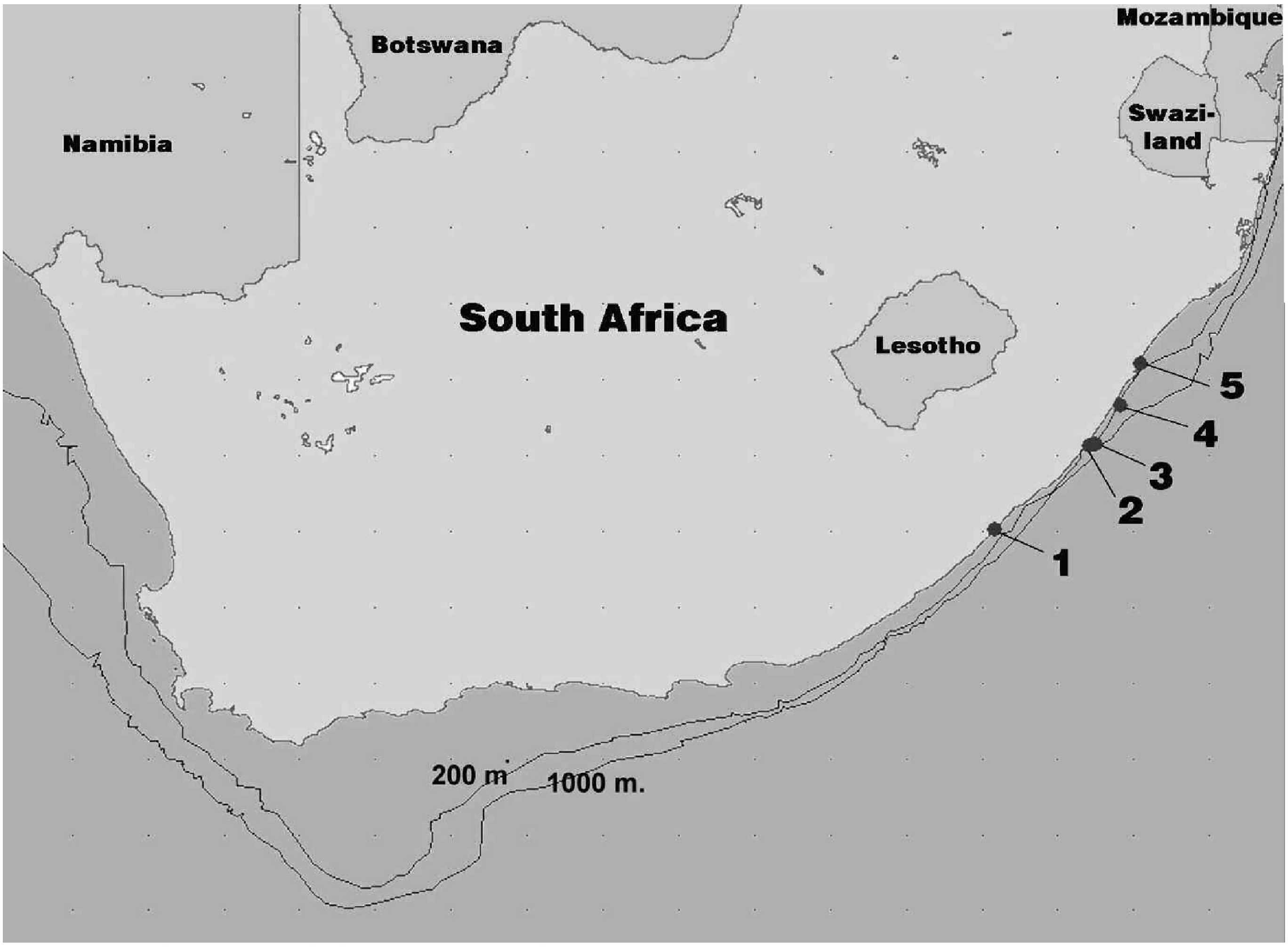

Figure 17. Digital map of South Africa showing localities for *Electrolux addisoni* (filled circles) and 200 m and 1000 m isobaths. Localities are numbered from southwest to northeast (1 from Eastern Cape, 2-5 from KwaZulu-Natal): 1, Coffee Bay; 2, Manaba Beach (type locality); 3, Protea Banks; 4, Aliwal Shoal; 5, Tee Barge, north of Durban.

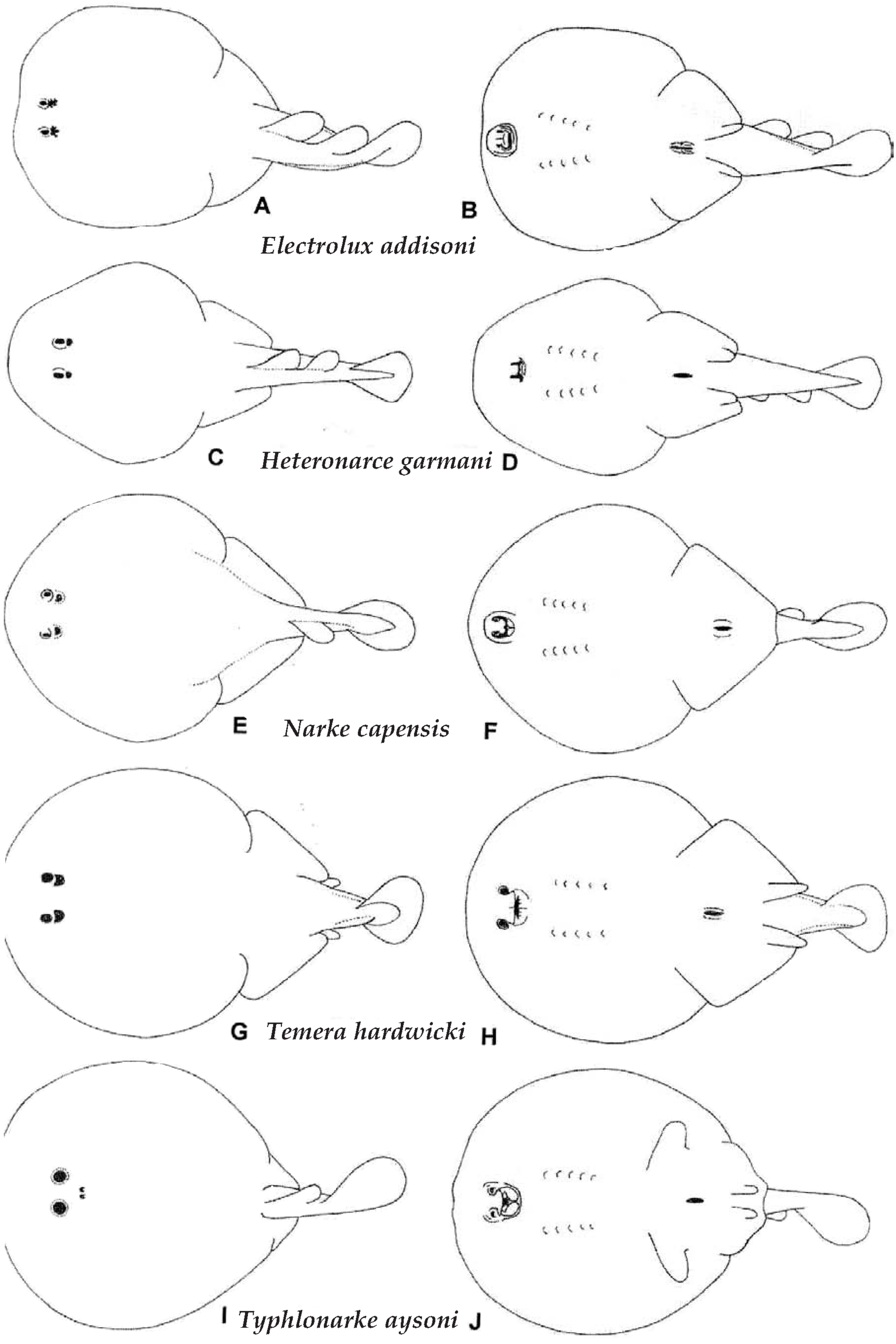

Figure 18. Dorsal (A, C, E, G, I) and ventral (B, D, F, H, J) views of A-B. *Electrolux addisoni*, holotype. C-D. *Heteronarce garmani*, 145 mm TL adolescent male, RV *Benguela* G13531 88N 30-08. E-F. Narke capensis, 231 mm TL adult female, RV *Africana* A12093 095 040 1035. G-H. *Temera hardwickii*, **SU** 35728, 104 mm TL adolescent male. I-J. *Typhlonarke aysoni*, 354 mm TL adult male. Drawings mostly by the senior author and Elaine Heemstra, I-J modified from a drawing in Garrick (1951).

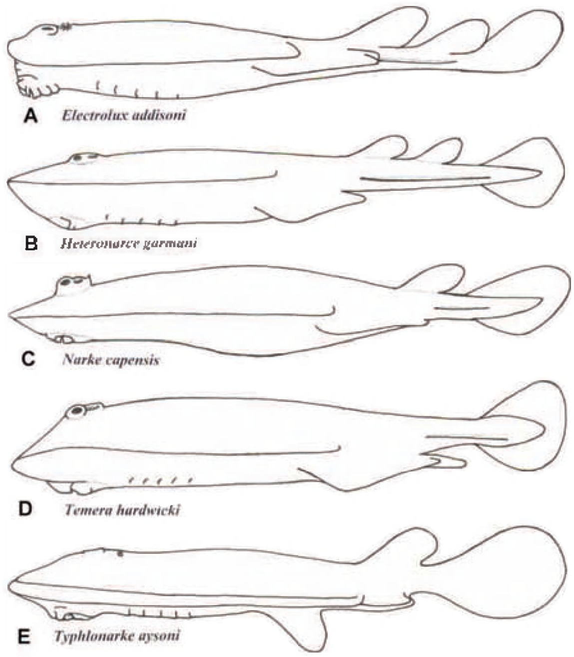

Figure 19. Lateral views of **A**, *Electrolux addisoni*. **B**, *Heteronarce garmani*. **C**, *Narke capensis*. **D**, *Temera hardwickii*. **E**. *Typhlonarke aysoni*. Same specimens and artists as in Fig. 18.

narcinids, are a major (if limited) concern for conservation, as are offshore scyliorhinid catsharks of the genus *Holohalaelurus* in the area (Human, 2006). *Electrolux addisoni* would be an appropriate subject for a dive survey project by fish-watchers, professional ichthyologists and conservationists on the numerous dive sites of the northeast coast of the Eastern Cape Province, kwaZulu-Natal and Mozambique to attempt to better understand its distribution and estimate its abundance for the purposes of assessing its conservation status.

TORPEDINOID CLASSIFICATION AND NOMENCLATURE

The classification and nomenclature of torpedinoids used here follows Gill (1862, 1895) and Compagno (1973, 1999a, 2005). For discussion in the text below, detailed data on nomenclature, authors, dates, synonymies and modern equivalents are given for torpedinoid family groups (Table 3), torpedinoid genera (Table 4), and species of Narkidae (Table 5). Citations of families, genera and species below are abbreviated by omitting the authors and dates except in formal synonymies. The electric rays (suborder Torpedinoidei or order Torpediniformes) have long been recognized as very distinct from other batoids, with a variety of classifications including a separate order Torpediniformes (eg., Compagno, 1973, 1977) or suborder Torpedinoidea or Torpedinoidei (Bigelow & Schroeder, 1953, Compagno, 2005). Discussion of the higher classification and interrelationships of torpedinoids to other batoids is not elaborated here but has been considered by many authors. Suffice it to note that in modern studies torpedinoids are always regarded as monophyletic and distinct from other batoid groups and have numerous shared derived characters not found in other batoids.

