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Torpedo adenensis, a New Species of Electric Ray from the Gulf of Aden, with Comments on Nominal Species of *Torpedo* from the Western Indian Ocean, Arabian Sea, and Adjacent Areas (Chondrichthyes: Torpediniformes: Torpedinidae)

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ABSTRACT

A new species of electric ray of the genus *Torpedo* is described from the eastern Gulf of Aden, northwestern Indian Ocean. *Torpedo adenensis*, n. sp., is placed in the subgenus *Torpedo* due to the presence of small, knoblike papillae around its spiracles. It is distinguished from all other congeners by its unique dorsal coloration, consisting of a uniform reddish-, rusty-, or orange-brown without any distinctive spots, blotches, or reticulations. A unique combination of characters further distinguishes *T. adenensis*, including the proximity of the spiracles and eyes, the distance between the second dorsal and caudal fin, which is greater than the distance between the first and second dorsal fins, and the presence of an integumental flap in the clasper glans region. *Torpedo adenensis* is sexually mature when between 280 and 395 mm in total length, is known from specimens of both sexes, including adults and subadults, and is the only species of *Torpedo* unequivocally reported from the Gulf of Aden to date. Examination of further material, including type material, confirms that at least four other valid species of *Torpedo* occur in the western Indian Ocean, Red Sea, Arabian Sea, and adjacent gulfs: *Torpedo panthera* von Olfers, 1831, *Torpedo sinuspersici* Kämpfer in von Olfers, 1831,

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Torpedo fuscomaculata Peters, 1855, and *Torpedo suessi* Steindachner, 1898a. We have attempted to clarify the status and distribution of these species, and confirm that all four do not occur sympatrically. All four species may be distinguished on dorsal color pattern, but intraspecific variation in coloration and the proper limits of all four species remain to be precisely determined. Lectotypes are designated for *T. panthera*, *T. fuscomaculata*, and *T. suessi*. *Torpedo smithii* Günther, 1870 is confirmed as a junior synonym of *T. fuscomaculata*. *Narcacion polleni* Bleeker, 1866 is provisionally regarded as a junior synonym of *T. sinuspersici*, but it may eventually prove to be a valid species from Réunion. *Torpedo zugmayeri* Engelhardt, 1912 is either a junior synonym of *T. sinuspersici* or valid, but more material from off Pakistan needs to be examined to determine its taxonomic fate. *Torpedo suessi* has not been recorded since originally described from off Yemen in the southern Red Sea, but evidence for its possible occurrence off Sudan is presented. To serve as a reference for future studies, type material of *T. panthera*, *T. fuscomaculata*, *T. polleni*, *T. smithii*, and *T. suessi* is described and illustrated for the first time since their original descriptions. *Torpedo panthera* and *T. adenensis* share the derived presence of an integumental flap in the clasper glans region, forming a monophyletic species group.

INTRODUCTION

Electric rays are a relatively diverse group of batoids, comprising some 55 valid species in 10 genera (Bigelow and Schroeder, 1953; Carvalho, 1999). They are unquestionably monophyletic, being easily distinguished from other batoids by presenting large pectoral electric organs derived from branchial muscles, anteriorly expanded and branched antorbital cartilages, a neurocranium lacking supraorbital crests, and posteriorly arched scapulocoracoids, among other features (Compagno, 1977; McEachran et al., 1996). The species-level systematics of electric rays has been relatively neglected, as studies to date have focused more on their electrogenic potential, known since antiquity, or on the development and physiology of the electric organs per se (e.g., Mellinger et al., 1978; see references in Moller, 1995). In species with a strong electric organ discharge (*Torpedo* spp.), the shock is produced to immobilize and capture prey (Belbenoit, 1979; Bray and Hixon, 1986), and one recent study has demonstrated that for at least one species, *Torpedo californica*, this may involve an ambush strategy from the substrate during the day, coupled with a more vigorous attack in the water column at night (Lowe et al., 1994).

Species of the electric ray genus *Torpedo* Houttuyn, 1764, are medium to large electric rays (recorded to 180 cm in total length), that occur in tropical and temperate waters circumglobally from the shoreline down to about 600 m on the continental slope. Larger specimens are capable of producing strong electric shocks reported to reach a discharge of 220 volts (Coates and Cox, 1942; Bigelow and Schroeder, 1953). Two subgenera are commonly recognized within *Torpedo*: *Tetronarce* Gill, 1862 and *Torpedo* Houttuyn, 1764. *Tetronarce*, with up to 11 valid species, includes forms that are uniformly drab, dark brown, or purplish-black dorsally, lack spiracular papillae (small knob- or tentacle-like projections bordering the spiracles), usually have relatively soft and fleshy discs, and occur primarily in deep waters of the continental slope region (only occasionally being caught in shallower coastal areas) and around oceanic islands. The nine or so valid species of the subgenus *Torpedo*, on the other hand, have more ornate and colorful dorsal patterns, occur primarily in more shallow continental shelf areas, and have papillae around the spiracles (more prominent in smaller specimens). Species of *Tetronarce* appear to attain larger sizes and are also relatively more widespread than species of *Torpedo*, but this generalization is not always valid.

Torpedo and *Tetronarce* are somewhat disjunct in distribution as well. Species of *Torpedo* occur primarily in the western and northern Indian Ocean, Mediterranean Sea, and around Africa in the eastern Atlantic, but there is only one occurrence of *Torpedo* in the western Atlantic (*T. andersoni* from the Bahamas) and only one in all of the Pacific (Fowler, 1941; Herre, 1953; but this requires verification, as it probably refers to a specimen of *Tetronarce*). Species of *Tetronarce* occur in both sides of the Pacific Ocean, including isolated Pacific islands (such as Hawaii, New Caledonia, and Vanuatu), and also in both sides of the Atlantic, but there are only a few isolated records of *Tetronarce* in the Indian Ocean (see Discussion). Therefore, blurry zones of demarcation may separate species of both subgenera, albeit imprecisely, as *Tetronarce* is predominant from the western Pacific to the western Atlantic, and *Torpedo* is predominant in the Indian Ocean, whereas species of both co-occur in the eastern Atlantic.

Specimens of the subgenus *Torpedo* with a uniform reddish-brown dorsal coloration were collected in 1989 aboard the former Soviet research vessel *Stefanov* in the Gulf of Aden, off eastern Yemen. This material was deposited in the Zoological Museum of the Ukrainian Academy of Sciences (Kiev) and appeared to be distinct from *T. panthera* and *T. sinuspersici*, species that may occur in the same general area. A more thorough examination and description of these specimens, however, was only recently possible in conjunction with revisionary studies of *Torpedo* that are currently underway by the first author and colleagues. This material is described below as a new species. Presently, our understanding of species of *Torpedo* from the Red and Arabian seas, Persian Gulf, and western Indian Ocean is highly unsatisfactory, due to reasons that will be discussed herein. To serve as a guide for future studies, and because additional undescribed species of *Torpedo* from the Red Sea and western Indian Ocean may exist, we also provide information concerning the type specimens and status of nominal species of *Torpedo* from these regions. This paper is therefore only a first approximation to resolve taxonomic issues concerning species of *Torpedo* in the western Indian Ocean, Arabian Sea, and adjacent basins.

MATERIALS AND METHODS

Specimens of *Torpedo* examined for this study are deposited in the institutions listed below. Measurements and meristics taken on the type series are presented in table 1. Measurements were taken in a straight line with calipers (to the nearest 0.1 mm) or ruler (to the nearest 1 mm), and they are presented as both original data and as percentages of total length (% of TL) to facilitate comparisons. Terminology and most measurements follow the protocol of Bigelow and Schroeder (1953) for batoids and Hubbs and Ishiyama (1968) for skates; further explanation is given for the following measurements: spiracular cavity length (from anterior to posterior margin of spiracular cavity [the spiracular cavity contains the smaller spiracular opening per se]); spiracular opening length (greatest anteroposterior length of spiracular opening); orbit + spiracle length (from anterior margin of eye to posterior margin of spiracle); height of dorsal fins (from mid-base length to apex); space between second dorsal and caudal fins (from insertion of second dorsal to origin of caudal fin); caudal fin overall height (greatest height between upper and lower apexes); caudal fin upper margin length (from superior origin to apex along dorsal margin); caudal fin lower margin length (from inferior origin to apex along lower margin); tail height at pelvic fin (measured vertically at level of posterior tips of pelvics); tail height at caudal origin (measured vertically at caudal peduncle); tail width at caudal origin (measured horizontally at caudal peduncle); ventral head length (from anterior snout margin to level of last gill slits); internarial width (between inner margins of nostrils); gill slit length (from outer-lateral to inner-medial margins of first, third, and fifth gill slits); interspace between gill slits (between inner-medial margins of first and fifth gill slits); pelvic fin length (measured ventrally from anterior edge of first pelvic fin-ray joint to posterior apex of pelvic fin); pelvic fin width (greatest width across apexes of both fins measured together); clasper post cloaca length (from posterior cloaca edge to distal clasper tip); clasper length from first hemal arch (from first caudal vertebral centrum to clasper tip); snout tip to dorsal and caudal fins (from anterior disc margin to origin of dorsal and caudal fins); cloaca to dorsal fins (mid-cloaca to origin of first and second dorsal fin); cloaca to tail tip (mid-cloaca to posterior margin of caudal fin at mid-height); electric organ length (greatest anteroposterior length, measured ventrally); electric organ width (greatest width, measured ventrally just anterior to first gill slit); electric organ at first gill slit (width at level of first gill slit). Measurements are also provided for type specimens of *Torpedo panthera*, *T. fuscomaculata*, and *T. smithii*, but because these specimens are not well preserved, they are not to be interpreted as strictly as those taken on freshly preserved material. (Some measurements are more reliable than others, e.g., distances between dorsal fins or between second dorsal and caudal fin are less affected by desiccation than are disc or pelvic fin lengths or widths.)

Meristic data were taken directly from specimens (pseudobranchial folds and tooth rows) or from radiographs of the type series, and are as follows: pseudobranchial folds (at anterior wall within each spiracle); trunk vertebrae (from first distinguishable centrum posterior to synarcual to first centrum bearing a complete or closed hemal arch, which is abruptly shorter than trunk and more posterior to caudal centra in radiographs); tail vertebrae to first dorsal fin (from first centrum with complete hemal arch to origin of first dorsal fin); tail vertebrae to second dorsal fin (from first centrum with complete hemal arch to origin of second dorsal); tail vertebrae to upper caudal fin (from first centrum with complete hemal arch to origin of upper caudal lobe); tail terminal vertebrae (centra confined to caudal fin); total tail vertebrae (all centra as of first centrum with closed hemal arch); pectoral radials (radial elements of pro-, meso-, and metapterygium combined); pelvic radials (all radials in pelvic fins, first radial counted as a single element). Differences in counts between both sides of a specimen (e.g., for pectoral and pelvic radials) are due to slight discrepancy in exposure during radiography. Tooth rows in pavement pattern were counted in an anterior-posterior orientation following Stehmann (1978), and are represented as fractions (numerator: upper tooth rows; denominator: lower tooth rows).

Our use of the term ''subadult'' is equivalent to ''sexually immature or adolescent'' and refers to the developmental stage prior to being ''adult'' or ''sexually mature.'' Sexual maturity was determined in males by clasper rigidity, which generally closely precedes gonadal maturation in batoids, and therefore the capacity to reproduce. Females of electric rays are usually reproductively mature at slightly larger sizes than males.

Institutional Abbreviations

AMNH	Department of Ichthyology, Division of Vertebrate Zoology, American Museum of Natural History, New York
DBAV-UERJ	Departamento de Biologia Animal e Vegetal, Universidade do Estado do Rio de Janeiro, Rio de Janeiro
ISH	Institut für Seefischerei (presently housed in the ZMH), Hamburg
MNHN	Muséum National d'Histoire Naturelle, Paris
NHM	The Natural History Museum, London
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA	Zoologisch Museum, Universiteit van Amsterdam, Amsterdam
ZMB	Museum für Naturkunde, Humboldt University, Berlin
ZMH	Zoologisches Institut und Museum, Universitat Hamburg, Hamburg
ZMUAS	Zoological Museum of the Ukrainian Academy of Sciences, Kiev

ORDER TORPEDINIFORMES BERG, 1940

FAMILY TORPEDINIDAE BONAPARTE, 1838

General Characters (modified from McEachran and Carvalho, in press): Batoids of small to moderately large size (total length to about 180 cm, but most species less than 100 cm in total length). Body very depressed; head, trunk, and enlarged pectoral fins forming more or less circular disc, usually wider than long and extending posterior to pelvic origins. Anterior contour of disc straight, truncate, or slightly arched, snout extremely short and sometimes with a median protrusion. Eyes usually bulging; eyes and spiracles small and generally close together on top of head. Posterior margin of spiracles smooth or with papillae on posterior and lateral margins; pseudobranchial folds or lamellae present on inner anterior spiracular wall. Two endolymphatic pore openings present posterior to spiracles. Nostrils circular to slightly transverse and relatively large, closer to mouth than to snout;

anterior lobe expanded posteriorly and medially to form a continuous nasal curtain in front of mouth (except for narrow isthmus), and with smooth posterior margin. Mouth of moderate size and highly arched, flanked by longitudinal furrows but without well-developed labial cartilages; numerous monocuspid, small oral teeth in quincunx arrangement on each jaw, with flat bases and prominent cusp, roughly similar in shape and in 30–65 rows in either jaw in adult specimens. Pectoral fins very thick near margin, completely attached from sides of head to at least origin of pelvic fins. Two pectoral electric organs well developed and kidney-shaped, capable of delivering strong electric shocks and generally visible externally on either side of head. Five usually arched and small gill openings on underside of disc, and without gill rakers internally. Pelvic fins broadly rounded and not divided into anterior and posterior lobes. Tail very stout, demarcated from disc, distinctly shorter than disc length, and with cutaneous fold along lower lateral margins. Two dorsal fins, with first distinctly larger than second, and located partially or totally above pelvic fin base; dorsal fins rounded to angular in shape; caudal fin large, much larger than dorsal fins, with subtriangular to rounded apices, and with upper and lower lobes continuous around vertebral column. Skin very soft and naked, without dermal denticles or thorns.