The classification of electric rays at the familial level had not varied much until the last half of the 20th Century and torpedinoids have usually been placed in a single family without subdivision. Bonaparte (1838) proposed a subfamily, Torpedinini, and Müller & Henle (1841) proposed a single family, Torpedines, for the four valid genera known at the time (*Astrape* = *Narke, Narcine, Torpedo* and *Temera*). Torpedinidae or its numerous synonyms (Table 3), were utilized by 19th Century and most 20th Century authors for all electric rays. Gill (1862) proposed the division of his family Torpedinoidae (or Narcaciontoidae) for all electric rays into three subfamilies and four subgroups (equivalent to tribes) as follows:

Subfamily Hypninae. Disc pyriform, formed by the union of the true disc with the ventrals, [pelvic fins] which are united beneath the tail; tail very short; head emarginated in front; spiracles far behind eyes; teeth with three points; dorsals [fins] two. *Hypnos*.

Subfamily Narcaciontinae. Disc and tail nearly equal; head emarginated in front; spiracles far behind eyes; teeth transverse, with one point. *Narcacion* (= *Torpedo*), with two subgenera *Narcacion* and *Tetronarce*

Subfamily Narcininae. Disc and tail nearly equally long; head entire or convex in front; spiracles close behind eyes; teeth rhombic or hexagonal.

[Tribe] Discopygae. Dorsals two, ventrals [pelvic fins] united beneath the tail; teeth rhombic, acute behind; disc orbicular. *Discopyge*.

[Tribe] Narcinae. Dorsals two, ventrals separated; teeth rhombic, with a median point. Narcine, with three subgenera *Narcine, Cyclonarce,* and *Gonionarce*.

[Tribe] Astrapae. Dorsal [fin] single. Teeth rhombic, each with a median point; disc sub-circular. *Astrape* (= *Narke*).

[Tribe] Temerae. Dorsal [fin] obsolete; teeth hexagonal and flat; disc sub-circular. *Temera.*

Gill (1893) mentioned the division of his family Torpedinidae into three subfamilies, Torpedininae, Narcininae and Hypninae with tribes and generic allocations not specified. Fowler (1934, 1941) proposed the division of the family Torpedinidae into three subfamilies based on presence and number of dorsal fins, as with Gill's (1862) tribal classification within his Narcininae, but with the union of two-dorsal fin taxa in subfamily Torpedininae for *Narcine, Heteronarce, Benthobatis, Hypnos* and *Torpedo*; subfamily Narkinae for the one-finned Narke (including *Bengalichthys*) and

Typhlonarke, and subfamily Temerinae for the finless *Temera*.

Bigelow & Schroeder (1953) followed Fowler's classification but raised the rank of his subfamilies to family (Temeridae, Narkidae, and Torpedinidae) and added *Discopyge* and *Diplobatis* to the Torpedinidae. Their classification was followed by a few subsequent authors, including Lindberg (1971) and Rass & Lindberg (1971). Bigelow & Schroeder (1953: 86) cautioned that Fowler's system based on the number of dorsal fins was artificial, and that it ran "counter to a dichotomous grouping based on the firmness of articulation of the upper and lower jaws and the presence or absence of labial cartilages, characters which are probably of greater importance phylogenetically than the number of dorsal fins." Bigelow and Schroeder retained Fowler's arrangement as a matter of convenience, as being appropriate to a general work, and because several of the torpedinoid genera had not been examined for jaw morphology. They expected that a torpedinoid classification based on jaw morphology would eventually replace the dorsal fin scheme.

Fowler (1970) retained a single family Torpedinidae but included a modified arrangement of five subfamilies with a somewhat different composition than his earlier work and apparently incorporating elements of Gill's (1862) arrangement: Temerinae for the no dorsal fin *Temera*; Narkinae for the one-dorsal *Narke, Typhlonarke* and *Bengalichthys* (= *Narke*); Discopyginae for the two-dorsal *Discopyge*; Hypninae for the two-dorsal *Hypnos*; and Torpedinidae for the one-dorsal *Crassinarke* (= *Narke*) and two-dorsal genera *Benthobatis, Diplobatis, Heteronarce, Narcine*, and *Torpedo*.

Compagno (1973, 1977, fig. 12) proposed a revised classification of the electric rays based on anatomical comparisons of members of all the torpedinoid genera. The torpedinoids were divided into two well-defined superfamilies, Torpedinoidea and Narcinoidea, that verified and expanded the alternate dichotomous arrangement suggested by Bigelow & Schroeder (1953) as follows:

Superfamily Narcinoidea: Mouth straight, with stout jaws; strong labial cartilages; rod-shaped hyomandibulae; well-developed ceratohyals; branched, antler-like antorbital cartilages; short and broad crania; well-developed frontoparietal fenestrae; rostrum present; occipital condyles not exserted; and disc rounded anteriorly. Families Narcinidae and Narkidae.

Family Narkidae: shallow groove around mouth; narrow, rod-shaped rostrum; nasal capsules anteroventrally directed, contiguous, with a narrow internasal plate; precerebral fossa very small and terminated anteriorly by abrupt constriction of the rostrum; jaws short, stout and weakly protrusile; anterior hypobranchial elements and ceratohyals enlarged; posterior hypobranchials narrow and separated from each other by a wide space; and basibranchial copula small. Genera: *Heteronarce, Narke, Temera,* and *Typhlonarke.*

Family Narcinidae. Deep groove entirely surrounding mouth and lips; rostrum broad, trough or shovel shaped; nasal capsules directed ventrolaterally, separated by a wide, flat internasal plate; precerebral fossa very large; jaws long, stout, and strongly protrusile; anterior hypobranchial elements and ceratohyals small; posterior hypobranchials very broad and nearly meeting mid-ventrally; and basibranchial copula moderately large. Genera: *Benthobatis, Diplobatis, Discopyge,* and *Narcine.*

Superfamily Torpedinoidea: Mouth arcuate, very extensile, with extremely slender jaws; no labial cartilages; flattened triangular hyomandibulae; no ceratohyals; pinnate antorbital cartilages; crania elongated and narrow; with poorly developed frontoparietal fenestrae; rostrum absent or reduced; occipital condyles exserted; disc truncate and emarginate anteriorly. Families: Hypnidae and Torpedinidae.

Family Hypnidae. Disc pear-shaped, tail rudimentary with two tiny dorsal fins and a small caudal fin; teeth tricuspid; "rostral appendices" articulating with cranium (Haswell, 1885); ethmoid region strongly bent ventrally, with nasal capsules expanded anteroventrally, contiguous, internasal plate narrow and compressed, not separating nasal capsules; preorbital processes absent; otic capsules large, with their outlines expanded abruptly from orbital walls; and one pair of hypobranchials articulating with basibranchial copula. Genus *Hypnos.*

Family Torpedinidae. Disc subcircular, tail well-developed, with two moderate-sized dorsal fins and large caudal fin; monocuspid teeth; "rostral appendices" (Holmgren, 1941) fused to cranium; ethmoid region not bent ventrally, nasal capsules expanded laterally and separate, internasal plate wide and flat; preorbital processes present; otic capsules small, their lateral surface sloping gradually into orbital walls; two pairs of hypobranchials articulating with basibranchial copula. Genus *Torpedo.*

This four-family torpedinoid classification was utilized by several authors including McEachran & Compagno (1982), Carroll (1988), Compagno (1990, 1999a,b, 2005), Last & Stevens (1994), McEachran *et al.* (1996), Compagno & Last (*in* Carpenter & Niem, 1999a, b, c), Compagno *et al.* (*in* Carpenter & Niem, 1999), and Carvalho *et al.* (*in* Carpenter & Niem, 1999). 'Downranked' variants of this classification include Nelson (1976, 1984) with a single family Torpedinidae and two subfamilies: Torpedininae and Narcininae with two tribes each. Torpedininae has the tribes

Torpedinini and Hypnini while Narcininae has the tribes Narcinini and Narkini. Nelson (1994) modifies these to two families (Torpedinidae and Narcinidae) with two subfamilies each. Zhu & Meng (1979) used the families Torpedinidae and Narkidae for the two main groups, while Eschmeyer (1990, 1998) used two families Torpedinidae and Narcinidae. Shirai (1996) used one family Torpedinidae and three subfamilies, Torpedininae for *Hypnos* and *Torpedo*, Narkinae for the narkids *Heteronarce, Narke, Temera,* and *Typhlonarke,* and Narcininae for *Benthobatis, Diplobatis, Discopyge,* and *Narcine.*

Our comparison of narkid genera with one another and with other torpedinoids reinforces the distinctiveness of the four families and their grouping into two higher groups (superfamilies) which corresponds to morphological similarities that reflect very different trophic specializations in the two superfamilies. Torpedinoidea feed on large prey that are stunned by the electric organs and swallowed whole through their distensible (snake-like) mouths and flexible jaws. Narcinoidea are bottom feeders that use their more or less protrusible jaws to feed on small prey on or in the substrate. Both groups can use their electric organs defensively against predators, but their utility in feeding is uncertain among the Narcinoidea. A detailed review of torpedinoid systematics and interrelationships of the families and a revision of the Narkidae (particularly *Narke* including describing new species) are needed, but these tasks are beyond the scope of this paper and more appropriate elsewhere. The present work concentrates on the systematics of *Electrolux* but has revealed numerous additional characters distinguishing the genera of Narkidae and provides materials for a future cladistic analysis of the genera that would be preliminary and inappropriate here without a revision of the family.

KEY TO TORPEDINOID FAMILIES

Key modified from Compagno *et al.* (*in* Carpenter & Niem, 1999)

1a. Mouth broadly arcuate, protrusile and greatly distensible; no labial folds and cartilages at corners of mouth **2**

1b. Mouth nearly straight, more or less protrusile but not much distensible; strong labial folds and cartilages at corners of mouth **3**

2a. Disc longer than wide, heart or pear-shaped; teeth tricuspid; tail much reduced; caudal fin about as high as dorsal fins .... **Hypnidae** (Australia)

2b. Disc transversely elliptical, not pear-shaped; teeth monocuspid; tail not greatly reduced, caudal fin much higher than dorsal fins .... **Torpedinidae** (Wide-ranging in all temperate and tropical seas)

3a. Snout firm, with broad, stiff, shovel-shaped rostral cartilage, readily felt by palpitation of snout; deep groove around mouth; teeth extending onto outer surfaces of jaws in most species .... **Narcinidae** Wide-ranging in most temperate and tropical seas except for Eastern Atlantic.

3b. Snout soft, with a slender, rod-shaped rostral cartilage; shallow groove around mouth; teeth not extending onto outer surfaces of upper and lower jaws .... **Narkidae**. (Eastern South Atlantic and temperate and tropical Indo-West Pacific from South Africa and Red Sea to Indonesia, Japan and New Zealand)

FAMILY NARKIDAE FOWLER, 1934. SLEEPER RAYS

Group Astrapae Gill, 1862: 387 (Family Torpedinoidae or Narcaciontoidae, subfamily Narcininae Gill, 1862). Type genus: *Astrape* Müller & Henle, 1837 (= Narke Kaup, 1826). Proposed as a group that is equivalent to tribe in rank for purposes of nomenclature.

Subfamily Narkinae Fowler, 1934: 240 (Family Torpedinidae). Type genus: *Narke* Kaup, 1826. Replaces Astrapae Gill, 1862. Family Narkidae Bigelow & Schroeder, 1953: 87; and Narkidae Compagno, 1973: 41.