INCLUDED GENUS: *Torpedo* Houttuyn, 1764 (family is monogeneric).

TORPEDO HOUTTUYN, 1764

TYPE SPECIES: *Raja torpedo* Linnaeus, 1758 (by tautonomy).

APOMORPHIC CHARACTERS: Derived skeletal features of the genus (and family) include paired, slender rostral extensions formed by anterodorsal outgrowths of the lamina orbitonasalis (Holmgren, 1940; Miyake et al., 1992), projecting anteriorly in a relatively straight fashion; conspicuous shape and extent of antorbital cartilages (very slender, curved, and with comblike projections extending anteriorly to support anterior disc area); first hypobranchial (basihyal?) continuous with first ceratobranchial cartilage; multiple and subdivided hypobranchial elements radiating anteriorly or anterolaterally from anterior margin of basibranchial copula.

SPECIES DIVERSITY: Of the 46–53 nominal species (the availability of 7 of these is problematical; cf. Eschmeyer [1998] and Carvalho [1999]), only 17–20 are here considered valid. At least five additional new species have been recognized and are presently being described.

Torpedo adenensis, new species

Figures 1–7, table 1

Torpedo sp.: Manilo, 1997: 11 (listed).

HOLOTYPE: ZMUAS 5121 (109204), 407 mm TL adult male, Gulf of Aden, 15°15′03″N, 52°00′04″ E, 125–140 m, R/V *Dm. Stefanov* (cruise 5, bottom trawl station no.125), 29 December 1989, collectors: S.I. Usachev and Y.G. Domaschenko (YugNIRO Kerch) (fig. 1).

PARATYPES: Four specimens: ZMUAS 5121 (109203), 397 mm TL adult male (same data as holotype) (fig. 2); ZMUAS 5418, 390 mm TL adult female, Gulf of Aden, 15°07′09″N, 51°58′02″E, 230 m depth, R/V *Dm. Stefanov* (cruise 5, bottom trawl station no. 126), 29 December 1989, collectors: S.I. Usachev and Y.G. Domaschenko (YugNIRO Kerch); AMNH 231441, 295 mm TL (subadult?) female (same data as holotype) (fig. 3a); ISH 4–1993, 277 mm TL subadult male, Gulf of Aden, 15°17′00″N, 51°34′05″E, 26–33 m, R/V *Dm. Stefanov* (cruise 5, bottom trawl station no. 120), 28 December 1989, collectors: S.I. Usachev and Y.G. Domaschenko (YugNIRO Kerch) (fig. 3b).

DIAGNOSIS: A species of *Torpedo* from the Gulf of Aden distinguished from all congeners by its unique dorsal coloration, a uniform reddish-, rusty-, or orange-brown without any distinctive spots, blotches, or reticulations. A unique combination of characters further distinguishes *Torpedo adenensis*: spiracles with few, knoblike, and somewhat inconspicuous spiracular papillae (at least in specimens sexually mature or almost mature); spiracles and eyes relatively close together (without large gap in between); base of first dorsal fin extending just posterior to level of pelvic fin axil (not entirely positioned over bases of pelvic fins); distance be-

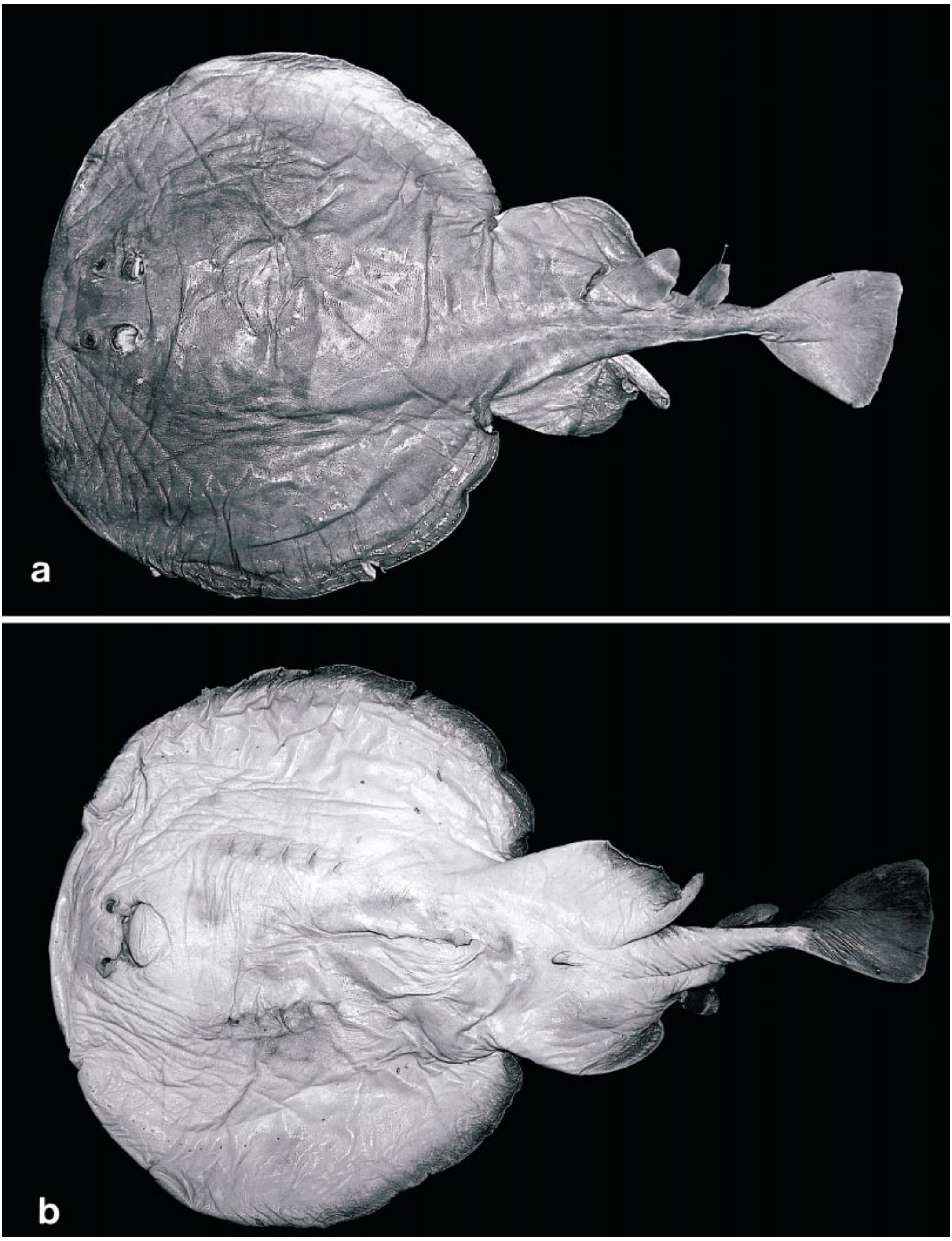

Fig. 1. Dorsal (**a**) and ventral (**b**) views of holotype of *Torpedo adenensis*, n. sp. (ZMUAS 5121 [109204], 407 mm TL adult male).

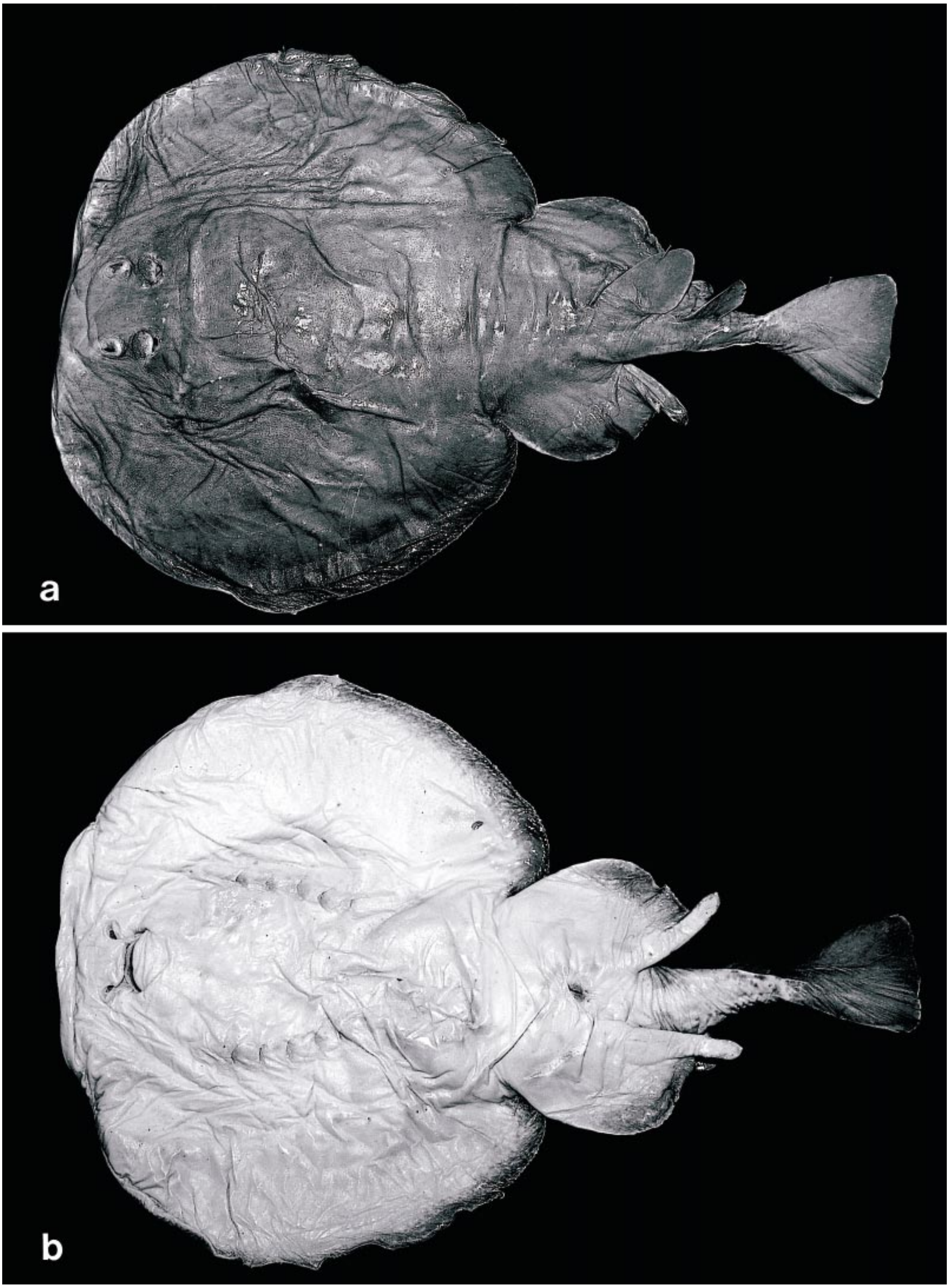

Fig. 2. Dorsal (**a**) and ventral (**b**) views of paratype of *Torpedo adenensis*, n. sp. (ZMUAS 5121 [109203], 397 mm TL adult male).

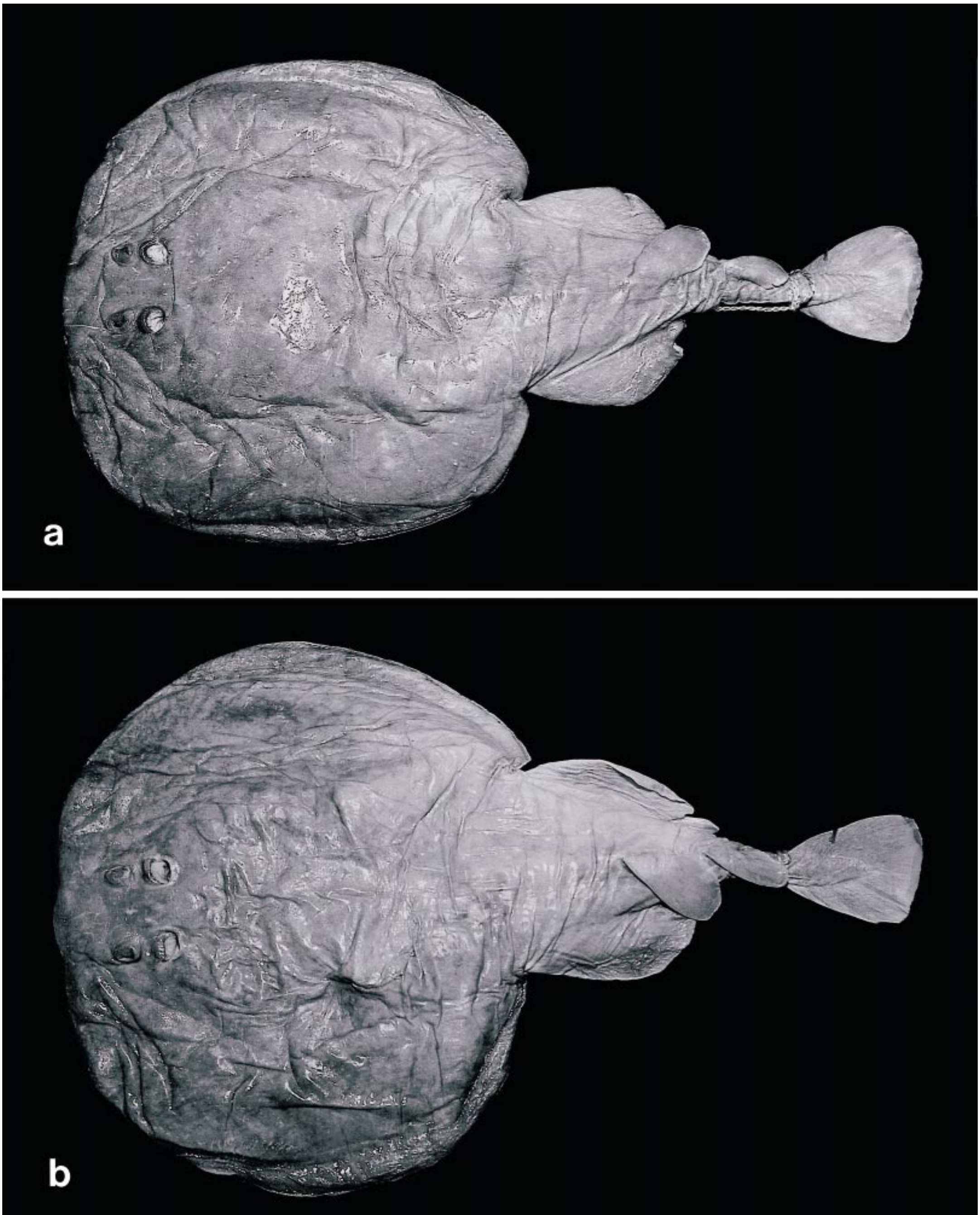

Fig. 3. Paratypes of *Torpedo adenensis*, n. sp. Dorsal views of (**a**) AMNH 231441, 295 mm TL female; (**b**) ISH 4–1993, 277 mm TL subadult male.

tween second dorsal and caudal fin greater than distance between first and second dorsal fins; claspers with fleshy integumental flap in clasper glans region.