Group Temerae Gill, 1862: 387 (Family Torpedinoidae or Narcaciontoidae, subfamily Narcininae). Type genus: *Temera* Gray, 1831. Subfamily Temerinae Fowler, 1934: 240 (Family Torpedinidae), Family Temeridae Bigelow & Schroeder, 1953: 87. Compagno (1973: 41) synonymized Temeridae with Narkidae although Temerae Gill, 1862 has priority.

FAMILY DIAGNOSIS (derived and expanded from Compagno, 1973, 1977, 1999a and Compagno & Last *in* Carpenter & Niem, 1999a): Electric rays with short preorbital snouts, 5-13% TL; snout broadly rounded anteriorly or nearly truncate (*Electrolux* and some *Heteronarce* species). Spiracles contiguous with posterior edges of eyeballs, not situated behind them; margins of spiracles usually smooth and flat or with a low ridge, elevated and occasionally with a few low papillae in *Narke capensis*, or with several long and prominent papillae that screen the spiracles (*Electrolux*). Nasal curtain elongated, narrow, posteriorly expanded and thickened, with prominent ampullal pores on its ventral surface. Mouth transverse, small and narrow, not highly distensible; shallow circumoral groove surrounding mouth and lips; labial folds and grooves strong. Tooth row counts low, 8-17 / 7-21 or 15-38 total rows; teeth concealed when mouth is closed; teeth small, rounded-oval, unworn crowns with keels or a single low blunt, broad cusp. Tail fairly large and stout but variably short to moderately elongated. Disc circular, ovate, rounded-angular or pear-shaped, often about as broad as long. Pectoral girdle crescentic; tubular section of lateral faces of scapulocoracoids greatly elongated, longer than medial fenestrated section. Suprascapulae V- or C- shaped, with fused midline above free vertebrae behind synarcual. Superscapulae articulating with scapulae entirely in front of coracoid bar or crossing above bar. Metapterygial axis subequal to propterygial axis or much shorter; propterygial radial count equal to metapterygial radial count or much more numerous. Puboischiadic bar with prominent short to greatly elongated iliac processes. Two dorsal fins (*Electrolux, Heteronarce*) or one dorsal fin (*Narke, Typhlonarke*) , or dorsal fin absent (*Temera*). Caudal fin larger than dorsal fins or fin (when present) and subequal to or somewhat smaller in size than pelvic fins (*Typhlonarke* with pelvic fins fused to disc); caudal fin without prominent ventral lobe. Cranium short and fairly broad; rostrum incomplete, medial floor reduced to narrow medial rostral cartilage and paired lateral rostral cartilages below it, lateral walls of rostrum truncated around precerebral cavity and fused to ethmoid region of cranium; medial rostral cartilage rod-shaped with short bifurcated rostral node, less than one-third nasobasal length. Rostral appendices small, separate from rostrum, just lateral to rostral node, and articulating with antorbital cartilages. Precerebral fossa very small and terminated anteriorly by an abrupt constriction of the lateral walls of the rostrum. Ethmoid region anteriorly directed or strongly bent ventrally (*Electrolux*); nasal capsules expanded anteroventrally or laterally; nasal cartilages (ala nasalis) greatly expanded posterolaterally from the nasal capsules to support the expanded and thickened nasal curtain; internasal plate narrow, compressed, narrowly separating the nasal capsules. Antorbital cartilages more or less branched and antler-like (narrower distally in *Electrolux* and in *Heteronarce garmani* than in other narkids examined); bases of cartilages articulating on posterolateral surfaces of nasal capsules; shafts of cartilages directed more or less anterolaterally; a lateroposteriorly directed spur or process present or absent on shafts of antorbital cartilages. Preorbital processes apparently absent. Cranial roof perforated by frontoparietal fenestra (*Narke, Temera, Typhlonarke*) or not (*Electrolux, Heteronarce*); when present long, U-shaped and contiguous with anterior fontanelle or separated from it by an epiphysial bridge. Otic capsules large and broad, length about 33-40% of nasobasal length, width across capsules about 59-68% of nasobasal length, capsules rather inflated and expanded laterally, distally rounded-angular; lateral outlines of otic capsules sloping gradually into orbital walls. Occipital condyles relatively short and low, not strongly exserted from occiput. Jaws stout and transverse, weakly protrusile. Palatoquadrates thick, straight and subtriangular, with strong overlapping processes on their articulation with Meckel's cartilages; orbital cartilages obsolete to strong on palatoquadrates. Meckel's cartilages very stout, flat and broad, strongly expanded symphysially and distally, with a weak to strong distal process. A large flat oval mental cartilage just posterior to lower symphysis in most genera (possibly absent in *Typhlonarke*). Well-developed upper and lower labial cartilages present and close to symphyses, dorsal labial cartilage simple or forked. Hyomandibulae heavy, elongated and sigmoid-shaped, with expanded bases and apices; ceratohyals well-developed and large, about size of anterior hypobranchials. Prespiracular cartilages present but postspiracular cartilages absent. Two pairs of hypobranchials, the posterior pair articulating with basibranchial copula; anterior hypobranchials large, as broad or broader than posteriors but not as long; posterior hypobranchials broad to very narrow and separated from each other by a narrow (*Electrolux*) to wide space (*Narke, Temera,* with *Heteronarce* intermediate). Basibranchial copula small and tack-shaped (*Narke* and *Temera*), larger and more rounded-angular in *Electrolux* and apparently *Heteronarce*. Dorsal surface usually brownish or reddish-brown, white or brownish below; dorsal surface either plain or with a few large dark spots or blotches, paired white spots, and white side bands on the tail and posterior pelvic bases, usually without a complex colour pattern or ocelli on pectoral fins (*Electrolux* exceptional with its elaborate colour pattern). Dwarf to moderate-sized batoids, adult males 82-515 mm TL and possibly longer (see size discussion for *Electrolux*, above).

Genera of Narkidae and status of Heteronarce: *Heteronarce, Narke, Temera*, and *Typhlonarke* were included in the Narkidae (Compagno, 1973), to which we add *Electrolux* as the second genus of two-dorsal narkid. We initially considered *Electrolux addisoni* as a possible species of *Heteronarce* but it soon became apparent that it was very different from any species of *Heteronarce* and that the four valid species of *Heteronarce* formed a coherent genus that is separable from *Electrolux* and other narkids. We present meristic data of *Heteronarce* and other narkids (Tables 6, 7 & 8) and morphometric data (Table 9) for *Heteronarce* and and can easily distinguish *Electrolux* and *Heteronarce* from each other and from other narkids. Figures 18 and 19 summarize external differences within narkid genera, Figures 6 and 7 show differences in mouth and nostril structures, Figures 5, 9, 10, 11 and 12 differences in head anatomy, Figure 13 pectoral girdle structure and Figure 14 pelvic girdle structure.

There has been considerable confusion in the literature on the status, familial position, and species of *Heteronarce*. Some authors have doubted its distinction from *Narcine* and have synonymized the two genera or have mistaken species of *Heteronarce* for *Narcine* or *vice versa*. Part of the problem is that

Heteronarce was originally defined on a few nasoral characters that although partially valid were not seen as definitive by some authors, particularly after a few species of Narcine were discovered with elongated, relatively narrow, *Heteronarce*-like nasal curtains.

The first valid species of *Heteronarce* was described by Lloyd (1907) as *Narcine mollis* from the Gulf of Aden at 238 m. This was distinguished from the Indian species *N. timlei* by its enlarged anterior nasal valves (circumnarial folds) and more elongated nasal curtains about as long as wide (about three times wider than long in *N. timlei*). Lloyd (1909) and Annandale (1909) gave additional information on *N. mollis* including illustrations of the whole ray, teeth, and oral anatomy. Garman (1913) included *N. mollis* in *Narcine* without comments.

The genus *Heteronarce* was proposed by Regan (1921) for a second new species of two-dorsal electric ray, *H. garmani*, collected about 15-22 miles off the Umvoti River, kwaZulu-Natal, South Africa, in 120-130 fms depth, and for *Narcine mollis* Lloyd, 1907. *Heteronarce* was distinguished from *Narcine* by "the minute nostrils, the length of the anterior nasal valves, which are confluent to form a curtain that is not much broader than long and is studded with pores, and the lateral position of the posterior nasal valves." (Regan, 1921). Regan noted that *H. garmani* was very similar to *H. mollis* but had much smaller eyes and spiracles, a longer snout, a smaller mouth and nasal valves, and different coloration (brown above and white below in *H. garmani*, dark brown above and gray-brown below in *H. mollis*). Regan did not assign a type species for *Heteronarce*, but this was subsequently designated as *H. garmani* by Fowler (1941).

Von Bonde & Swart (1923) described a third species, *Heteronarce regani* from a 190 mm specimen from kwaZulu-Natal, South Africa (two stations mentioned, depth 211-329 m), but didn't compare or distinguish it from *H. garmani* which they also recognized. Their specimen (pl. 22, fig. 2) had a truncated caudal fin tip that is unusual compared to the rounded caudal tips of other *Heteronarce* species and might be abnormal. The genus *Heteronarce* was not characterized by these authors.

Fowler (1925a) described a fourth species of *Heteronarce* as *Narcine natalensis*, from a 260 mm specimen trawled from off kwaZulu-Natal at 40 fathoms, but didn't refer to Regan's or von Bonde & Swart's accounts and didn't compare it with either *H. garmani* or *H. regani*. Fowler (1925b) subsequently synonymized his *N. natalensis* with *H. garmani*, and later (Fowler, 1941) included both *N. natalensis* and *H. regani* in synonymy of *H. garmani*. Fowler's (1941) synonymy was recognized by Wallace (1967) and is followed here. Fowler (1941) included *H. mollis* and *H. garmani* in *Heteronarce* and separated this genus from *Narcine* by its more elongated nasal curtain.

Bigelow & Schroeder (1953) included *Heteronarce* and *Narcine* in their Family Torpedinidae as separate genera, but noted that *Heteronarce* (including *H. garmani* and *H. mollis*) was so close to *Narcine* that its generic validity was doubtful, and differed only in its more elongated nasal curtain. However Compagno (1973) noted that *Heteronarce* "had two dorsals, and had usually been placed in the vicinity of Narcine, but examination of its exterior and skeleton revealed its affinity with *Narke*.

McKay (1966) described *Narcine westraliensis* from Western Australia which has an unusually elongated nasal curtain for a narcinid that resembles that of *Heteronarce*. McKay used this similarity to synonymize *Heteronarce* with *Narcine*. However, the chondrocranium and oral structure of *N. westraliensis* as described by McKay is like that of other *Narcine* species and of narcinids and unlike that of *Heteronarce* and other narkids.

Talwar (1981) reviewed *Heteronarce* and named a fifth species from the southwest coast of India, *H. prabhui*. Talwar recognized three valid species, including *H. garmani* from southern Africa (with synonyms *H. regani* and *Narcine natalensis*), *H. mollis* from the Arabian Sea, and *H. prabhui* from India. Talwar defined *Heteronarce* as having the disc rounded anteriorly, a shallow groove around the mouth, jaws short and weakly protractile, eyes well developed and almost contiguous with spiracles, nasal curtain only slightly broader than long, and two dorsal fins.

Baranes & Randall (1989), described *Narcine bentuviai* from 80-200 m. in the Gulf of Aqaba, Red Sea, which proved to be a sixth and unusual species of *Heteronarce. Heteronarce bentuviai* has a unique bold and black-blotched color pattern and a second dorsal fin noticeably smaller than the first dorsal. *H. mollis, H. garmani*, and *H. prabhui* in contrast are uniformly colored and have second dorsal fins about as large as the first. According to Baranes & Randall's detailed account, the external morphology and anatomy of *H. bentuviai* agrees with that of other narkids and particularly with other species of *Heteronarce* but not with *Narcine* or other narcinids. These authors tentatively placed their species in *Narcine* because they considered *Heteronarce* a junior synonym following McKay (1966), but noted that an alternate generic arrangement might remove it from Narcine. De Carvalho (1999) excluded *H. bentuviai* from *Narcine* in his revision of the genus.

Lloris & Rucabado (1991) described a seventh species, *Heteronarce rierai* from off Mozambique, but this proved to be a narrow-bodied *Narcine* with a narrow nasal curtain as in *N. westraliensis* but like that species has mouth and anatomical characteristics typical of narcinids (Compagno, *in* Smith & Heemstra, 1995, de Carvalho, 1999). There are several other narrow-bodied species of *Narcine* in Australian waters (MacKay, 1966, Last & Stevens, 1994, de Carvalho, 1999).

The superficial external similarity of *Heteronarce* to *Narcine* is contradicted by its anatomical and external differences (particularly in the oral and chondrocranial morphology) which are similar to those of other narkids rather than *Narcine* or other narcinids. Based on our examination of *Heteronarce* specimens, as well as literature data, we confirm that *Heteronarce* is a valid and well-defined genus including the four species *H. bentuviai, H. garmani, H. mollis*, and *H. prabhui*, with the latter species morphologically very similar to *H. mollis*. *Heteronarce* is separable from narcinids by characters in the key to families and definition of the Narkidae above, and separable from other narkids in the key to narkid genera and in comparison with *Electrolux*.

KEY TO NARKID GENERA

1a. No dorsal fins .... ***Temera*** (Indo-West Pacific from Andaman Sea near southern Thai-Burma border through Straits of Malacca and Malay Peninsula to Singapore, Thailand and Viet-Nam, doubtful from Philippines)

1b. One or two dorsal fins 2

2a. One dorsal fin 3

2b. Two dorsal fins 4

3a. Eyes not visible externally; anterior lobes of pelvic fins form isolated leg-like structures protruding from ventral surface of pectoral disc, posterior lobe of pelvic fins fused to pectoral disc .... ***Typhlonarke*** (New Zealand)

3b. Eyes usually visible externally; no separate pelvic fin lobes .... ***Narke*** (Southeastern Atlantic and Indo-West Pacific, South Africa, northern Arabian Sea, India, Malaysia, Singapore, Indonesia, Thailand, Viet-Nam, Philippines (doubtful), China, Taiwan, Japan, Korea)

4a. Spiracles with long, slender, stiff papillae (Fig. 5A); nostrils and mouth projecting ventrally as prominent nasoral turret near front of disc (Figs 3B; lower lips thin, without a chin (mental) groove and with labial cartilages not meeting at midline (Fig. 7A & 12A); tooth rows numerous, 32-34 total; dorsal side of disc with numerous pale spots on dark brown background, live ray with elaborate concentric pattern of black lines and pale spots; underside of disc white medially, the broad distal margin dark brown, with numerous small pale spots .... ***Electrolux***, (Western Indian Ocean, South Africa)

4b. Spiracles without papillae (Fig. 5B); nostrils and mouth not projecting as a prominent nasoral turret at front of disc, more posterior and slightly projecting from ventral surface of disc; lower lips thick, with prominent mental groove and labial cartilages meeting at symphysis (Figs 7B & 12B); tooth rows fewer, 20-24 total; uniform pale to dark brown or grayish above, without markings or with a few large black blotches on disc, first dorsal fin and caudal fin, white, grayish or gray-brown below .... ***Heteronarce*** (Western Indian Ocean, South Africa to Gulf of Aqaba, Arabian Sea and west coast of India)

MATERIAL EXAMINED

Institutional abbreviations: Institutional abbreviations for specimens of Narkidae mostly follow Compagno (1988): **BMNH** - Natural History Museum, London, UK, formerly British Museum (Natural History). **CAS** - California Academy of Sciences, San Francisco, California, USA. **GVF** - George Vanderbilt Foundation fish collection, Stanford University, Stanford, California, USA, housed at the California Academy of Sciences. **ISH** - Institut für Seefischerei, Hamburg, Germany. **KUMF** - Kasetsart University. Faculty of Fisheries, Museum, Bangkok, Thailand. LJVC - XXXX and **LJVC** - YYMMDD (Year, Month, Day), L.J.V. Compagno accession number and field-accession number. **PCH** - Phillip C. Heemstra field numbers. **NMS** - National Museum of Singapore (formerly Raffles Museum) zoology collection, housed in the Department of Zoology, National University of Singapore. **SAIAB** - South African Institute of Aquatic Biodiversity, formerly **RUSI**, for the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. **SAM** - Iziko - South African Museum, Natural History Division, department of Marine Biology, Cape Town, South Africa. **SIO** - Scripps Institution of Oceanography, La Jolla, California, USA. **SU** - Stanford University fish collection, Stanford, California, USA, housed at the California Academy of Sciences. **USBCF** - United States Bureau of Commercial Fisheries, Department of the Interior field number. Now US National Marine Fisheries Service, Department of Commerce. **ZRC** - Zoological Reference Collection, Department of Zoology, National University of Singapore.

COMPARATIVE MATERIAL - FAMILY NARKIDAE

'Crassinarke dormitor' (? = Narke japonica), **SIO** 4-257-6B, 278 mm TL adult male, Yellow Sea.

Heteronarce garmani: **BMNH** 1921.3.1.3, holotype, adult male, 169 mm TL, 77 mm DW, 1921, Umvoti River, kwaZulu-Natal, South Africa, 220-238 m. **SAM** 34813, two adult males, 256-289 mm TL and 124-135 mm DW, RV Algoa, C00813 014 011-3115, 19940612, Western Indian Ocean, Mozambique, 23° 28.0′ S, 35°43.00′ E, 185 m. **SAM** uncataloged, two females, 125-132 mm TL and 65-72 mm DW, adolescent male, 145 mm TL and 64 mm DW, RV Benguela G13531 88N 30-08, 19880822, kwaZulu-Natal, South Africa, 29°44.0′ S, 31°23.00′ E, 154 m.

Heteronarce mollis: **CAS** 58352, 206 mm TL, 92 mm DW adult male, RV Anton Bruun, AB 9-444, 19641216, N. Indian Ocean, Somalia, 9° 36.00′N, 51° 1.00′E, 78-82 m. **CAS** 58351, 6 females, 217, 226, 255, 218, 211 and 212 mm TL, 115, 120, 122, 111, 108 and 100 mm DW, 2 adult males, 220 and 199 mm TL, 118 and 100 mm DW; immature male, 165 mm TL and 90 mm DW, RV Anton Bruun, AB 9-464, 19641218, N.

Indian Ocean, Somalia, 11° 37.00'N, 51° 27.00'E, depth? **ISH** 254/75, adult male, 199 mm TL, 100 mm DW, Dr. F. Nansen, FAO, 19750303, North coast, N. Indian Ocean off Somalia, 11°41.00' N, 51°36.00'E, 82 m.

Narke capensis: (all from South Africa): *Africana* A04752 048 030-1039, immature males, 87, 94, 98 mm TL, 52, 53, 57 mm DW, adult males, 206, 250 mm TL, 142, 165 mm DW, immature female, 89 mm TL, 49 mm DW, adult (?) females, 205, 215, 223, 233, 255 mm TL, 133, 133, 137(?), 153, 164 mm DW, adult females, 193, 208, 220, 220, 224, 232, 234, 245 mm TL, 120, 139, 136, 145, 146, 156, 146, 173 mm DW, 19860920, southeastern Cape coast, , 34°16.0' S, 22°1.0'E, depth 42 m. Africana A04770 048 043-1093, adult males, 176, 237, 245 mm TL, 119, 153, 154 mm DW, immature female (?), 155 mm TL and 101 mm DW, females, 145, 165, 171, 192, 218 mm TL, 96, 108, 105, 128, 140 mm DW, 19860923, southeastern Cape coast, , 33°48.0'S, 26° 7.0' E, depth 56 m. Africana A06215 056 023-1042, adult males, 243 and 253 mm TL, 154 and 153 mm DW, adult females, 196 and 213 mm TL, 115 and 120 mm DW, 19870917, southeastern Cape coast, , 34°7.0'S, 22° 15.0'E, depth 40 m. Africana A07115 063 011-2123, adult male 243 mm TL and 172 mm DW, 19880513, southeast Cape coast, 34°30.0'S, 21°14.0'E, depth 59 m. Africana A07116 063 012 2132, male (adult?) 253 mm TL, 155 mm DW, 19880513, East coast cruise, Cape coast, 34°31.0'S, 21°17.0'E, depth 58 m. *Africana* A07128 063 020-1039, immature female, 118 mm TL, 75 mm DW, adult females, 225, 229, 246, 254, 263 mm TL, 136, 143, 156, 162,169 mm DW, adolescent male, 257 mm TL, 168 mm DW, adult males, 243, 253 mm TL, 173 mm DW (253 mm TL), 19880515, southeastern Cape coast, 34°16.0'S, 22°1.0'E, depth 35 m. *Africana* A07152 063 038-1093, adult males, 175, 178, 215, 255 mm TL, 117, 123, 134, 170 mm DW, adult females, 155, 175 mm TL., 95, 112 mm DW, 19880519, southeastern Cape coast, 33°45.0'S, 26°5.0' E, depth 32 m. *Africana* A13339 102 014-2332, immature male 73 mm TL, 50 mm DW, 1992040, southeastern Cape coast, 33°53.0'S, 26°46.0'E, depth 90 m. *Africana* A16338 122 043-1042, immature male, 105 mm TL, 68 mm DW, adult female, 176 mm TL, 109 mm DW, 19940618, eastern Cape coast, 34°9.0'S, 22°13.0'E, depth 39 m. **SAM** 34347, adult male, 174 mm TL, 118 mm DW, *Africana* A18168 135 077-1090, 19960429, southeastern Cape coast, , 33°45.0'S, 26°1.0'E, depth 27 m. depth. **LJVC** 961014, **SAM** uncataloged, adult male, 265 mm TL, 180 mm DW, M. Marks site 1, 19961013, Buffels Bay, False Bay, Western Cape, , 34°19.06'S, 18° 27.75'E, depth 4.5 m. **RUSI** 11932, adult male, 195 mm TL, 115 mm DW , TBD-3, off Swartkops, Eastern Cape, . **SAM** 22796, female, 188 mm TL, 120 mm DW, 19590919, Algoa Bay, Eastern Cape, . **SAM** 22799, female 170 mm TL, 101 mm DW, 19590916, Sandy Point, Mazeppa Bay, Eastern Cape, 32°27.00'S, 28°39.00'E. **SAM** 30992, adult male, 239 mm TL, 156 mm DW, 19781103, Muizenberg, False Bay, Western Cape.

Narke dipterygia: **BMNH** 1909.7.12.13, female, 121 mm TL, 57 mm DW, **syntype** of *Bengalichthys impennis* Annandale, 1909, Balasore Bay, Orissa coast, India. **CAS** uncataloged, female ca 120 mm TL, 50 mm DW, Indo-West Pacific. **CAS** 66840, female, 146 mm TL, 78 mm DW, collected by J. Mee, 19890222, Sudah, Oman, 6 m depth. **LJVC** 0508, five females, 170, 150, 150, 162 and 155 mm TL, immature male, 165 mm TL, F. Steiner, 19751006, Taiwan straits?, Taiwan. **LJVC** 0514, 157 mm TL adult (?) female, F. Steiner, 19751006(?), Taiwan straits, Taiwan? **LJVC** 0515, adult (?) females, 146 and 151 mm TL, F. Steiner, 19751006, Taiwan straits, Taiwan(?). J. Randall uncataloged, female, 131 mm TL, India. **NMS** 3119, adult males, 150 and 131 mm TL, 84 and 70 mm DW, A. K. Tham, 1964, Fisheries Biology Unit, SPR 425, Singapore. **SU** 32406, adult male, ca. 135 mm TL, 65 mm DW, India. **SU** 41717, adult male ca 150 mm TL and female ca 135 mm, India. **USBCF** F.H. Berry no number, two adult males, 170 and 180 mm TL, five females, 178, 153, 166, 130, 153 mm TL, Porto Novo, Madras, India. **USBCF** F.H. Berry, SOSC-381, female ca 160 mm TL, Porto Novo, Madras, India, 15-22 m. depth,

Narke cf. dipterygia, **KUMF** 2464, female, 120 mm TL, 75 mm DW, 19740105, Samut Songkram, Thailand,. **KUMF** 0807, female, 123 mm TL, 69 mm DW, 1968, collected by P. Wongrat, Prachuat Khiri Khan, Gulf of Thailand, **KUMF** 0834, females 109, 114 and 112 mm TL, 64, 66, 66 mm DW, 1972021-10, collected by P. Wongrat, offshore near Sataheys, Gulf of Thailand.