DESCRIPTION: Measurements and counts are summarized in table 1. **External morphology**—Disc broadly rounded in outline with relatively straight anterior margin, but some specimens (e.g., ISH 4–1993) with a slight median protuberance anteriorly. Disc wider than long (disc width ranging from 58.6 to 67% of TL and disc length ranging from 52.3 to 55.9% of TL), and widest anteriorly at about one-third of its length. Disc only faintly overlaps origin of pelvic fins, not leaving a prominent free lobe posteriorly (e.g., ZMUS 5121 [109203]), but in most specimens disc does not appear to overlap pelvic fins due to slight postmortem shrinking. Preorbital snout length about one-seventh of disc length and just greater than prenasal length (ranging from 6.9 to 8.4% of TL compared to 5.5 to 6.9% of TL, respectively), and smaller than preoral snout length in all specimens. Snout anterior to orbits about equal to length of eyes and spiracles combined. Eyes moderately small, horizontal eye diameter ranging from 2.8 to 3.4% of TL, much smaller than spiracles. Eyes and spiracles relatively close together, space in between them not as great as horizontal eye diameter. Spiracles relatively large and rounded, with slightly elevated rims, especially on posterior contour. Very small, inconspicuous knoblike spiracular papillae are present around posterior margin of spiracle, sometimes only clearly seen under magnification; eight papillae in subadult male paratype (277 mm TL, ISH 4–1993), but only three in holotype (407 mm TL adult male). Papillae relatively closely spaced on inner margin of spiracle in ISH 4–1993 (fig. 4), but more sparsely grouped on spiracular outer margin. Pseudobranchial folds present inside spiracles, lining anterior spiracular wall, ranging from 8 in smaller male paratype to 12 in larger male paratype. Spiracular opening itself constricted by anterior spiracular wall in some specimens, and relatively small and crescent-shaped. Distance between eyes greater than interspiracular distance in all specimens. Electric organs without a clearly visible outline dorsally, but easily observed in ventral view. Electric organs originate very close to anterior disc contour, well anterior to eyes and nostrils, and terminate posteriorly just caudal to last gill openings. Electric organs with concave inner margins posteriorly and convex outer contours, and widest anteriorly in between mouth and first gill slit. Electric organ length about twice its width at widest point. Anterior to gill openings, electric organs inflect somewhat abruptly toward midline.

First gill slit situated at about anterior one-third of disc length; last gill slit just anterior to two-thirds of disc length. Gill slits crescent-shaped, situated lateral to level of outer corners of mouth and nostrils (more or less level with pelvic fin origin). Distance between first gill slits just slightly greater than distance between last gill slits. Third gill slit larger than others, and fifth gill slit smallest. The nasal curtain short and wide, its length just a little smaller than internarial width. Nasal curtain extends posteriorly in a more or less straight line to mouth opening. Posterior margin of nasal curtain with a slight median lobe present (median lobe may be obscured because nasal curtain distorts easily in preservative). Nostrils with prominent folds mostly surrounding outer margins (fig. 5); outer margins of nostrils situated just lateral to level of mouth corners. Posterior contour of nostrils confluent with conspicuous median lobes that contact nasal curtain at its corners and separate nostrils from mouth. Mouth arched, with a relatively large gape. Width of mouth is slightly greater than or equal to distance between nostrils. Teeth in 33/32–47/39 rows in type series (from 277 mm TL to 407 mm TL). Teeth amber in color, set in quincunx, somewhat flattened labial-lingually. Tips of individual cusps overlap bases of teeth positioned in next inner tooth row. Teeth morphologically similar among both upper and lower jaws, with well-developed single cusps, these more prominent toward central rows. Cusps slightly oriented toward lateral mouth corners on all teeth, but more prominently on teeth with longer cusps. Teeth of outermost rows with relatively wider bases and smaller cusps, but cusps also slender. Cusps of inner and middle rows tall, pointed, and somewhat sharp. Tooth bases slightly arched at center.

TABLE 1

Proportional Morphometrics and Meristics of Holotype and Four Paratypes of *Torpedo adenensis*, n. sp. (in mm and as % of total length)[a]

	ZMUAS 5121 (109204) Mature male Holotype		ZMUAS 5121 (109203) Mature male Paratype		ZMUAS 5418 Mature male Paratype		AMNH 231441 Female Paratype		ISH 4-1993 Subadult male Paratype	
	mm	%	mm	%	mm	%	mm	%	mm	%
TL	407	100	397	100	390	100	295	100	277	100
Disc										
Width	263	64.6	266	67	244	62.6	173	58.6	184	66.4
Length	213	52.3	220	55.4	218	55.9	158.5	53.7	151	54.5
Snout length										
Preorbital	28	6.9	33.3	8.4	31.1	8	20.5	6.9	20.5	7.4
Preoral	38.3	9.4	37	9.3	33.4	8.6	23	7.8	24	8.7
Prenasal	25.4	6.2	25.6	6.4	21.5	5.5	17.2	5.8	19.2	6.9
Eye diameter	12.1	3	12.7	3.2	11.2	2.9	8.2	2.8	9.4	3.4
Interorbital width	17	4.2	15	3.8	15	3.8	9	3.1	13.5	4.9
Spiracle										
Cavity length	19.3	4.7	15.7	4	16	4.1	12.8	4.3	12.6	4.5
Opening length	14.6/12.0	3.6/2.9	7.7	1.9	11.4	2.9	8.5	2.9	9.3/8.7	3.4/3.1
Interspiracular width	19.7	4.8	18.3	4.6	17.9	4.6	14.4	4.9	14.8	5.3
Orbit + spiracle length	34	8.4	31	7.8	30.2	7.7	22	7.5	23.5	8.5
D1										
Height	43.3	10.6	41.5	10.5	38.5	9.9	22.5	7.6	24	8.7
Base length	26.7	6.6	29	7.3	31.3	8	19.2	6.5	20	7.2
D2										
Height	28	6.9	23.7	6	28	7.2	16.2	5.5	18.6	6.7
Base length	18	4.4	19	4.8	19	4.9	14.5	4.9	14	5.1
Interdorsal space	16.6	4.1	13.5	3.4	11.5	2.9	11	3.7	6	2.2
Space D2 to upper C	22	5.4	21.5	5.4	19.8	5.1	16	5.4	14	5.1
C										
Overall height	66.8	16.4	62.5	15.7	54	13.8	41.5	14.1	34.7	12.5
Height upper lobe	30.8	7.6	32	8.1	29	7.4	22	7.5	17.8	6.4
Height lower lobe	34	8.4	32	8.1	26	6.7	24	8.1	16.2	5.8
Length upper margin	73.5	18.1	64	16.1	60.7	15.6	42.4	14.4	46	16.6
Length lower margin	62.7	15.4	62	15.6	57.3	14.7	45	15.3	43.5	15.7
Tail										
Postdorsal length	89	21.9	86	21.7	72.4	18.6	58	19.7	56	20.2
Height at pelvic tips	19	4.7	17.5	4.4	20	5.1	12	4.1	10	3.6
Width at pelvic tips	27	6.6	31.5	7.9	25	6.4	21	7.1	21	7.6
Height at C origin	12.3	3	12	3	13.5	3.5	8	2.7	7.7	2.8
Width at C origin	11.7	2.9	15.3	3.9	12.8	3.3	8.5	2.9	9	3.2
Lateral tail fold length	44.0/40.0	10.8/9.8	50.0/46.0	12.6/11.6	48.5	12.4	45.5	15.4	34	12.3
Head length										
Ventral	135	33.2	134.5	33.9	134.5	34.5	95	32.2	90	32.5
Dorsal	103	25.3	98	24.7	72	18.5	50.5	17.1	59.5	21.5
Mouth width	29	7.1	28.2	7.1	28.2	7.2	20.7	7	22.3	8.1
Internarial width	20.3	5	20.2	5.1	17.3	4.4	13.3	4.5	14.5	5.2
Nasal curtain length	10.5	2.6	8	2	7.2	1.8	5.3	1.8	5	1.8
Gill slit length										
1st	12	2.9	13	3.3	11	2.8	10.0/7.8	3.4/2.6	8.2	3
3rd	14	3.4	14.2	3.6	12.8	3.3	10.2	3.5	9.6	3.5
5th	8	2	8.5	2.1	9.3	2.4	7.4	2.5	5	1.8

TABLE 1
(Continued)

	ZMUAS 5121 (109204) Mature male Holotype		ZMUAS 5121 (109203) Mature male Paratype		ZMUAS 5418 Mature male Paratype		AMNH 231441 Female Paratype		ISH 4-1993 Subadult male Paratype	
	mm	%	mm	%	mm	%	mm	%	mm	%
Space betw. 1st gill slits	71	17.4	68.5	17.3	68.8	17.6	50.8	17.2	52	18.8
Space betw. 5th gill slits	57	14	53	13.4	58.7	15.1	42.5	14.4	47	17
Pelvic fin										
Length	96.0/92.0	23.6/22.6	97	24.4	93.5	24	63	21.4	57	20.6
Width	116.3	28.6	131.5	33.1	108	27.7	78	26.4	84.4	30.5
Clasper-cloaca length	65.0/66.5	16.0/16.3	66.5/71.5	16.8/18.0	0	0	0	0	41	14.8
Clasper, 1st hemal sp.	58.0/55.0	14.3/13.5	65.0/70.0	16.4/17.6	0	0	0	0	38	13.7
Snout										
To mid-cloaca	232	57	235	59.2	237.5	60.9	175	59.3	163	58.8
To D1 origin	250	61.4	251	63.2	256	65.6	193	65.4	180.5	65.2
To D2 origin	292	71.7	284	71.5	294	75.4	220	74.6	205	74
To upper C	333	81.8	324.5	81.7	327.5	84	250.5	84.9	230.5	83.2
To max. disc width	95	23.3	110	27.7	120	30.8	88	29.8	82	29.6
Mid-cloaca										
To D1	19	4.7	19	4.8	16.5	4.2	18	6.1	16	5.8
To D2	66	16.2	58.5	14.7	58	14.9	49	16.6	41.5	15
To tail end	163.5	40.2	158.5	39.9	154.5	39.6	119	40.3	111	40.1
EO										
Length	132.3	32.5	136.4	34.4	?	?	88	29.8	91	32.9
Greatest width	71.1	17.5	64.2	16.2	?	?	50	16.9	41.3	14.9
Width at first gill slit	43	10.6	45.2	11.4	?	?	33	11.2	32.1	11.6
Pseudobranchial folds (l/r)	10/10		11/12		10/11		10/10		8/8	
Trunk vertebrae	29		27				25		26	
Tail vertebrae to D1	ca. 15		ca. 14				ca. 18		14	
Tail vertebrae to D2	32		?				ca. 32		29	
Tail vertebrae to upper C	ca. 42		ca. 42		x-ray		52		42	
Tail terminal vertebrae	30		27		not available		21		29	
Total tail vertebrae	72		69				73		71	
Pectoral radials (l/r)	ca. 44/40+		ca. 43/ca. 43				?		?	
Pelvic radials (l/r)	16/16		15/15				18+/20		15/15	
Tooth rows										
Upper jaw	47		44		40		38		33	
Lower jaw	39		36		37		35		32	

[a]Both values are given if different bilateral measurements/counts exist for a specimen.

Abbreviations: TL, total length; D1, first dorsal fin; D2, second dorsal fin; C, caudal fin; EO, electric organ; (l/r), left/right side of specimen.

Pelvic fins originate just anterior to posterior disc margins. Pelvic fins long but not very wide, greatest width of pelvic fins just less than one-half of disc width, and slightly wider in male specimens. Anterior margins of pelvics relatively straight, not projecting laterally to a large degree. Posterior margins of pelvics more convex. Pelvic fins much longer than wide; pelvic fin length ranging from 20.6 to 24.4% of TL. Pelvics widest posteriorly, at about two-thirds of their length. Cloaca situated at about midlength of pelvic fins. Claspers project significantly from distal tip of pelvic fins in all male specimens, mature or subadult, reaching posteriorly to at least level of midbase of second dorsal fin. Claspers relatively slender and not tapered greatly from origin to distal tip. Clasper groove extends on dorsolateral aspect of clasper from pelvic fin to about three-

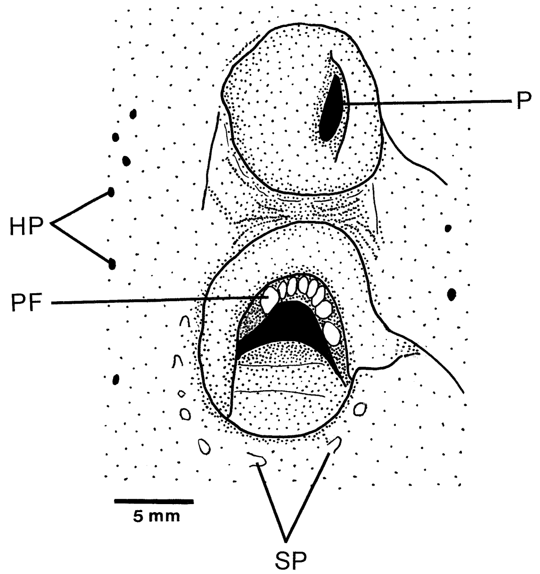

Fig. 4. Eye and spiracle of *Torpedo adenensis*, n. sp., from paratype ISH 4–1993. Abbreviations: HP, head sensory pores; P, pupil; PF, pseudobranchial folds; SP, spiracular papillae.

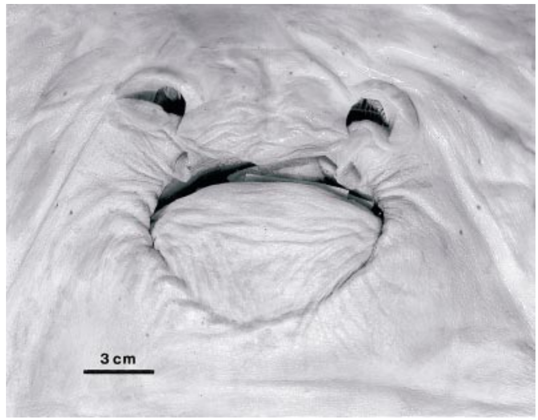

Fig. 5. Nasoral region of holotype of *Torpedo adenensis*, n. sp. (ZMUAS 5121 [109204], 407 mm TL adult male).

fourths of its length, where it curves toward the midline and continues to clasper tip. A fleshy integumental flap, bearing a distinctive notch, present close to the hypopyle (fig. 6). Both ventrolateral and dorsolateral slits (presumably the ventral pseudosiphon and dorsal pseudosiphon, respectively) present, continuing posteriorly to close to level of integumental flap.

Tail relatively short and stout, ranging from 18.6 to 21.9% of TL as measured from second dorsal fin origin, but tail length from cloaca is about 40% of TL. Tail tapers considerably from posterior tips of pelvic fins toward caudal fin. Tail oval in cross-section close to pelvic and dorsal fins, being much wider than tall almost along its entire extent, but at caudal fin origin tail more circular in cross-section. Lateral tail folds ridgelike and not very prominent in preserved specimens, extending from underneath level of anterior second dorsal fin base to end posteriorly on ventral aspect of caudal peduncle. Lateral tail-folds ranging from 9.8 to 15.4% of TL, and may vary slightly in length among both sides of the same specimen. First dorsal fin origin anterior to level of posterior axil of pelvic fins. First dorsal fin base entirely anterior to pelvic fin posterior apex, but posterior free lobe of first dorsal just posterior or at same level of posterior apex of pelvic fins (fig. 7). Posterior insertion of first dorsal fin just posterior to pelvic fin axil in all specimens, but more so in holotype and other males. First dorsal fin originates at about same level of greatest pelvic fin width. First

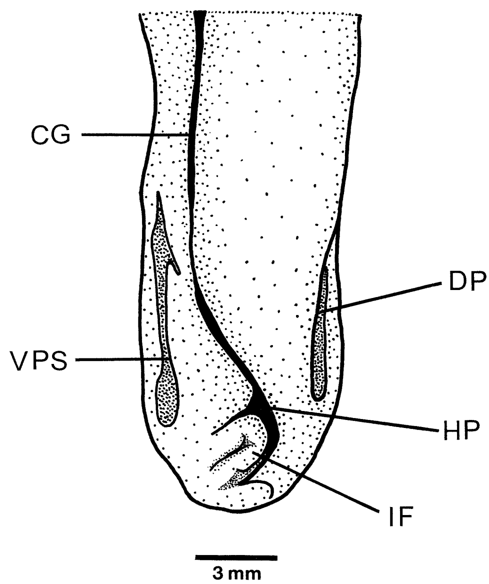

Fig. 6. Left clasper of holotype (ZMUAS 5121 [109204]) of *Torpedo adenensis*, n. sp., in dorsal view. Abbreviations: CG, clasper groove; DPS, dorsal pseudosiphon; HP, hypopyle; IF, integumental flap; VPS, ventral pseudosiphon.

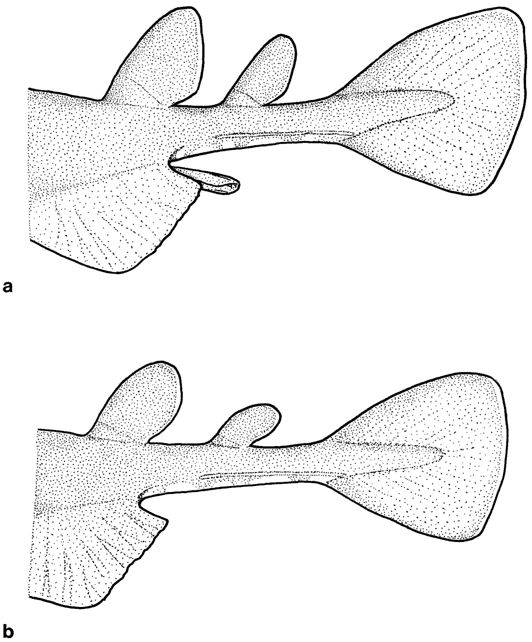

Fig. 7. Lateral tail region of *Torpedo adenensis*, n. sp. **a,** Mature male (holotype ZMUAS 5121 [109204], 407 mm TL adult male); **b,** female paratype (AMNH 231441, 295 mm TL female). Figures are not to scale.

dorsal fin moderately slanted at its anterior margin, with a posterior free lobe about equal to one-third of its base length (less so in the female paratype). First dorsal fin greater than second in both height and length of base in all specimens (first dorsal fin height ranges from 7.6 to 10.6% of TL; second dorsal fin height ranges from 5.5 to 7.2% of TL). Dorsal fins more or less similar in shape, but second dorsal fin more slanted and lower, with a more acute apex and relatively greater free lobe posteriorly in the male specimens. Female paratype (AMNH 231441, 295 mm TL) with relatively smaller dorsal fins in relation to male specimens, even smaller proportionally than smaller male paratype (ISH 4–1993, 277 mm TL). Dorsal fins of female also more broadly rounded at apex and less slanted. Distance between dorsal fins clearly smaller than distance between second dorsal and caudal fin (in ISH 4–1993, distance between dorsals less than half of distance between second dorsal and caudal). Caudal fin moderately tall, ranging from 12.5 to 17.2% of TL, and taller proportionally in larger specimens. Upper lobe of caudal fin longer than lower lobe in all male specimens, but lower lobe just longer than upper in the female paratype (AMNH 231441). Upper lobe of caudal fin slightly more sloping than lower lobe (especially in the holotype), and relatively straight from origin to apex. Posterior margin of the caudal fin more or less straight, especially in males, but it may have a small protrusion at mid-height. Both upper and lower apexes of caudal fin slightly acute and not broadly rounded (fig. 7). **Coloration**—In preservative, dorsal coloration uniform reddish-, rusty-, or orange-brown without distinctive blotches, spots, vermiculations, or reticulations. Tip of claspers dorsally slightly darker than rest of dorsal surface. Very small faint whitish spots, roughly the size of sensory pores, may be present on dorsal disc surface, unevenly scattered over outer and central disc, electric organs, and to some extent over tail region (these are more apparent on the female paratype and are perhaps preservational, as they are very faint, irregular, and inconspicuous). Posterior margin of dorsal and caudal fins with a very narrow edging of light cream color. Some specimens (e.g., ISH 4–1993) have a lighter brown dorsal color, but this may be preservational. Coloration when freshly captured not significantly different (perhaps more intense). Holotype dorsally with a small unpigmented area at center of disc (an abrasion). Ventral coloration uniform creamy-white, but disc and pelvic fins clearly have darker margins similar to dorsal color. This edging stronger on the ventral surface at lateral and posterior disc and posterior margins of pelvic fins. Ventral surface of tail irregularly blotched with rusty-brown in most specimens (slightly less in the holotype). Irregular blotches also present on ventral snout region of female paratype (AMNH 231441), and at cloaca of one male paratype (ZMUAS 5121). Pores of ampullary system highlighted with a reddish-brown pigmentation on ventral disc surface, particularly those outlining electric organs. Holotype with faint, indistinct blotches of darker color on ventral surface of mid-disc and right pelvic fin region. **Selected skeletal features**—Superficial calcification present on most skeletal elements, but more pronounced on neurocranium (except nasal capsules), synarcual cartilage, and pectoral and pelvic girdles. Neurocranium slender and somewhat hourglass-shaped, about one-third of disc length. Rostral structures not visible in radiographs. Antorbital cartilages slender and anterolaterally directed, forming a partial anterior border to electric organs. Jaws slender and highly arched; labial cartilages absent. Hyomandibulae short, devoid of rays, with very stout proximal portions that articulate with neurocranium, and taper greatly to contact outer jaw corners. Synarcual relatively long and wide, extending posteriorly to level of suprascapulae; its total length (including posterior segment with distinct centra) about equal to neurocranial length. Anteriorly, synarcual notched on either side of foramen magnum. Anterolateral margin of lateral stays sloping and concave; posterior margin more straight. About 12 spinal nerve foramina exiting from synarcual anterior to first separate vertebral centrum. Basibranchial copula large, trapezoidal, and widest just posterior to its midlength. Hypobranchials 2 and 3 radiating from anterior margin of copula obliquely, extending anteriorly underneath neurocranium. Ceratobranchial and epibranchial elements slender, but last ceratobranchial relatively large, articulating with basibranchial copula posterolaterally, and contacting scapulocoracoid posteriorly. Scapulocoracoid slender medially but stouter at corners, where it articulates with pectoral pterygia; ascending scapular processes not fused with suprascapula. Pro- and mesocondyles protrude slightly (metacondyle not visible in dorsoventral view). Propterygium stout, divided into six segments (decreasing in size distally from procondyle), and also contacting mesopterygium posteriorly. Mesopterygium small and slender, extending laterally obliquely and articulating with anteriorly situated procondyle at its midlength. Metapterygium very slender and inconspicuous, articulating with very few weakly calcified radials. Puboischiadic bar slender, with concave anterior margin and laterally projecting prepelvic processes at anterior corners. Posterior margin of girdle convex, with median indentation at level of vertebral column. At least three obturator foramina present at each anterolateral aspect of pelvic girdle, mesial to small triangular process that projects laterally from each corner. Each basipterygium about as long as half of pelvic girdle width, and with sinuous external margin for articulation with pelvic radials. First pelvic radial about twice as stout as remaining radials, and articulating distally with small additional radial element. Dorsal caudal radials more elongate than ventral caudal radials; radial elements with slight proximal thickening.

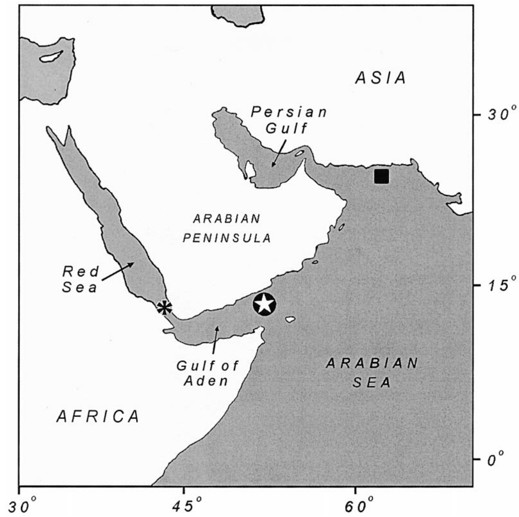

Fig. 8. Northwestern Indian Ocean, indicating approximate localities of type specimens of *Torpedo adenensis*, n. sp. (star) and *T. suessi* (asterisk), and type locality of *T. zugmayeri* (square).

ETYMOLOGY: The specific epithet *adenensis* (an adjective) is in reference to the only known locality, the Gulf of Aden. Gender masculine.

GEOGRAPHIC DISTRIBUTION: *Torpedo adenensis* has been collected from three distinct but adjacent localities from the eastern Gulf of Aden, close to the Yemen coastline, at depths ranging from 26 to 140 m (fig. 8).