Narke japonica: **CAS** Acc. 1972:1:5, female, 233 mm TL, 19711200, East. China Sea, between Japan and Korea. **GVF** Naga 60-61 (**GVF**-2077), adult male ca 225 mm, 19600227, South China Sea, 15°40.00'N, 109°25.50'E. **PCH** Jan. 1988, female 168 mm TL, 93 mm DW, 1988, from Tachi, South China Sea, Taiwan. **SU** 3363, adult male, ca. 365 mm TL, Japan. **SU** 61723, female ca 215 mm TL, Japan. **SU** 7267, adolescent male, ca 195 mm TL, Japan.

Narke spp. **CAS** Acc 1972-XII: 18, immature male, 67 mm TL, adolescent males, 94 and 109 mm TL, adult males, 99 and 103 mm TL, females, 58 and 93 mm TL, southwest of Kao Ksiung, Taiwan. *Anton Bruun*, AB 4B-263, immature male, 100 mm TL, adult males, 143 and 147 mm TL, females, 117, 121, 127, 127, 132, and 139 mm TL, Arabian Sea, 22°54'N, 68°06'E. **GVF**-2430, female ca 150 mm TL, Gulf of Thailand, Thailand. **GVF**-2449, adult males, 153 and 154 mm TL, female, ca. 125 mm TL, Gulf of Thailand, Thailand. **GVF**-2663, female ca 150 mm TL, Gulf of Thailand, Thailand. **CAS** *Anton Bruun* AB 4B-223A, females, 130, 150 and 165 mm, Arabian Sea, 22°54'N, 68°06'E, depth 16 m.

Temera hardwickii: **BMNH** 1953.8.10.9-10, female, 139 mm TL, 73 mm DW, and adult male, 108 mm TL, 55 mm DW, from Penang, Malaysia, ***syntypes*** of *Temera hardwickii* Gray, 1831. **CAS** 58369, adolescent males, 74 and 84 mm TL, 44 and 49 mm DW, female, 108 mm TL, 59 mm DW, *Anton Bruun* Sta. 0248, 9°54'N, 97°42'E, Andaman Sea, SSW of Kawthaung, Isthmus of Kraa, Burma, 0-200 m. **KUMF** 0014, female, 136 mm TL, 86 mm DW, 19650823, Phuket (Puket), Thailand, depth 91-105 m. **KUMF** 2916, females, 78 and 142 mm TL, 36 and 85 mm DW, adult or late adolescent male, 88 mm TL, 44 mm DW Songkhla Research Vessel, S. Mongkolprasit, 198412, Thailand. **NMS** 2090, adult female, 148 mm TL, 76 mm DW, M. Tweedie, identified by A.W.C.T. Herre, 1940, fish market, Singapore. **NMS** 2110, adult (?) female, 140 mm TL, 81 mm DW, R.L. Chermin, 1954, det. E.R. Alfred, 680615, Changi, Singapore. **SU** 35728, adolescent male, 104 mm TL, 64 mm DW, A.W.C.T. Herre, 1936-1937, Telok Kurau, Perak, Malaysia, **SU** 35736, immature female, 74 mmTL, 38 mm DW, adolescent female, 105 mm TL, 62 mm DW, adult female, 119 mm TL, 62 mm DW (cranium dissected), A.W.C.T. Herre, Singapore. **ZRC** no number, adult male, 82 mm TL, 48 mm DW, no locality data or other information, presumably Singapore, **ZRC** no number, female (possibly adult), 121 mm TL, 72 mm DW, Ahmad Draman, 19630811, Ponggol, Singapore. **ZRC** 10588, adult male, 109 mm TL, 66 mm DW adult male, Ahmad Draman, 19640801, Ponggol, Singapore. **ZRC** 38918, adult female, 122 mm TL, 78 mm DW, K. Lim, P.K.L. Ng, et al., June 1995, Pulau Bintan, north coast, Tanjung Tondang, Sumatra, Indonesia.

Typhlonarke aysoni: **LJVC** 0424, adult male, 205 mm TL, 110 mm DW, Kaikoura coast, South Island, New Zealand, 110 m. **SIO** 61-149-6A, immature female, 92 mm TL, 48 mm DW, 19610129, NW of Mernoo Bank, South Island, New Zealand, 43°39.0'S, 175°15.0'E, 0-119 m.

ACKNOWLEDGEMENTS

We thank Mark Addison and his father Brent Addison for their efforts in collecting and donating the two specimens of *Electrolux addisoni* to the South African Institute for Aquatic Biodiversity. We are grateful for the images of the live fish supplied by Stefania and Peter Lamberti, Dennis King, Avril and Len Fish, and Peter Chrystal through Rudy van der Elst. We thank Elaine Heemstra for her assistance with the drawings. Thanks also to Mark Marks, Mike Bougaardt and Liz Hoenson of Iziko-South African Museum. The first author thanks the curators and collection managers at the following institutions for allowing him to examine narkid specimens in their collections: Natural History Museum, London, UK; California Academy of Sciences, San Francisco, California, USA; Institut für Seefischerei, Hamburg, Germany; Kasetsart University. Faculty of Fisheries, Museum, Bangkok, Thailand; National Museum of Singapore (formerly Raffles Museum) zoology collection and Zoological Reference Collection in the Department of Zoology, National University of Singapore; Scripps Institution of Oceanography, La Jolla, California, USA.

Table 1. Morphometric abbreviations and definitions for torpedinoids

Code	Description	Code	Description
ANF	anterior nasal flap length, from anterior edge of incurrent apertures to rear end of nasal curtain	IG5	distance between medial ends of fifth gill slits
CDM	dorsal caudal margin, upper caudal fin origin to rear tip of fin	INO	least inter-orbital width between eyeballs
CH	greatest vertical height of caudal fin	INS	least width between spiracles
CLB	width across base of clasper	INW	inter-narial width, least distance between excurrent narial apertures
CLI	clasper medial length from anterior end of vent	IOW	inter-narial outer width, nasal curtain base width at incurrent apertures
CLO	clasper length, from pelvic fin base to clasper tip	MOL	mouth length, mid upper lip to line joining corners
COH	height of exposed cornea	MOW	mouth width, distance between mouth corners
COL	anterior – posterior length of exposed cornea	NOW	nostril width from lateral edge of incurrent aperture to medial edge of excurrent aperture
CPH	peduncle height at upper caudal fin origin	PCS	pelvic fin insertion to ventral origin of caudal fin
CPW	caudal peduncle width at upper caudal origin	PDI	least distance between verticals at pelvic fin insertion and first dorsal fin insertion
CVM	ventral caudal fin margin, from ventral fin origin to rear tip	PDO	pelvic fin origins to first dorsal fin origin
DCS	dorsal caudal space, D2 insertion to upper caudal fin origin	PD1	pre-D1, snout tip to first dorsal fin origin
DL	disc length, snout tip to line at rear tips of disc	PD2	pre-D2, snout tip to second dorsal fin origin
DT	greatest thickness at middle of disc	PGL	prebranchial length, snout tip to level of first gill slits
DW	greatest transverse width across disc	PGW	snout tip to level of greatest disc width
D1A	D1 anterior margin from origin to fin apex	PIW	body width at pectoral fin insertions
D1B	first dorsal fin base, from origin to insertion	POB	pre-orbital, snout tip to line at front edge of eyes
D1H	D1 height, vertical distance from fin base to apex	POR	pre-oral length, snout tip to front edge of mouth
D1I	D1 inner margin, from insertion to rear edge	PP2	pre-pelvic length, snout tip to level of pelvic fin origins
D1L	D1 length, from origin to rear edge of fin	PRC	pre-caudal length, from snout tip to dorsal caudal fin origin
D1P	D1 posterior margin from apex to free rear tip	PRN	pre-narial length, midline snout tip to level of nostrils
D2A	D2 anterior margin from origin to fin apex	PSP	pre-spiracular length, snout tip to level of spiracles
D2B	length D2 base, from origin to insertion	P1I	pectoral disc insertion to free rear tip
D2H	D2 height, vertical distance from base to apex	P2A	pelvic fin anterior margin from fin origin to apex
D2I	D2 inner margin from insertion to rear edge of fin	P2B	pelvic fin base from pelvic fin origin to insertion
D2L	D2 length, from origin to rear edge of fin	P2H	pelvic fin height, perpendicular distance from base to apex of fin
D2P	D2 posterior margin, from apex to free rear tip	P2I	pelvic fin inner margin, pelvic fin insertion to rear tip
ESL	distance from rear edge of eyeball to spiracle	P2L	pelvic fin length, from pelvic fin origin to rear tip
EH	height of protruding eyeball	P2P	pelvic fin postero-lateral margin, fin apex to rear tip
EL	anterior-posterior length of protruding eyeball	P2S	pelvic fin span, distance between pelvic fin apices
GS1	width from medial to lateral ends of first gill slit	SPL	anterior-posterior length (diameter) of spiracle
GS2	width of second gill slit	SPW	lateral-medial width (diameter) of spiracle
GS3	width of third gill slit	SVL	snout tip to anterior end of vent
GS4	width of fourth gill slit	TBH	tail base vertical thickness at pelvic fin insertions
GS5	width of fifth gill slit	TBW	tail base width at pelvic fin insertions
HL	head length, tip of snout to level of fifth gill slits	TL	total length, from snout tip to rear end of caudal fin
IDS	interdorsal distance, D1 insertion to D2 origin	VNL	anterior-posterior length of vent (cloaca)
IG1	distance between medial ends of first gill slits		

Table 2. Measurements in mm and proportions as %TL for type specimens of *Electrolux addisoni*. Abbreviations for measurements are defined in Table 1.