COMPARISONS WITH CONGENERS AND COMMENTS ON RELEVANT NOMINAL SPECIES

The status, identification, and distribution of many species of *Torpedo* are poorly known and rather difficult, and the species occurring in the western Indian Ocean, Arabian Sea, and adjacent areas are no exceptions. The existence of poorly described nominal species in regions where the diversity of species of *Torpedo* has been underestimated—such as the basins relevant to this study—along with the lack of accurate verifiable occurrences for some species, contribute to the present state of taxonomic confusion. Also, there is significant intraspecific variation in color pattern in species with ornate coloration (e.g., *T. fuscomaculata*, *T. sinuspersici*), much of which has yet to be properly described. A similar situation exists with species of *Narcine* Henle, 1834, from around the Indian subcontinent and west Indo-Pacific region (Carvalho, 1999; Carvalho et al., 2000). Complicating the issue further is the fact that collected specimens of electric rays are commonly poorly preserved and deformed, thus affecting proportional characters sometimes used in identification, especially those of the disc and pelvic fins (Carvalho, 1999). Furthermore, some compilations do not rely on collected material but rather on inaccurate previous accounts, propagating misleading identifications or information (e.g., Sommer et al., 1996). Caution is therefore necessary in descriptions of new species of *Torpedo*.

We have compared the type series of *Torpedo adenensis* with type specimens of five of the seven nominal species of *Torpedo* from the Indian Ocean, Arabian Sea, Red Sea, and Persian (Arabian) Gulf (type locality in parentheses, comparisons and details of types provided in paragraphs to follow): *Torpedo panthera* von Olfers, 1831 (Red Sea), *Torpedo fuscomaculata* Peters, 1855 (Mozambique), *Narcacion polleni* Bleeker, 1866 (Réunion), *Torpedo smithii* Günther, 1870 (probably from South Africa), and *Torpedo suessi* Steindachner, 1898a (Red Sea). There are no extant type specimens of *Torpedo sinuspersici* Kämpfer (in von Olfers, 1831) (Persian Gulf) and probably of *Torpedo zugmayeri* Engelhardt, 1912 (Gwadar, Pakistan). Only photographs were examined of the extant syntypes of *Torpedo suessi* Steindachner, 1898a. Along with *T. adenensis*, these seven nominal species are referred to the subgenus *Torpedo* (containing species with spiracular papillae, which are more obvious during subadult stages). *Torpedo* is currently under review both regionally and globally by the first author and various colleagues.

Faunal revisions and compilations that address the western Indian Ocean, Arabian Sea, Red Sea, or Persian Gulf have commonly recognized a total of three valid species of *Torpedo* occurring in these areas: *T. panthera*, *T. sinuspersici*, and *T. fuscomaculata* (e.g., Wallace, 1967; Compagno and Randall, 1985; Compagno, 1995; Randall, 1995; Carpenter et al., 1997). To date, all three species have not been correctly reported to co-occur in any one of these regions (contrary to the claims of Bianchi, 1985; Sommer et al., 1996), but two species are occasionally sympatric along the east African coast (*T. fuscomaculata* and *T. sinuspersici*), in the Red Sea (*T. panthera* and *T. sinuspersici*), and perhaps elsewhere (*T. suessi* is also present in the Red Sea, as we report below). The correct identification, limits, and distribution of these species are problematical (and beyond the scope of this paper), but it is clear that *T. adenensis* is distinct from all of them by presenting a uniform reddish-, rusty-, or orange-brown dorsal color without any significant spots, blotches, vermiculations, or other distinctive markings. *Torpedo panthera*, *T. sinuspersici*, *T. fuscomaculata*, and *T. suessi* all present characteristic spots, ocelli, irregular blotches, and/or vermiculations dorsally. This distinction in coloration is not a function of size or sex, as specimens of roughly equal sizes and of both sexes have been compared.

Our preliminary conclusions regarding the validity and identification of *T. panthera*, *T. sinuspersici*, and *T. fuscomaculata* essentially agree with those of Fraser-Brunner (1949; however, we disagree in relation to *T. suessi*). Fraser-Brunner's partial review of the subgenus *Torpedo*, although brief, is relatively accurate. We have examined many of the same specimens he consulted in the NHM and largely agree with his identifications. However, the arrangement and number of spiracular papillae and the more posterior placement of the first dorsal fin base in relation to pelvic fin base are not consistent enough features, if used separately, to distinguish among species of the subgenus as he advocated. Bigelow and Schroeder (1953) relied heavily on Fraser-Brunner's (1949) characters to compose their own account, and many subsequent authors have followed suit (e.g., Bianchi, 1985). These characters are in need of further verification, as they have either been inaccurately described by previous authors or they are variable within species according to specimens we have examined (Wallace, 1967, also reported on the variability of spiracular papillae for *T. sinuspersici*). There is abundant material of *Torpedo* in collections from the western Indian Ocean (including the Seychelles, Mauritius, Réunion, and the Comoros), Red Sea, and India (but not from the Gulf of Aden), and the examination of this material, presently ongoing, will hopefully clarify the proper limits of *T. panthera*, *T. sinuspersici*, and *T. fuscomaculata*. Below we present further information on these species, focusing on their coloration and type specimens when available, and provide additional distinctions from *T. adenensis*.

Torpedo panthera

Figures 9, 10a, table 2

Torpedo panthera von Olfers, 1831: 15 (original description, as ''Var. γ'' of *T. marmorata* Risso, 1810, based on several specimens [number not precisely known], not figured; lectotype [herein designated]: ZMB 4560, adult male 281 mm TL; Red Sea; collected by Hemprich and Ehrenberg).

The remaining syntype of *T. panthera* (lectotype) is in relatively good condition (ZMB 4560; fig. 9), as it is not significantly desiccated (measurements in table 2). However, no trace of its original coloration remains, which was described by von Olfers (1831: 15) as darker brown with small whitish spots (''dunkler braun mit wenigen weisslichen Flecken''; darker presumably in reference to *T. marmorata*). ZMB 4560 was identified as the sole remaining syntype by Paepke and Schmidt (1988: 172; but not by Klausewitz, 1960), and it presumably was the only specimen available only a decade later to Müller and Henle (1841: 193). The lectotype is roughly equal in total length to one of the paratypes of *T. adenensis* (ISH 4–1993), allowing for a detailed comparison. It contains within its viscera an undigested teleost, ingested head-first, which is about one-third of its total length.

We have examined specimens of *T. panthera* from the northern Red Sea (Egypt; fig. 10a), and reliable literature records confirm its presence in the southern Red Sea (Rüppel, 1835) and Gulf of Oman (Randall, 1995). Annandale (1909) recorded a specimen of *Torpedo* (misidentified as *T. marmorata*) from Puri (off eastern India, in the Bay of Bengal) that is very similar in coloration to *T. panthera* (see his photograph on plate 5, fig. 3), thus greatly increasing its range if confirmed. Bianchi (1985) cited this species from Pakistan, but perhaps not based on hard evidence, even though it probably does occur there. *Torpedo panthera* apparently does not extend farther south than the Red Sea along the east African coast (contrary to Sommer et al., 1996), and it has not been recorded from the Gulf of Aden even though it probably occurs there as well. Further reliable Red Sea references include Klunzinger (1871), Bamber (1915), Gohar and Mazhar (1964), Dor (1984), Baranes and Golani (1993), and Field and Field (1998), but not Fowler (1956, both species mentioned may be *T. sinuspersici*). Fowler's (1934) mention of this species from South Africa is also a misidentification. The accounts of Blegvad (1944) and Kuronuma and Abe (1986) of *T. panthera* from the Persian Gulf are based on misidentifications (see below). Carpenter et al. (1997) also record *T. panthera* from the Persian Gulf, but whether this is compiled or based on specimens is not clear.

Specimens of *T. panthera* from throughout its confirmed range present small clusters of more or less isolated, and sometimes blurry, whitish spots over the disc, pelvic fins, and tail, contrasting with the more uniform coloration of *T. adenensis*. There is some variation in the amount, size, and arrangement of spots in different specimens of *T. panthera*, but whether this variation is significant systematically is unknown (Rüppell's stylized depiction of *T. panthera* from the Red Sea is similar to Annadale's specimen from the Bay of Bengal). The very small (sensory pore-sized), faint lighter markings irregularly present in the female paratype of *T. adenensis* (which may be preservational) are very distinct from the much larger and conspicuous spots of *T. panthera,* which are constantly present and much larger than sensory pore

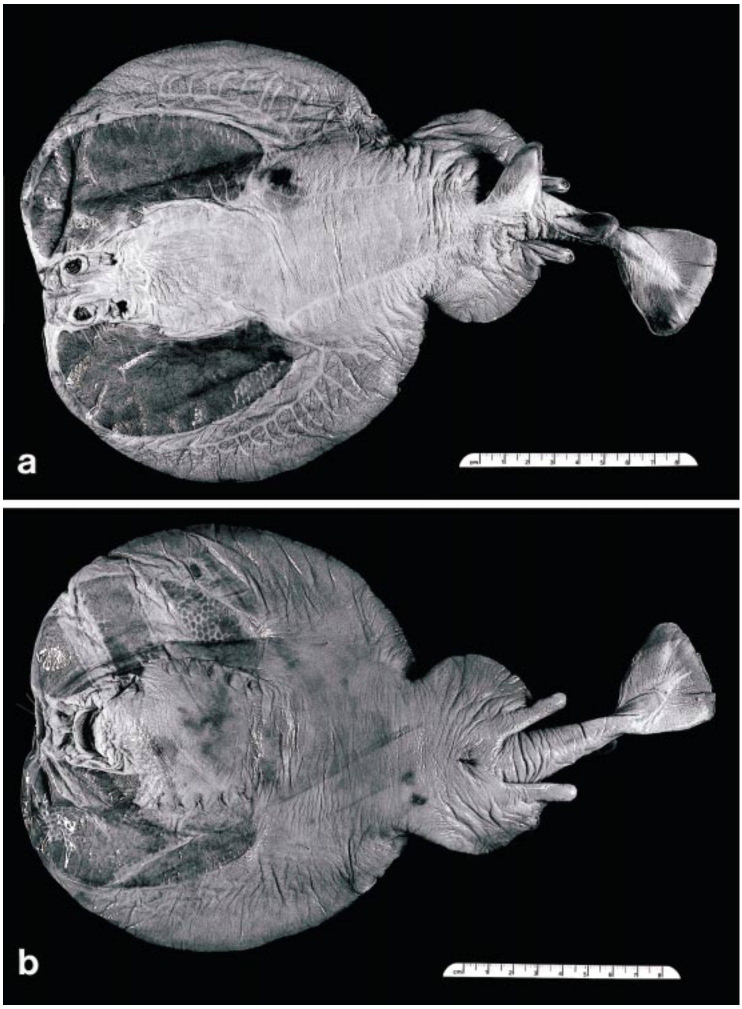

Fig. 9. Dorsal (**a**) and ventral (**b**) views of lectotype of *Torpedo panthera* von Olfers, 1831 (ZMB 4560, 281 mm TL adult male). Note that caudal fin is pointing downward in **a.**

diameter (may be as large as eye diameter) (fig. 10a). *Torpedo adenensis* can be further distinguished from *T. panthera* by having the distance between the second dorsal and caudal fin markedly greater than interdorsal distance. In *T. panthera*, the interdorsal distance is roughly equal to the distance between the second dorsal and caudal fin (according to all reliable accounts and specimens examined, including the lectotype). Compared to *T. panthera*, *T. adenensis* has spiracles relatively closer together, less pronounced spiracular papillae (comparing individuals of roughly equal dimensions; specimens of *T. panthera* also commonly have a more pronounced postero-central papilla), and a straighter posterior caudal fin margin (in many specimens of *T. panthera* the posterior margin is more curved). *Torpedo adenensis* also has more tail vertebrae (and hence total vertebrae) than does *T. panthera* (tables 1, 2). The lectotype of *T. panthera* has 61 tail vertebrae (and 86 total vertebrae), compared to the AMNH and ISH paratypes of *T. adenensis* (which are roughly the same size as the lectotype of *T. panthera*), which have, respectively, 73 (98 total) and 71 (97 total) vertebrae (however, more specimens of *T. panthera* need to be compared). Both species are similar in external clasper structure, presenting a unique me-

TABLE 2

Proportional Measurements (in mm and as % of total length) for Lectotype of *T. panthera*, Lectotype and Paralectotype of *T. fuscomaculata*, and Holotype of *T. smithii*

	T. panthera ZMB 4560 Lectotype Mature male		*T. fuscomaculata* ZMB 4573 Lectotype ?Mature male		*T. fuscomaculata* ZMB 4573 Paralectotype Subadult male		*T. smithii* NHM1852.8.12.46 Holotype Mature female	
	mm	%	mm	%	mm	%	mm	%
TL	281.0	100	223.0	100	126.0	100	365.0	100
Disc								
Width	183.0	65.1	117.0	52.5	74.0	58.7	172.0	47.1
Length	166.0	59.1	122.0	54.7	71.0	56.3	151.0	41.4
Snout length								
Preorbital	19.2	6.8	18.2	8.2	—[a]	—	30.0	8.3
Preoral	21.0	7.5	22.1	9.9	—	—	34.1	9.3
Prenasal	15.4	5.5	14.3	6.4	—	—	22.3	6.1
Eye diameter	6.3	2.2	4.1	1.8	—	—	4.5	1.2
Interorbital width	14.3	5.1	16.5	7.4	—	—	22.3	6.1
Spiracle								
Cavity length	7.2	2.6	6.4	2.9	—	—	8.0	2.2
Opening length	5.1	1.8	5.2	2.3	—	—	7.0	1.9
Interspiracular width	14.3	5.1	12.7	5.7	—	—	16.2	4.4
Orbit + spiracle length	22.0	2.6	17.4	7.8	—	—	18.1	5.0
D1								
Height	29.1	10.4	21.1	9.5	—	—	33.3	9.1
Base length	19.2	6.8	16.3	7.3	—	—	26.1	7.2
D2								
Height	19.1	6.8	16.1	7.2	—	—	26.4	7.2
Base length	13.4	4.8	12.0	5.4	—	—	16.2	4.4
Interdorsal space	15.4	5.5	11.2	5.0	7.1	5.6	19.1	5.2
Space D2 to upper C	14.0	5.0	14.5	6.5	7.3	5.8	25.3	6.9
C								
Overall height	42.1	15.0	30.2	13.5	—	—	45.2	12.4
Height upper lobe	20.1	7.2	13.2	5.9	—	—	22.3	6.1
Height lower lobe	21.2	7.5	14.1	6.3	—	—	21.7	5.9
Length upper margin	45.2	16.1	33.1	14.8	—	—	—	—
Length lower margin	36.1	12.8	31.2	13.9	—	—	—	—
Tail								
Postdorsal length	55.6	19.8	46.0	20.6	—	—	—	—
Height at pelvic tips	16.4	5.8	16.2	7.3	—	—	—	—
Width at pelvic tips	25.7	9.1	15.1	6.8	—	—	—	—
Height at C origin	10.2	3.6	9.2	4.2	—	—	—	—
Width at C origin	6.1	2.8	7.3	3.3	—	—	—	—
Lateral tail fold length	25.3	9.0	—	—	—	—	—	—
Head length								
Ventral	102.0	36.3	80.0	35.9	—	—	—	—
Dorsal	58.0	20.6	43.0	19.3	—	—	—	—
Mouth width	21.1	7.5	19.1	8.6	—	—	26.0	7.1
Internarial width	14.3	5.1	8.2	3.7	—	—	14.2	3.9
Nasal curtain length	7.3	2.6	—	—	—	—	7.1	1.9

TABLE 2
(Continued)

	T. panthera ZMB 4560 Lectotype Mature male		*T. fuscomaculata* ZMB 4573 Lectotype ?Mature male		*T. fuscomaculata* ZMB 4573 Paralectotype Subadult male		*T. smithii* NHM1852.8.12.46 Holotype Mature female	
	mm	%	mm	%	mm	%	mm	%
Gill slit length								
1st	7.2	2.6	—	—	—	—	—	—
3rd	9.1	3.1	—	—	—	—	—	—
5th	5.6	2.0	—	—	—	—	—	—
Space betw. 1st gill slits	47.2	16.8	23.1	10.4	—	—	53.0	14.5
Space betw. 5th gill slits	38.1	13.6	—	—	—	—	50.0	13.7
Pelvic fin								
Length	58.0	20.6	38.0	17.0	—	—	86.0	23.6
Width	97.0	34.5	46.0	20.6	—	—	125.0	34.2
Clasper—cloaca length	43.2	15.4	37.3	16.7	—	—	—	—
Clasper from 1st hemal sp.	—	—	—	—	—	—	—	—
Snout								
To mid-cloaca	177.0	63.0	127.0	57.0	—	—	235.0[b]	64.4
To D1 origin	182.0	64.8	130.0	58.3	—	—	242.0	66.3
To D2 origin	215.0	76.5	161.0	72.2	—	—	—	—
To upper C	238.0	84.7	182.0	81.6	—	—	—	—
To max. disc width	75.0	26.7	—	—	—	—	81.0	22.2
Mid-cloaca								
To D1	—	—	—	—	—	—	—	—
To D2	—	—	—	—	—	—	—	—
To tail end	107.0	38.1	86.0	38.6	—	—	128.0[b]	35.1
EO								
Length	92.0	32.7	78.0	35.0	—	—	121.0	33.2
Greatest width		17.8	35.0	15.7	—	—	—	—
Width at first gill slit	35.0	12.5	26.0	11.7	—	—	43.0	11.8
Pseudobranchial folds (l/r)	—		—		—		—	
Trunk vertebrae	25		25		24		x-ray not available	
Tail vertebrae to D1	9		12		11			
Tail vertebrae to D2	25		27		29			
Tail vertebrae to upper C	40		46		44			
Tail terminal vertebrae	21		17		18			
Total tail vertebrae	61		63		62			
Pectoral radials (l/r)	43		36		39			
Pelvic radials (l/r)	15		14		14			
Tooth rows								
Upper jaw	—		—		—		54	
Lower jaw	—		—		—		—	

[a]Dashes indicate parameter not available or measurements/counts not taken.
[b]Parameter is an approximation.
Abbreviations: TL, total length; D1, first dorsal fin; D2, second dorsal fin; C, caudal fin; EO, electric organ; (l/r), left/right of specimen.

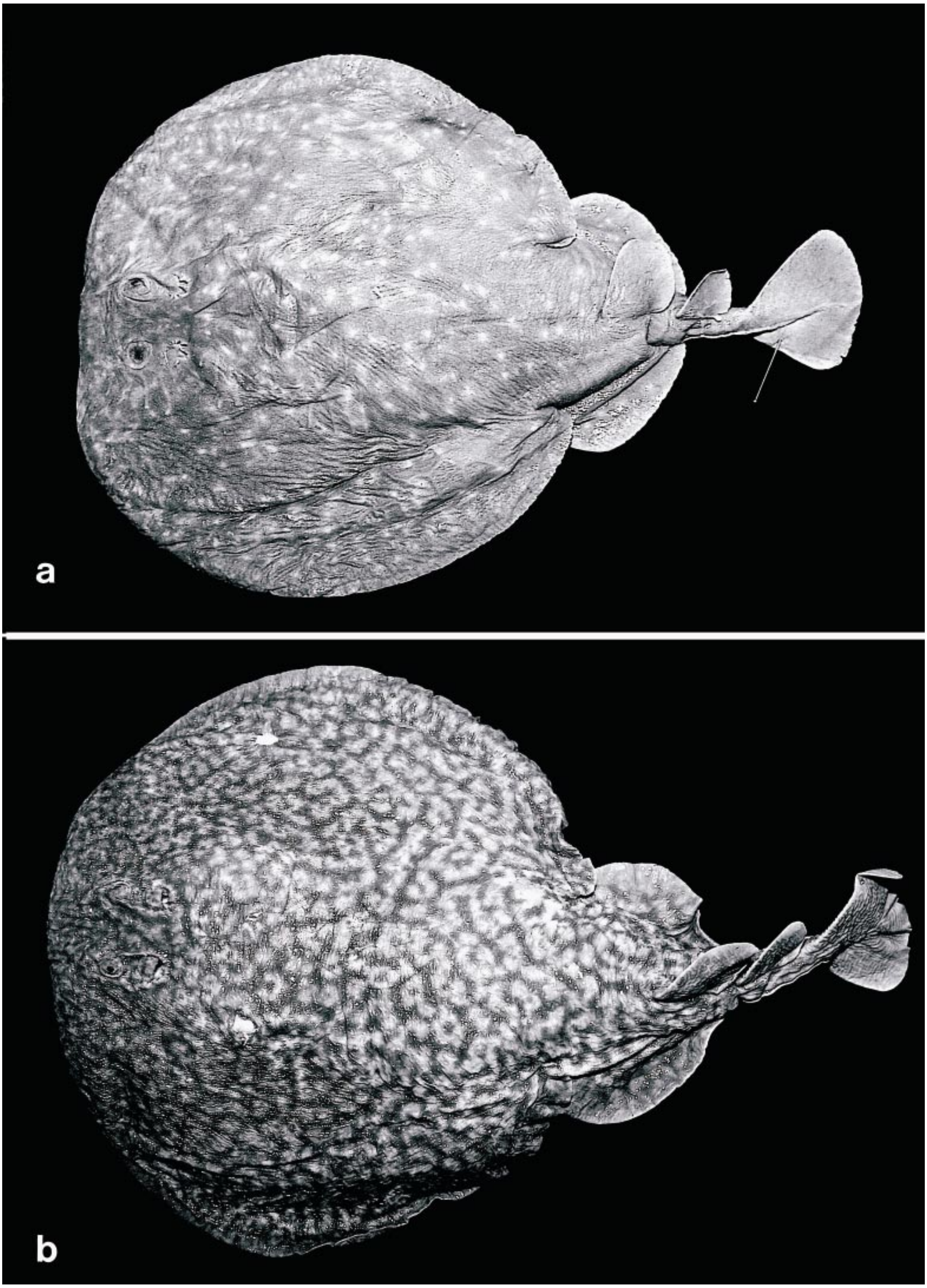

Fig. 10. **a,** Dorsal view of *Torpedo panthera* (USNM 222524, 193 mm TL female) from Egypt; **b,** dorsal view of *Torpedo sinuspersici* (USNM 222527, 300 mm TL adult male) from off Iran, Persian Gulf (type locality of species).

dian integumental flap in the clasper glans region, interpreted as a derived feature supporting their monophyly as a species pair (fig. 6). Judging from the lectotype, *T. panthera* reaches sexual maturity at least before 281 mm TL as its claspers are fully calcified, and therefore probably at a smaller size than *T. adenensis* (paratype ISH 4–1993 is a subadult male at 277 mm TL; this species matures sexually between 280 and 395 mm TL). This may constitute further evidence distinguishing both species.

Torpedo sinuspersici

Figure 10b

Torpedo sinus Persici Kämpfer in von Olfers, 1831: 15 (original description, as ''Var. ϵ'' of *T. marmorata* Risso, 1810, credit given to pre-Linnean work by Kämpfer, dated 1712 in von Olfers, 1831; no specimens mentioned or figured, type locality: Persian Gulf [''Persischer Meerbusen'']).

Torpedo sinuspersici was originally used by von Olfers (1831) as a variation of *T. marmorata* (as was *T. panthera*), a variation that also included ''*Raja maculata*'' and ''*R. bicolor*'' of Shaw (1804) (both names are referred to *Narcine*; Carvalho, 1999), as von Olfers (1831) erroneously regarded these nominal species as synonymous. The brief original description of *T. sinuspersici* only mentions the presence of two dorsal fins and a white- and dark brown-spotted dorsal coloration pattern as diagnostic characters (von Olfers, 1831: 17, citing and translating Kämpfer's original Latin diagnosis). No type specimen exists, and designating a neotype is premature at present.

According to published accounts and material examined, this species appears to be the most widespread of the four previously described western Indian Ocean forms, with a reported range extending to South Africa (Wallace, 1967; van der Elst, 1993; Compagno, 1995), Somalia (Sommer et al., 1996), the Red Sea (e.g. Compagno and Randall, 1985), the Arabian Sea (Bianchi, 1985; Qureshi, 1972), the Gulf of Oman (Debelius, 1993, 1999; Randall, 1995), the Persian Gulf (Carpenter et al., 1997), Sri Lanka, and the Andaman Sea (Kuiter and Debelius, 1997). Specimens or more reliable records of *T. sinuspersici* are still required from the northern Arabian and Andaman seas (we have not examined material from the Red Sea either, even though it is commonly reported from there). Fourmanoir (1963) may have misidentified *T. sinuspersici* as *T. fuscomaculata* from Madagascar, and Smith and Smith's (1963) *T. fuscomaculata* from the Seychelles may also include *T. sinuspersici* or another similar form. Jones and Kumaran (1980) illustrated a specimen from the Laccadive Islands, misidentified as *T. marmorata*, that is probably this species as well. Other misidentifications of *T. sinuspersici* as *T. marmorata* in the literature of the western Indian Ocean include Günther (1870), von Bonde and Swart (1923), Smith (1961), Qureshi (1972) and perhaps Prashad (1920). We have examined material of *T. sinuspersici* from Sri Lanka and the Persian Gulf (Iran).

Dorsal coloration appears to be the most secure means of identifying *T. sinuspersici* (Compagno et al., 1989; Compagno, 1995), even though it may be somewhat variable, and also easily distinguishes it from *T. adenensis* with which it may co-occur in the Gulf of Aden (although no records or material of *T. sinuspersici* in the Gulf of Aden were found). In the Persian Gulf (type locality), its coloration is composed of strong cream or whitish and rather thick vermiculations over disc, pelvic fins, and tail, with many cream-colored and irregular spots, no larger than eye diameter, on anterior and lateral disc regions (fig. 10b). These vermiculations may be formed from fused irregular spots. A specimen from South Africa, of undetermined size, has cream-colored brain-shaped figures or rosettes over disc and tail, decreasing in size toward disc margins, along with numerous small spots laterally on disc and the anterior snout region (van der Elst, 1993). Compagno et al. (1989) and Compagno (1995) illustrated roughly the same arrangement (based on a specimen from Natal), but with more closely packed brain-shaped figures and rosettes, approaching the pattern of specimens from the Persian Gulf and Sri Lanka (see also illustration in Wallace, 1967: fig. 27). Field and Field (1998) depicted a specimen identified as *T. sinuspersici* from the northern Red Sea that varies considerably from the typical pattern, resembling *T. marmorata* from the Mediterranean more than

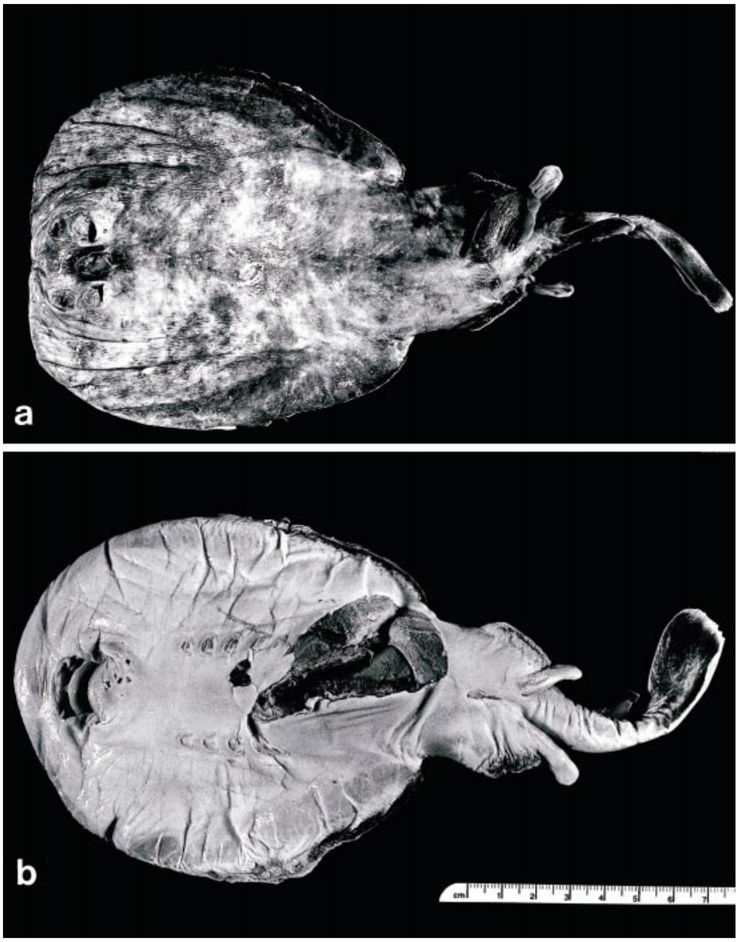

Fig. 11. Dorsal (**a**) and ventral (**b**) views of lectotype (ZMB 4573, 223 mm TL subadult male) of *Torpedo fuscomaculata* Peters, 1855 (from Mozambique).

typical *T. sinuspersici* (if confirmed, this would indicate that the former species probably dispersed through the Suez Canal). Specimens from the full distribution of *T. sinuspersici* need to be compared in detail to determine if it can be subdivided into more than one species.