	Holotype		Paratype			Holotype		Paratype	
TL	515 mm	%TL	502 mm	%TL		mm	%TL	mm	%TL
PRC	425	83	410	82	GS3	10	1.9	9	1.8
DW	305	59	291	58	GS4	10	1.9	9	1.8
DL	264	51	255	51	GS5	5	1.0	7	1.4
DT	46	8.9	53	11	IG1	50	9.7	51	10
PRN	37	7.2	41	8.2	IG5	34	6.6	27	5.4
POR	32	6.2	42	8.4	VNL	24	4.7	22	4.4
POB	42	8.2	32	6.4	PIW	99	19	80	16
PSP	46	8.9	40	8.0	TBH	32	6.2	36	7.2
PGL	79	15	71	14	TBW	62	12	55	11
HL	132	26	127	25	CPH	15	2.9	15	3.0
PGW	137	27	129	26	CPW	13	2.5	16	3.2
PP2	194	38	186	37	P1I	25	4.9	27	5.4
SVL	225	44	221	44	P2L	123	24	126	25
PD1	300	58	282	56	P2A	81	16	82	16
PD2	369	72	357	71	P2B	82	16	81	16
IDS	33	6.4	27	5.4	P2H	63	12	68	14
DCS	21	4.1	22	4.4	P2I	48	9.3	51	10
PCS	144	28	142	28	P2P	116	23	116	23
PDO	132	26	62	12	P2S	202	39	197	39
PDI	64	12	58	12	CLO	22	4.3	24	4.8
COL	9	1.7	9	1.8	CLI	102	20	95	19
COH	5	1.0	5	1.0	CLB	9	1.7	10	2.0
EL	11	2.1	12	2.4	D1A	75	15	76	15
EH	10	1.9	8	1.6	D1B	31	6.0	36	7.2
INO	24	4.7	24	4.8	D1H	56	11	57	11
NOW	12	2.3	12	2.4	D1I	16	3.1	18	3.6
INW	6	1.2	5	1.0	D1L	52	10	53	11
IOW	18	3.5	16	3.2	D1P	44	8.5	39	7.8
ANF	17	3.3	15	3.0	D2A	73	14	75	15
SPL	14	2.7	13	2.6	D2B	30	5.8	31	6.2
SPW	13	2.5	12	2.4	D2H	48	9.3	46	9.2
INS	17	3.3	17	3.4	D2I	21	4	23	4.6
ESL	0	0.0	0	0.0	D2L	46	8.9	43	8.6
MOL	3	0.6	5	1.0	D2P	35	6.8	37	7.4
MOW	22	4.3	20	4.0	CDM	81	16	80	16
GS1	12	2.3	9	1.8	CVM	58	11	66	13
GS2	10	1.9	9	1.8	CH	63	12	56	11

Table 3. Torpedinoid family-group taxa assigned to the two superfamilies of Compagno (1973), and sorted into currently recognized families.

Taxon	Original Family	Current Family
Superfamily Narcinoidea (Narcinidae + Narkidae) Compagno 1973		
Tribe (group) Astrapae Gill, 1862	Narcaciontoidae	Narkidae
Tribe (group) Discopygae Gill, 1862	Narcaciontoidae	Narcinidae
Subfamily Discopyginae Gill, 1895	Narcobatidae	Narcinidae
Tribe (group) Narcinae Gill, 1862	Narcaciontoidae	Narcinidae
Family Narcinidae Compagno, 1973		Narcinidae
Subfamily Narcininae Gill, 1862	Narcaciontoidae	Narcinidae
Subfamily Narcininae Gill, 1893	Torpedinidae	Narcinidae
Family Narkidae Bigelow & Schroeder, 1953		Narkidae
Family Narkidae Compagno, 1973		Narkidae
Subfamily Narkinae Fowler, 1934	Torpedinidae	Narkidae
Tribe (group) Temerae Gill, 1862	Narcaciontoidae	Narkidae
Family Temeridae Bigelow & Schroeder, 1953		Narkidae
Subfamily Temerinae Fowler, 1934	Torpedinidae	Narkidae
Superfamily Torpedinoidea (Hypnidae + Torpedinidae) Compagno 1973		
Subfamily Hypninae Gill, 1862	Narcaciontoidae	Hypnidae
Subfamily Hypninae Gill, 1893	Torpedinidae	Hypnidae
Family Hypnidae Compagno, 1973		Hypnidae
Family Narcaciontoidae Gill, 1862		Torpedinidae
Subfamily Narcaciontinae Gill, 1862	Narcaciontoidae	Torpedinidae
Family Narcobatidae Gill, 1895		Torpedinidae
Subfamily Narcobatinae Gill, 1895	Narcobatidae	Torpedinidae
Subfamily Torpedinae Fowler, 1934	Torpedinidae	Torpedinidae
Family Torpedines Müller & Henle, 1841		Torpedinidae
Family Torpedinidae Owen, 1866		Torpedinidae
Family Torpedinidae Bigelow & Schroeder, 1953		Torpedinidae
Family Torpedinidae Compagno, 1973		Torpedinidae
Subfamily Torpedinini Bonaparte, 1838	Rajidae	Torpedinidae
Subfamily Torpedinini Gill, 1893	Torpedinidae	Torpedinidae
Family Torpedinoidae Gill, 1862		Torpedinidae

Table 4. Torpedinoid genera and synonyms. Genus group names that are apparently incorrect subsequent spellings of previously described names are designated by an asterisk (*). Citations for incorrect subsequent spellings are not included in Literature Cited list.

Superfamily Narcinoidea		Superfamily Torpedinoidea	
Genus	**Valid genus**	**Genus**	**Valid genus**
Astrape Müller & Henle, 1837	*Narke*	*Eunarce* Fowler, 1910	*Torpedo*
Bengalichthys Annandale, 1909	*Narke*	*Fimbriotorpedo* Fritsch, 1886	*Torpedo*
Benthobatis Alcock, 1898	*Benthobatis*	*Gymnotorpedo* Fritsch, 1886	*Torpedo*
Crassinarke Takagi, 1951	*Narke*	*Hypnarce* Waite, 1902	*Hypnos*
Cyclonarce Gill, 1862	*Narcine*	*Hypnarea** Sharp, 1903	*Hypnos*
Diplobatis Bigelow & Schroeder, 1948	*Diplobatis*	*Hypos** Cappetta, 1988	*Hypnos*
Discopyge Heckel *in* Tschudi, 1846	*Discopyge*	*Hypnos* Dumeril, 1852	*Hypnos*
Gonionarce Gill, 1862	*Narcine*	*Narcacion* Gill (Klein) 1862	*Torpedo*
Heteronarce Regan, 1921	*Heteronarce*	*Narcobatis** Blainville, 1825	*Torpedo*
*Narcina** Jordan & Seale, 1905	*Narcine*	*Narcobatus* Blainville, 1816	*Torpedo*
Narcine Henle, 1834	*Narcine*	*Notastrape* Whitley, 1932	*Torpedo*
Narcinops Whitley, 1940	*Narcine*	*Tetranarce** Gill, 1895	*Torpedo*
Narke Kaup, 1826	*Narke*	*Tetronarce* Gill, 1862	*Torpedo*
Syrraxis Jourdan *in* Bonaparte, 1835	*Narcine*	*Tetronarcine** Tanaka, 1908	*Torpedo*
Temera Gray, 1831	*Temera*	*Torpedo* Houttuyn, 1764	*Torpedo*
Temerara Tirant, 1929	*Temera*	*Torpedo* Dumeril, 1806	*Torpedo*
Typhlonarke Waite, 1909	*Typhlonarke*		

Table 5. Family Narkidae: species and synonyms, including name changes and one species (*Heteronarce rierai*) originally allocated to the Narcinidae

Nominal species	Valid species
Astrape aysoni Hamilton, 1902	*Typhlonarke aysoni*
Narcine bentuviai Baranes & Randall, 1989	*Heteronarce bentuviai*
Raja capensis Gmelin, 1788	*Narke capensis*
Raja dipterygia Bloch & Schneider, 1801	*Narke dipterygia*
Crassinarke dormitor Takagi, 1951	? = *Narke japonica*
Heteronarce garmani Regan, 1921	*Heteronarce garmani*
Temera hardwickii Gray, 1831	*Temera hardwickii*
Temerara hardwickii Tirant, 1929	*Temera hardwickii*
Bengalichthys impennis Annandale, 1909	*Narke dipterygia*
Torpedo japonica Temminck & Schlegel, 1850	*Narke japonica*
Narcine mollis Lloyd, 1907	*Heteronarce mollis*
Narcine natalensis Fowler, 1925	*Heteronarce garmani*
Heteronarce prabhui Talwar, 1981	*Heteronarce prabhui*
Heteronarce regani von Bonde & Swart, 1924	*Heteronarce garmani*
Heteronarce reirai Lloris & Rucabado, 1991	*Narcine reirai*
Typhlonarke tarakea Phillipps, 1929	? *Typhlonarke tarakea*

Table 6. Vertebral counts of representative narkids. Counts of vertebral centra, and sums of totals and percent vertebral groups. Abbreviations follow text; n = number of specimens.

COUNTS	n	SYN	SYS	SYC	MPN	MPR	MP	DPR	DPN	DP	DC
Electrolux addisoni	2	14 –16	9 --11	5	6 -- 7	23 – 24	30	6 -- 8	54 -- 55	61 -- 62	27 -- 28
Heteronarce	21	10 --14	7 --10	2 -- 5	3 -- 6	15 – 22	19 -- 26	3 -- 10	34 -- 50	34 -- 64	21 -- 29
H. bentuvai	6									57 -- 64	22 -- 25
H. garmani	6	10 --14	7 -- 9	2 -- 5	4 -- 6	15 –20	19 -- 25	8 -- 10	45 --50	45 -- 56	21 -- 29
H. mollis	9	11 --13	7 -- 10	2 -- 4	3 -- 5	16 – 22	21 -- 26	3 -- 7	34 -- 49	34 -- 53	21 --26
Narke	51	8 -- 13	5 -- 10	1 -- 4	2 -- 7	15 – 25	20 -- 29	1 -- 9	19 -- 42	21 -- 51	16 – 28
N. capensis	6	10 --13	7 -- 10	2 -- 4	3 -- 7	21 – 24	26 -- 29	1 -- 4	28 -- 31	31 -- 35	24 -- 28
N. dipterygia	14	8 -- 11	5 -- 9	1 -- 4	2 -- 6	15 –21	20 -- 25	1 -- 5	19 -- 42	21 -- 42	19 -- 25
N. japonica	6	9 -- 12	6 -- 9	2 -- 3	4 -- 5	16 – 25	20 -- 29	5 -- 9	37 -- 42	37 -- 51	16 – 26
N. spp	24	8 -- 11	5 -- 9	1 -- 3	2 -- 5	16 – 25	20 -- 29	2 -- 9	27 -- 42	27 -- 51	17 -- 26
'Crassinarke dormitor'	1	11	9	2	2	16	18	8	38	46	27
Temera hardwickii	7	8 -- 10	5 -- 8	2 -- 3	2 -- 4	20 – 23	24 -- 25	29 --30	24 -- 28	24 -- 30	16 -- 19
Typhlonarke aysoni	2	11 --14	10 --10	1 -- 4	8 -- 8	18 – 24	24 -- 26	3 -- 3	37 -- 48	40 -- 48	22 -- 32
SUMS & RATIOS	**n**	**PCC**	**PC**	**TF**	**TC**	**TS**	**SYN%**	**MP%**	**DP%**	**DC%**	
Electrolux addisoni	2	96 --97	105 -- 108	118 -- 120	123 -- 125	132 -- 136	12 -- 13	25 -- 18	52	23	
Heteronarce	21	63 - 79	71 - 86	84 - 104	81 - 108	95 – 115	10 -- 15	18 -- 31	41 -- 56	22 -- 29	
H. bentuvai	6				81 -- 86						
H. garmani	6	73 --79	82 -- 86	94 -- 104	98 -- 108	106 -- 115	10 -- 15	18 --25	48 -- 56	22 -- 28	
H. mollis	9	63 -- 78	71 -- 86	84 -- 99	87 -- 102	95 -- 111	11 -- 14	21 – 31	41 -- 54	23 -- 29	
Narke	51	48 -- 75	53 -- 82	65 -- 92	69 -- 95	74 -- 102	10 -- 16	22 -- 37	32 -- 57	18 – 32	
N. capensis	6	61 -- 66	70 -- 75	83 -- 88	87 -- 90	96 -- 99	12 -- 16	31 -- 33	36 -- 40	27 -- 32	
N. dipterygia	14	48 -- 63	53 -- 71	65 -- 85	69 -- 86	74 -- 94	10 -- 14	24 -- 35	32 -- 49	256 – 32	
N. japonica	6	66 -- 75	73 -- 82	87 – 92	90 -- 95	97 -- 102	10 -- 14	22 -- 32	40 -- 57	18 – 28	
Narke spp.	24	54 -- 75	61 -- 82	71 -- 92	73 -- 95	79 -- 102	10 -- 13	26 -- 34	37 -- 57	23 -- 40	
'Crassinarke dormitor'	1	66	75	91	93	102	12	20	51	30	
Temera hardwickii	7	51 -- 58	59 -- 63	65 -- 74	67 -- 77	75 -- 82	11	33 -- 39	37 -- 41	24 -- 26	

Table7. Narkid intestine spiral valve counts (number of turns); total lengths in mm.