Torpedo fuscomaculata

Figures 11–13, table 2

Torpedo fuscomaculata Peters, 1855: 278 (original description, not illustrated, based on two syntypes; lectotype [herein designated]: ZMB 4573, 223 mm TL subadult or adult male; paralectotype: ZMB 4573, 126 mm TL subadult male; Mozambique, Angoxe [= Angoche]).

Torpedo smithii Günther, 1870: 451 (original description, not illustrated; holotype: NHM 1852.8.12.46, 365 mm TL adult female; probably South Africa; A. Smith).

Peters (1855) described the original coloration of *T. fuscomaculata* as having a yellowish- to reddish-brown background with closely packed brownish-black spots and brownish-black dorsal fins with a white periphery. The type specimens are slightly distinct in coloration (cf. figs. 11 and 12), as the smaller paralectotype is more markedly spotted and less faded, but both specimens retain details of their original color. The lectotype has faded dark brown blotches over dorsal disc, pelvic fins, dorsal and caudal fins, and tail, and is probably late subadult or adult, as

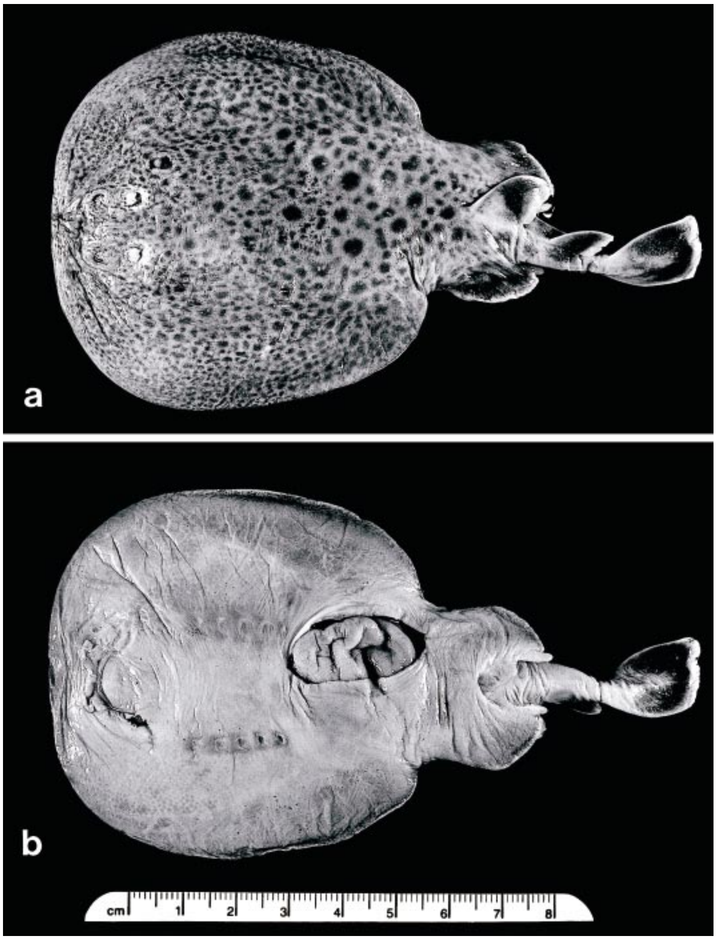

Fig. 12. Dorsal (**a**) and ventral (**b**) views of paralectotype (ZMB 4573, 126 mm TL subadult male) of *Torpedo fuscomaculata* Peters, 1855 (from Mozambique).

the clasper is somewhat rigid with calcified terminal cartilages. Accurate measurements could not be made on the ventral surface of the lectotype, and the disc and pelvic fins are distorted (our measurement of TL is more or less equivalent to that of Peters at 223 mm, but other measurements cannot be directly compared). The paralectotype is about one-half the length of the lectotype, and it was not measured (table 2). Its coloration is composed of numerous spots that become progressively smaller toward disc margins (much smaller than eye diameter), with larger spots (larger than spiracles) over posterior mid-disc area. The distance between the second dorsal and caudal fin is greater than the distance between both dorsal fins in the lectotype (this is also reported for 13 specimens from South Africa by Wallace, 1967), but these dimensions are about equivalent in the paralectotype. This is in contrast to the assertion by Fraser-Brunner (1949; repeated by Bigelow and Schroeder, 1953; Sommer et al., 1996), who used the greater distance between the first and second dorsal fins to separate this species from *T. sinuspersici*. The first dorsal fin base appears to be entirely above the pelvic fin base. The lateral tail fold of the lectotype is ridgelike, extending from about midlength of the second dorsal fin base to the lower caudal peduncle. The clasper does not have the integumental flap in the clasper glans region as in *T. adenensis* and *T. panthera*. Specimens of *T. fuscomaculata* are easily separated from *T. adenensis* on the basis of coloration, but size at maturity may provide another distinction if the lectotype of *T. fuscomaculata* (223 mm TL) is either adult or close to adult, and if sexual maturation closely follows clasper rigidity.

The differences in coloration in both original syntypes may be because of their distinct sizes, but a complete ontogenetic series of *T. fuscomaculata* from Mozambique still needs to be studied. Alternatively, both specimens may represent distinct color morphs of this species. Variation in coloration has been previously reported by many authors, such as Playfair and Günther (1866) from Zanzibar, and Wallace (1967) and Compagno et al. (1989; also Compagno,1995) from South Africa. The variation in coloration of *T. fuscomaculata* is confined not only to number, size, and disposition of the darker spots, but also to whether they are present at all, because some examined specimens from South Africa, roughly the same size of the paralectotype, have a uniform dark grayish- or blackish-brown dorsal coloration without any spots. Other specimens are reported to have gray flecks along with darker spots, or even a gray background color (e.g., Smith, 1961; Compagno, 1995). As in *T. sinuspersici*, this variation still awaits a more thorough documentation. A lectotype is chosen for *T. fuscomaculata* so as to avoid taxonomic confusion in case its type series is shown to be heterogeneous.

The holotype of *Torpedo smithii* Günther, 1870 (fig. 13) agrees with the lectotype of *T. fuscomaculata* in coloration (even though faded), being dark brown with darker brownish-black irregular spots, about the same size as the spiracles, over the disc. The specimen has a shrunken disc and pelvic fins and dried dorsal fins. As in the lectotpye of *T. fuscomaculata*, the distance between the second dorsal and caudal fin is greater than the distance between both dorsal fins (also as in *T. adenensis*). The eyes are deeply embedded and set apart from the spiracles by a small gap, and the central posterior spiracular papilla is larger than the remaining inconspicuous papillae, similar to the holotype of *T. panthera*. There are some 50–54 upper tooth rows, and teeth are very sharp with pointed cusps and relatively wide bases. The lateral tail folds remain as slight ridges, similar in extension to *T. fuscomaculata*. The second dorsal fin is smaller and more slanted than the first dorsal fin. There is no reason to consider *T. smithii* a separate species distinct from *T. fuscomaculata*, as previous authors have suggested (e.g., Fraser-Brunner, 1949; Compagno, 1995).

Torpedo fuscomaculata appears to be more restricted geographically than *T. sinuspersici*, being distributed in the western Indian Ocean from South Africa (Wallace, 1967; Compagno et al., 1989; Compagno, 1995) to Zanzibar (Playfair and Günther, 1866) and perhaps as far north as the Kenyan coast (Sommer et al. [1996] reported it as possibly occurring off Somalia, but more definite records do not exist). It has also been recorded from Madagascar (as *Torpedo* sp.; Fourmanoir, 1963), Seychelles (perhaps only in part; Smith and Smith, 1963), and Mauritius (Fraser-Brunner, 1949). We have examined material from Mauritius (Agalega Islands), South Africa, and Mozambique, but specimens from Mauritius may in fact be distinct, as they have a lighter background color with smaller and more regularly displayed spots.

Torpedo suessi

Figures 14, 15

Torpedo suessi Steindachner, 1898a: 199 (original description, not figured, based on three syntypes further specified in Steindachner, 1898b; lectotype [herein designated]: NMW 88240, adult female, 291 mm TL; paralectotype: NMW 78016, adult male, 232 mm TL; Red Sea at Mocca [= Mocha], Yemen; fig. 8).

Torpedo suessi was described by Steindachner (1898a) in an abstract preceding his more detailed account of it (Steindachner, 1898b). Two of his three original specimens remain in Vienna and are depicted in figures 14 and 15. *Torpedo adenensis* is distinct from *T. suessi* in coloration, described originally as having a bright brown background with eight large, deep brown spots with lighter outlines (ocelli), with slender reticulations over the disc and disc edges, and with smaller dark spots on the anterior disc region, pelvic fins (in the female syntype, an anterior pelvic spot merges with a larger ocellus from the disc), and dorsal fin bases (Steindachner,

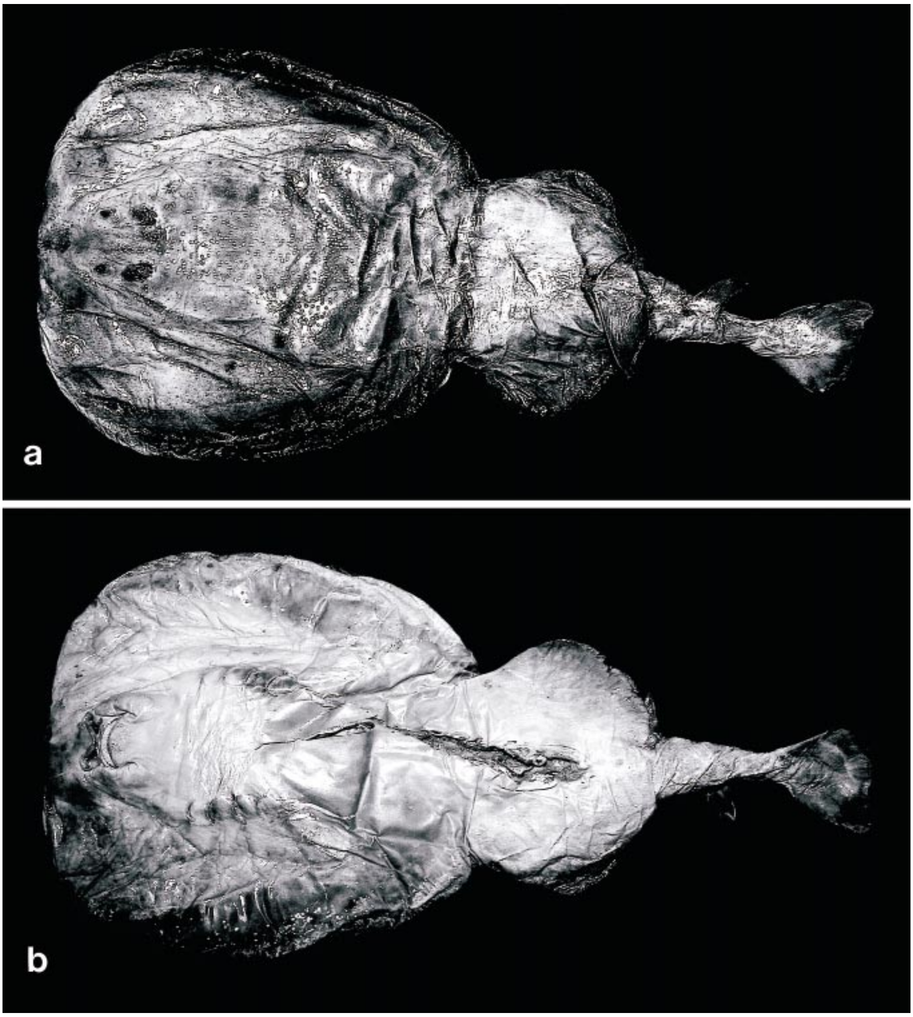

Fig. 13. Dorsal (**a**) and ventral (**b**) views of holotype of *Torpedo smithii* Günther, 1870 (NHM 1852.8.12.46, 365 mm TL adult female), probably from South Africa.