Species	Specimens	Count
Electrolux addisoni: SAM-36908, adult male, 502 mm		17
Heteronarce garmani: SAM-34813, adult male, 256 mm		9
Heteronarce garmani: SAM-34813, adult male, 289 mm		8
Narke capensis: A12093 +040-1035, adult female, 231 mm		10
Narke capensis: A14742 111 010-2074, adult male, 215 mm		10
Typhlonarke aysoni: LJVC-0424, adult male, 208 mm		10

Table 8. Tooth row counts of narkids; total lengths in mm; upper jaw rows / lower jaw rows.

Species	Specimens and counts
Electrolux addisoni	SAIAB - holotype adult male, 515 mm; 15 / 17
Electrolux addisoni	SAM – paratype, adult male, 502 mm; 16 / 18
Heteronarce bentuvai	HUJ - holotype, adult male, 191 mm; 11 / 11
Heteronarce garmani	SAM-34813, adult male, 256 mm; 11 / 11
Heteronarce garmani	SAM-34813, adult male, 289 mm; 11 / 10
Heteronarce mollis	Lloyd (1907): 10 – 12 / 10 -- 12
Heteronarce prabhuai	Talwar (1981): Types: 10 – 12 / 11 – 12
Narke capensis	A12093 adult female, 231 mm; 16 / 14
Narke dipterygia	SU? adult female, 164 mm; 17 / 21
Typhlonarke aysoni	Garrick (1951): 10 – 12 / 10 – 12
Typhlonarke aysoni	LJVC-0424, adult male, 205 mm; 10 / 11
Typhlonarke aysoni	SIO-61-149-6A, immature female, 92 mm; 8 / 7
Typhlonarke tarakea	Garrick (1951): 11 / 11

Table 9. Measurements of *Heteronarce* spp. in %TL for *H. garmani* and holotypes of *H. bentuvai* (after Baranes & Randall, 1989) and H. prabhui (after Talwar, 1981)

	garmani	*garmani*	*garmani*	*garmani*	*garmani*	*garmani*	*bentuvai*	*prabhui*
	SAM-	SAM-	Benguela	Benguela	Benguela	BMNH-	HUJ	ZSI
	34813	34813	30-98	30-98	30-98	1921.3.1.3	13612	F7614/2
						Holotype	Holotype	Holotype
	Adult	Adult	Adolescent	Juvenile	Immature	Adolescent	Adult	Adult
	male	male	male	female	female	male	male	male
TL	256	289	145	132	127	164	191	220
PRC	82	80	83	80	84	85	79	79
DW	48	43	48	52	51	42	48	51
DL	47	45	50	49	50	49	48	49
DT	13	12	13	12	12	9.8		
PRN	10	10	9.9	8.0	11	12	3.7	
POR	12	12	12	10	13	10	7.3	11
POB	9.4	11	13	10	13	13	8.4	11
PSP	12	13	15	13	15	19	13	
PGI	17	17	18	18	19	30	16	
HL	29	28	31	31	31	24	26	
PGW	31	32	36	37	35	43		
PP2	44	41	42	43	43	49		
SVL	47	47	49	51	50	45	49	46
PD1	61	61	63	63	64		58	57
PD2	71	70	72	70	72	74	71	67
IDS	4.4	4.4	3.1	2.4	1.6	5.8	4.7	4.8
DCS	3.4	2.0	4.2	2.7	2.4	5.5	3.7	
PCS	23	24	23	15	15	27		
PDO	21	19	20	18	19	23		
PDI	11	9.6	9.7	5.5	6.3	11		
COL	1.7	1.6	2.0	1.8	1.9	1.2		
COH	1.0	0.6	1.0	1.0	0.2	0.6		
EL	3.2	2.7	3.1	4.2	3.6	1.8	2.6	
EH	3.0	2.1	2.4	2.0	1.9	1.2		
INO	5.1	5.5	4.7	6.3	6.3	7.9	8.9	
NOW	1.8	1.3	1.4	2.3	2.0	2.1		
INW	1.2	0.9	1.6	1.2	1.6	0.6		
IOW		3.3	3.6	3.8	3.1	3.4	5.2	
ANF	3.4	2.8	2.9	2.2	2.4	1.8	3.7	
SPL	1.3	1.7	1.4	1.0	1.3	1.2	2.1	
SPW	1.7	1.7	1.5	1.4	0.9	1.2		
INS	6.5	6.9	6.4	7.0	7.9	6.7	6.8	6.1
ESL	0.4	0.3	0.3	0.7	0.0	0.3	1.0	
MOL	0.0	0.3	0.0	0.0	0.0	1.2		
MOW	3.0	2.9	3.4	3.5	1.8	4.3	5.2	4.8
GS1	1.5	1.0	1.6	1.2	1.3	1.2		

Table 9 continued

GS1	1.5	1.0	1.6	1.2	1.3	1.2		
GS2	1.1	1.1	1.3	1.4	1.3	1.8		
GS3	1.3	1.1	1.5	1.4	1.2	1.8		
GS4	1.3	1.2	1.7	1.3	1.1	1.8		
GS5	1.4	1.1	1.6	1.3	0.9	1.2		
IG1	10	9.3	12	11	12	12	13	15
IG5	6.4	6.2	6.4	6.4	6.3	7.3	8.9	8.2
VNL	5.6	3.3	3.4	4.5	3.9	4.9		
PIW	20	17	20	24	22			
TBH	5.3	5.8	6.2	6.7	5.5	6.7		
TBW	11	9.9	12	13	11	11		
CPH	3.4	3.0	3.0	2.5	2.4	3.0		
CPW	4.0	3.8	4.3	4.1	4.7	3.0		
P1I	43	41	43	47	0.0	41		
P2L	5.2	2.7	5.9	6.1	0.0	0.0		
P2A	22	21	21	24	24	20		
P2B	13	14	12	11	11	11	11	
P2H	16	17	17	20	21	15		
P2I	9.7	9.2	9.6	10	15	9.1		
P2P	6.2	4.7	6.9	6.1	3.9	4.0	1.6	
P2S	16	15	16	17	17	14	19	
CLO	34	30	35	33	33	28		
CLI	5.2	4.2	3.0			5.5	11	
CLB	20	21	15			15		
D1L	2.5	2.4	2.1			2.4		
D1A	7.6	8.6	8.5	7.8	10	7.9		
D1B	9.3	12	9.1	10	11	9.5	9.4	
D1H	5.3	6.3	5.2	5.1	5.8	5.5	7.3	5.7
D1I	6.6	5.7	4.0	6.1	5.5	5.5	6.8	
D1P	2.3	2.6	2.7	2.4	1.6	3.4		
D2L	4.9	3.9	4.2	5.2	3.9	4.9		
D2A	7.7	9.4	8.3	9.2	8.7	8.5		
D2B	11	13	10	12	11	11	6.8	
D2H	6.1	6.9	5.5	6.3	5.5	4.9	3.1	5.7
D2I	7.1	5.6	4.9	6.2	6.3	4.3	1.6	
D2P	1.8	2.4	2.0	2.4	1.6	5.5		
CDM	5.0	4.2	4.6	4.9	4.7	4.6		
CVM	17	18	17	17	16	15	24	
CH	12	14	13	13	13	13	18	

LITERATURE CITED

ANNANDALE, N. 1909. Report on the fishes taken by the Bengal fisheries steamer "Golden Crown". Part I. - Batoidei. *Memoirs of the Indian Museum*, **2**(1): 1-60.

BARANES, A., & J.E. RAMDALL. 1989. *Narcine bentuviai*, a new torpedinoid ray from the northern Red Sea. *Israel Journal of Zoology*, **36**: 85-101, pl. 1, fig. 1-9.

BIGELOW, H.B., & W.C. SCHROEDER. 1953. Chapter one, Sawfishes, Guitarfishes, Skates and Rays. *In* Fishes of the Western North Atlantic. Memoirs of the Sears Foundation for Marine Research (1) **2**: 1-514.

BONAPARTE, C.L. 1838. Selachorum tabula analytica. Nuovi Annali delle Scienze Naturali, Bologna, series 1, **2**: 195-214.

CARROLL, R.L. 1988. Vertebrate paleontology and evolution. W.H. Freeman, New York, pp. i-iv, 1-698.

COMPAGNO, L.J.V. 1973. Interrelationships of living elasmobranchs. *In* P. H. Greenwood, R. S. Miles and C. Patterson (editors), Interrelationships of fishes. *Zoological Journal of the Linnaean Society*, London, Supplement 1, **53**: 15-61.

COMPAGNO, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**(2): 303-322

COMPAGNO, L.J.V. 1984. FAO Species Catalogue. Vol. 4, Sharks of the World. An annotated and illustrated catalogue of shark species known to date. *FAO Fisheries Synopsis No. 125*, **4**(1): i-viii, 1-250, **4**(2): i-x, 251-655.

COMPAGNO, L.J.V. 1986. Family Narkidae, *in* M.M.Smith & P.C. Heemstra, *eds. Smith's Sea Fishes, 1st edition, first impression.* Macmillan South Africa Publishers, Johannesburg, South Africa, 113-114.

COMPAGNO, L.J.V. 1988. *Sharks of the Order Carcharhiniformes.* Princeton University Press, Princeton, New Jersey, pp. i-xxii, 1-572. Reprinted by Blackburn Press, 2003, pp. i-xxii, 1-572, with new forward.

COMPAGNO, L.J.V. 1990. Evolution and diversity of sharks. *In* S. H. Gruber, *ed.*, Discovering sharks. A volume honoring the work of Stewart Springer. Underwater Naturalist, Bulletin of the American Littoral Society, **19-20**(4/1): 15-22, figs

COMPAGNO, L.J.V. 1995. Additions to and revisions of Family Narkidae and Narcinidae, *in* M.M.Smith & P.C. Heemstra, *eds. Smith's Sea Fishes, 1st edition, third impression (revised).* Southern Book Publishers, Johannesburg, South Africa, vi-vii.

COMPAGNO, L.J.V. 1999a. Chapter 1. Systematics and body form. Chapter 3. Endoskeleton. Appendix. Checklist of living elasmobranchs. *In* W. C. Hamlett, *ed.. Sharks, skates and rays. The biology of elasmobranch fishes.* Johns Hopkins Press, pp. 1-42, 69-92, 471 to 498, figs. 1.1-1.15, 3.1-3.8.

COMPAGNO, L.J.V. 1999b. An overview of chondrichthyan systematics and biodiversity in southern Africa. *Transactions of the Royal Society of South Africa,* 1999 **54**(1): 75-120, fig. 1-9, tab. 1-2.

COMPAGNO, L.J.V. 2001, Sharks of the World. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). An annotated and illustrated catalogue of the shark species known to date. FAO Species Catalogue for Fisheries Purposes (1): i-v, 1-269, figs. 1-163, 160 maps.

COMPAGNO, L. J. V. 2005. Chapter 16. Checklist of living Chondrichthyes. *In* W. C. Hamlett, *ed., Reproductive biology and phylogeny of Chondrichthyes.* Enfield, New Hampshire, USA, Science Publishers, Inc.: 503-548.

COMPAGNO, L.J.V., M. DANDO & S. FOWLER. 2005. *A Field Guide to the Sharks of the World.* First printing, first impression. Harper-Collins, London. Pp i-vii, 9-368, monochrome figs. 1-60, color pls. 1-64.

COMPAGNO, L.J.V., D.A. EBERT & M.J. SMALE. 1989. *Guide to the sharks and rays of southern Africa.* Struik Publishers, Cape Town, 160 pp.

COMPAGNO, L.J.V., & P.R. LAST. 1999a. Order Torpediniformes. Narkidae. Sleeper rays. In Carpenter, K.E. and V.H. Niem *(eds)*, 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific.* Rome, FAO, 3: 1443-1446, figs.

COMPAGNO, L.J.V., & P.R. LAST. 1999b. Order Torpediniformes. Hypnidae. Coffin rays. In Carpenter, K.E. and V.H. Niem (eds), 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific.* Rome, FAO, 3: 1447-1448.

COMPAGNO, L.J.V., & P.R. LAST. 1999c. Order Torpediniformes. Torpedinidae. Torpedos. In Carpenter, K.E. and V.H. Niem (eds), 1999. FAO species identification guide for fishery purposes. *The living marine resources of the Western Central Pacific.* Rome, FAO, 3: 1449-1451,

COMPAGNO, L.J.V., P.R. LAST, B. SERET, & M. DE CARVALHO. 1999. Batoid Fishes. In Carpenter, K.E. and V.H. Niem *(eds)*, 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific.* Rome, FAO, 3: 1398-1409, figs.

COMPAGNO, L.J.V., & T.R. ROBERTS. 1982. Freshwater stingrays (Dasyatidae) of Southeast Asia and New Guinea, with description of a new species of *Himantura* and reports of unidentified species. *Environmental Biology of Fishes*, **7**(4): 321-339.

COMPAGNO, L.J.V., & T.R. ROBERTS. 1984. Marine and freshwater stingrays (Dasyatidae) of West Africa, with description of a new species. *Proceedings of the California Academy of Sciences*, series 4, **43**: 283-300, fig. 1-10.

DE CARVALHO, M.R. 1999. *A systematic revision of the electric ray genus Narcine Henle, 1834 (Chondrichthyes, Torpediniformes: Narcinidae), and the higher level-phylogenic relationships of the orders of elasmobranch fishes (Chondrichthyes).* Unpublished Ph.D. Thesis, City University of New York, pp. i-xxxii, 1-704, fig. 1-116.

DE CARVALHO, M.R., L.J.V. COMPAGNO, & P.R. LAST. 1999. Order Torpediniformes. Narcinidae. Numbfishes. *In* Carpenter, K.E. and V.H. Niem *(eds)*, 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific.* Rome, FAO, **3**: 1433-1442, figs.

DE CARVALHO, M.R., B. SERET, & L.J.V. COMPAGNO. 2002. A new species of electric ray of the genus *Narcine* Henle, 1834 from the southwestern Indian Ocean (Chondrichthyes: Torpediniformes: Narcinidae). *South African Journal of Marine Science*, **24**: 135-149, figs. 1-7, tab. 1.

EBERT, D.A. 1990. *The taxonomy, biogeography and biology of cow and frilled sharks (Chondrichthyes: Hexanchiformes).* Unpub. Ph.D. thesis, Rhodes University, Grahamstown, 308 pp.

ESCHMEYER, WILLIAM N. 1990. *Catalog of the genera of Recent fishes.* California Academy of Sciences, San Francisco, 697 pp.

ESCHMEYER, WILLIAM N. 1998. *Catalog of fishes.* Vol. 1, Introductory materials. Species of fishes (A-L): 1-958. Vol.

2. Species of fishes (M-Z): 959-1820. Vol. 3. Genera of Fishes. Species and genera in a classification. Literature Cited. Appendices: 1821-2905. Also CD-ROM with Access database.

FOWLER, H. W. 1925a. Descriptions of three new marine fishes from the Natal coast. *Annals of the Natal Museum*, **5**(2): 195-200. fig. 1-3.

FOWLER, H. W. 1925b. Fishes from Natal, Zululand and Portuguese East Africa. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 1925, **77**: 187-268, fig. 1-4.

FOWLER, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **85**: 233-367

FOWLER, H.W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by United States Bureau of Fisheries Steamer Albatross in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin of the United States National Museum* (100) **13**: 1-879.

FOWLER, H. W. 1970. A catalog of world fishes (XII). *Quarterly Journal of the Taiwan Museum* **23**(1-2): 39-126.

GARMAN, SAMUEL. 1913. The Plagiostoma. *Memoirs of the Museum of Comparative Zoology, Harvard*, **36**: 1-515.

GARRICK, J. A. F. 1951. The blind electric rays of the genus *Typhlonarke* (Torpedinidae). *Zoological Publications, Victoria University College*, (15): 1-6.

GILL, T. 1862. Analytical synopsis of the Order of Squali; and revision of the nomenclature of the genera. Squalorum generum novorum descriptiones diagnosticae. *Annals of the Lyceum of Natural History of New York*, 7: 367-413.

GILL, T. 1893. Families and subfamilies of fishes. *Memoirs of the National Academy of Sciences, United States of America*, **6**(6): 125-138.

GILL, T. 1895. Notes on the synonymy of the Torpedinidae or Narcobatidae. *Proceedings of the United States National Museum*, **18**(1050): 161-165.

HASWELL, W.A. 1885. Studies on the elasmobranch skeleton. *Proceedings of the Linnaean Society of New South Wales*, **9**: 71-119.

HENLE, F. G. J. 1834. *Ueber* Narcine, *eine neue Gattung electrischer Rochen nebst einer synopsis der electrischer Rochen*. Königlichen anatomischen Museum, Berlin, 1, pp. 1-44, pls. 1-4.

HOLMGREN, N. 1941. Studies on the head in fishes. Embryological, morphological, and phylogenetical researches. Part II. Comparative anatomy of the adult selachian skull, with remarks on the dorsal fins in sharks. *Acta Zoologica*, **22**: 1-100. figs. 1-74.

HUMAN, B. A. 2006. A taxonomic revision of the catshark genus *Holohalaelurus* Fowler 1934 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae), with descriptions of two new species. *Zootaxa* (1315): 1-56, figs. 1-17, figs. 1-5, append. 1.

IUCN. 2006. International Union for the Conservation of Nature, Species Survival Commission. Red List web site at http://www.iucnredlist.org

KOORHNHOF, A. 1995. *The dive sites of South Africa. Comprehensive coverage of diving and snorkeling*. New Holland Publishers, London, Cape Town, Sydney, Singapore, 1-183.

LAST, P.R., & J.D. STEVENS. 1994. *Sharks and rays of Australia*. CSIRO, Australia, pp. i-ix, 1-513, 1400 black and white ill., color pls. 1-84.

LEIGH-SHARPE, W. H. 1922. The comparative morphology of the secondary sexual characters of Holocephali and elasmobranch fishes. Memoir IV. *Journal of Morphology* **36**: 199-220.

LEIGH-SHARPE, W. H. 1924. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir VI. *Journal of Morphology* **39**: 553-566.

LEIGH-SHARPE, W. H. 1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir VIII. *Journal of Morphology* **42**: 307-320.

LINDBERG, G. U. 1971 (1974). *Fishes of the world. A key to families and a checklist*. Pp. 1-545, fig. 1-986. Translated by Israel Program for Scientific Translations, 1974. Halsted Press, New York.

LLORIS, D. & J.A. RUCABADO. 1991. *Heteronarce rierai*, a new narkid ray from Mozambique, Western Indian Ocean. *Japanese Journal of Ichthyology*, **37**(4): 327-332, fig. 1-3.

LLOYD, R. E. 1907. Contributions to the fauna of the Arabian Sea, with descriptions of new fishes and crustacea. *Records of the Indian Museum*, **1**(1): 1-12.

LLOYD, R. E. 1909. A description of the deep sea fish caught by the R.I.M.S. Ship *Investigator* since the year 1900, with supposed evidence of mutation in *Malthopsis*. *Memoirs of the Indian Museum*, 2(3): 139-180.

MCEACHRAN, J.D., & L.J.V. COMPAGNO. 1982. Class Chondrichthyes. In S. Parker, ed. *Synopsis and classification of living organisms*. McGraw-Hill, **2**: 831-858, figs, 1113-1114.

MCEACHRAN, J.D., K.A. DUNN, & T. MIYAKE. 1996. Interrelationships of the batoid fishes (Chondrichthyes: Batoidei). *In* M.L.J. Stiassny, L.R. Parenti, & G.D. Johnson, Eds, *Interrelationships of fishes*. Academic Press, San Diego, London, 63-84, fig. 1-13.

MCKAY, R.J. 1966. Studies on western Australian sharks and rays of the families *Scyliorhinidae, Urolophidae*, and *Torpedinidae*. *Journal of the Royal Society of Western Australia*. **49**(3): 65-82.

MÜLLER, J. & F. G. J. HENLE. 1841. *Systematische Beschreibung der Plagiostomen*, (part 3) pp. 103-200. Veit, Berlin.

NELSON, J. S. 1976. Fishes of the world. Pp. i-ix, 1-416. Wiley-Interscience, New York.

NELSON, J. S. 1984. Fishes of the world, second edition. Pp. i-xv, 1-523. Wiley-Interscience, New York.

NELSON, J. S. 1994. Fishes of the world, third edition. Pp. i-xvi, 1-600. John Wiley & Sons, Inc., New York.

RASS, T. S., & G. U. LINDBERG. 1971. Modern concepts of the classification of living fishes. *Journal of Ichthyology* **11**: 302-319 (translated by the American Fisheries Society).

REGAN, C. T. 1921. New fishes from deep water off the coast of Natal. Annals and Magazine of Natural History, series 9, **7**(41): 412-420.

SHIRAI, S. 1996. Phylogenetic interrelelationships of neoselachians (Chondrichthyes, Euselachii). *In* M.L.J. Stiassny, L.R. Parenti, & G. D. Johnson, *Eds, Interrelationships of fishes*. Academic Press, San Diego, London, 9-34, fig. 1-4.

SMITH, H. M. 1912. The squaloid sharks of the Philippine Archipelago, with descriptions of new genera and species. *Proceedings of the United States National Museum*, **41**(1877): 677-685, figs. 1-4, pls. 50-54.

TALWAR, P. K. 1981. The electric rays of the genus *Heteronarce* Regan (Rajiformes; Torpedinidae), with the description of a new species. *Bulletin of the Zoological Survey of India*, **3**(3): 147-151, fig. 1.

Von Bonde, C., & D. B. Swart. 1923. The platosomia (skates and rays) collected by the S. S. "Pickle". *Union of South Africa, Fisheries Marine Biological Survey, Report (3), 1922,* special Report (5), pp. 1-22 pls. 20-23.

Wallace, J.H. 1967. The batoid fishes of the east coast of southern Africa. Part III: Skates and electric rays. *South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report* (17): 1-62, fig. 1-29.

Whitley, G. P. 1940. *The fishes of Australia. Part I. The sharks, rays, devilfish, and other primitive fishes of Australia and New Zealand.* Australian Zoology Handbook, pp. 1-280. Royal Zoological Society of New South Wales, Sydney.

Zhu Yuanding & Meng Quingwen. 1979. A study of the lateral-line canals system and that of Lorenzini ampullae and tubules of Chondrichthyes fishes of China. *Monographs of Fishes of China*, Science and Technology Press, Shanghai, i-iv, 1-132, figs. 1-71.