1989b: 786). Even though slightly faded, the striking original coloration of *T. suessi* is still present in the type specimens (figs. 14, 15), easily separating it from congeners from the western Indian Ocean, the Red Sea, and adjacent gulfs. Steindachner's original plate (taf. II) appears to be of the lectotype (there are no signs of claspers in the illustration), but it may also be a composite (the ocelli are not in strict accord with any of the two remaining types) or the missing original syntype (a 130 mm TL male specimen). The lectotype of *T. suessi* (originally reported to be 300 mm TL) can be directly compared to the AMNH and ISH paratypes of *T. adenensis*, as they are similar in TL, confirming that their distinction in coloration is not dependent on size. The paralectotype of *T. suessi* has elongated claspers devoid of the integumental flap present in both *T. adenensis* and *T. panthera*.

Torpedo suessi has been considered a junior synonym of *T. sinuspersici* by almost all previous authors, following Fraser-Brunner (1949; e.g., Bigelow and Schroeder, 1953; Dor, 1984), but those authors did not examine the type specimens or provide other justification. Garman (1913) considered *T. sues-*

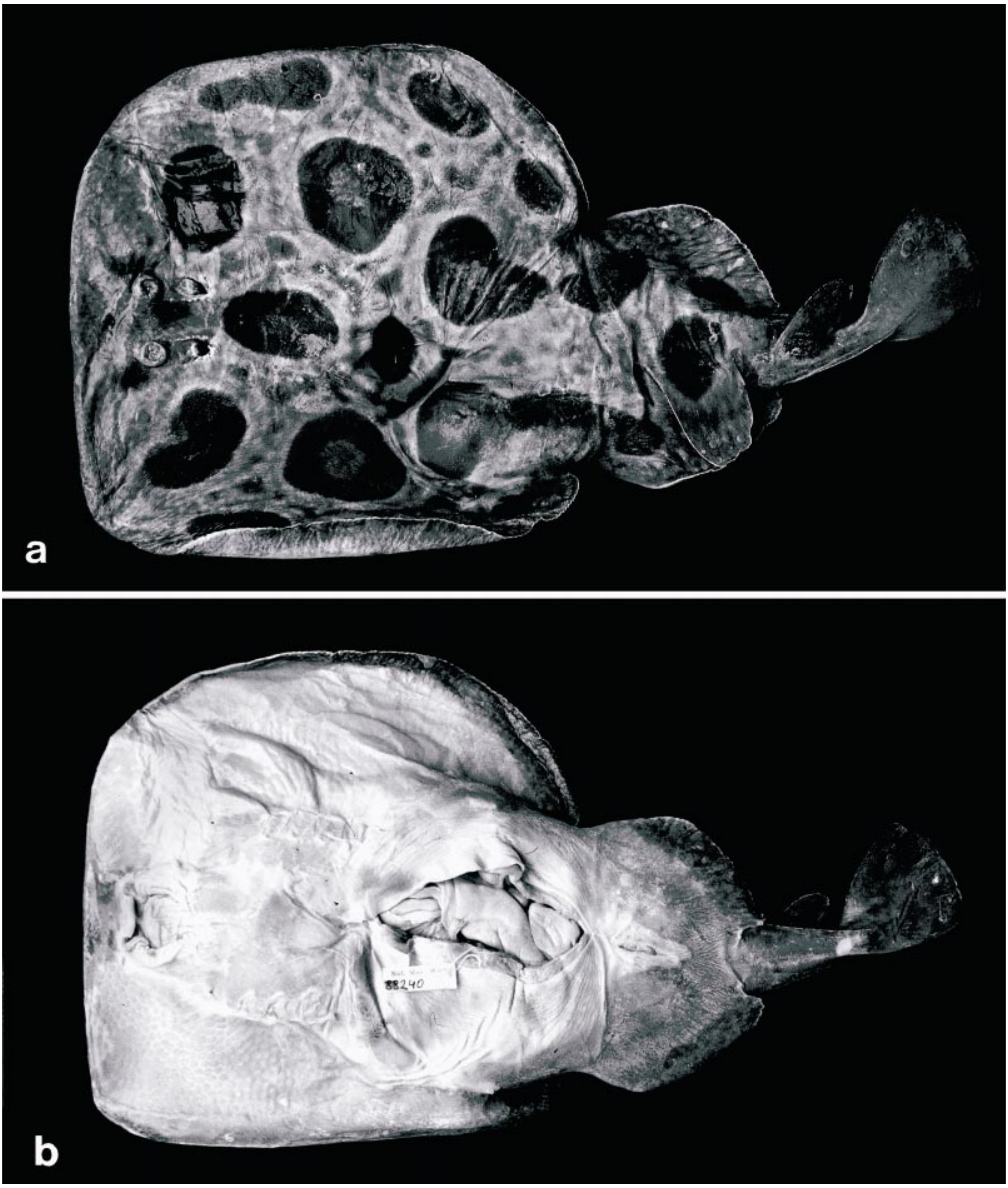

Fig. 14. Lectotype of *Torpedo suessi* Stendachner, 1898a (NMW 88240, 291 mm TL, 186 mm disc width, 163 mm disc length; adult female) in dorsal (**a**) and ventral (**b**) views.

si to be a valid species, but noted that it may synonymous with *T. panthera*. It is inconceivable that the ornate color pattern of *T. suessi*, originally described in specimens of 130, 240, and 300 mm TL, will transform into the typical pattern of small, irregular whitish spots present in *T. panthera*, or into the vermiculate or marbled whitish pattern over a dark brown background of *T. sinuspersici*. We have examined specimens of *T. panthera* smaller than 200 mm TL (fig. 10a) and confirm that the color pattern of juve-

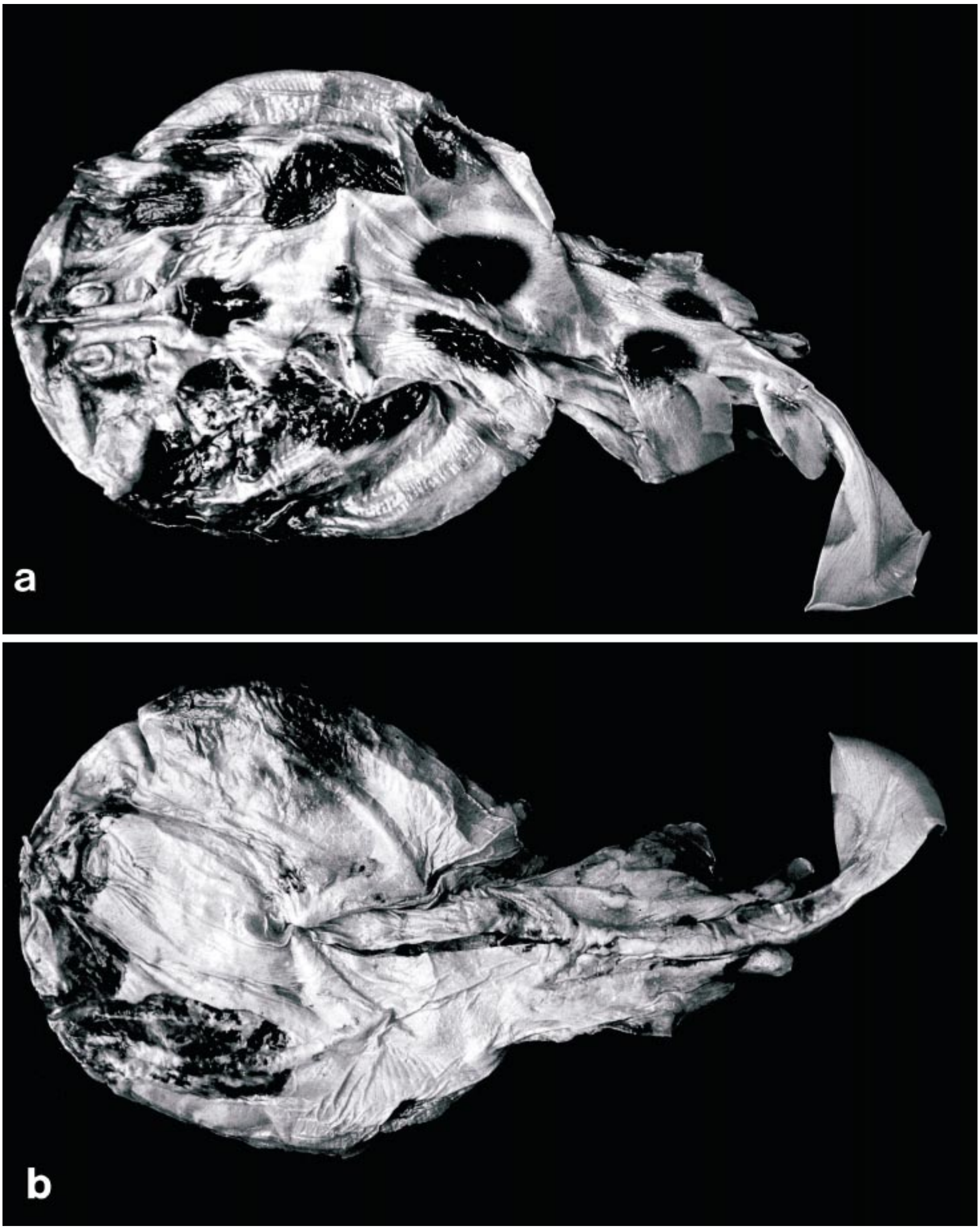

Fig. 15. Paralectotype of *Torpedo suessi* Stendachner, 1898a (NMW 78016, 232 mm TL, 114 mm disc width, 122 mm disc length; adult male) in dorsal (**a**) and ventral (**b**) views.

niles is essentially the same as in adults, and never composed of dark brown spots or ocelli. We have also examined specimens of *T. sinuspersici* smaller than 240 and 300 mm TL, and clearly the same typical color pattern of larger specimens is present. We therefore refute that *T. suessi* is a synonym of any one of these two species, and consider it a valid species that occurs at least in the southern Red Sea, known from two extant type specimens.

Photographs of a species of *Torpedo* taken by Jack Randall in the Sudanese Red Sea (fig. 16) may constitute a further record of *T.*

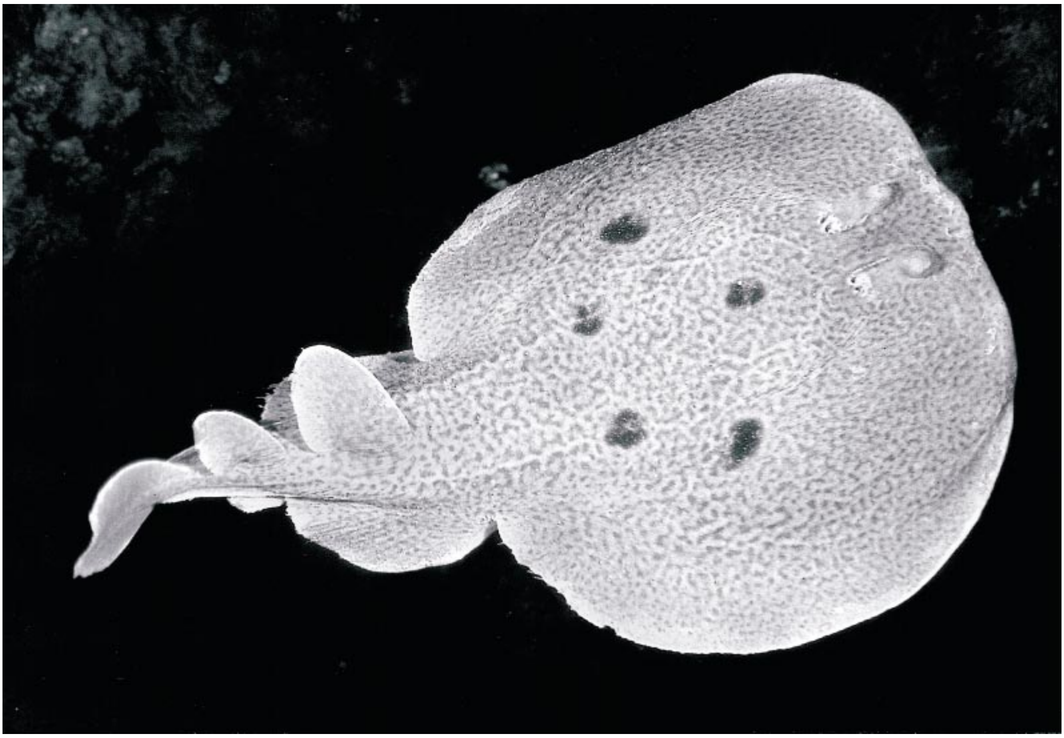

Fig. 16. Adult male specimen (not collected), possibly of *Torpedo suessi* Steindachner, 1898a, from the Sudanese Red Sea (off Port Sudan) (courtesy of Jack Randall).

suessi. The specimens photographed resemble *T. suessi* in dorsal background coloration (composed of a slender reticulate pattern) and in having large brown spots over the dorsal disc region (another photo of this species by J. Randall is featured in Michael [1993: 79] as ''Ocellated torpedo ray or *Torpedo* sp. 1''). The differences in color pattern between the type specimens of *T. suessi* and the specimens from Sudan may be ontogenetic or intraspecific. The transformation from proportionally larger and prominent ocelli into more uniformly colored and fewer spots is possible, as a similar transformation has been recorded previously for another electric ray species (*Narcine entemedor*; Carvalho, 1999). Specimens of this distinctive *Torpedo* from off Port Sudan are needed for comparisons to clarify if they represent an undescribed species or simply a range extension for *T. suessi*.

Another possibility (not supported here) is that *T. suessi* can be identified with the paralectotype of *T. fuscomaculata* (ZMB 4573; fig. 12). This specimen presents larger brown spots posteriorly over the disc that may be encircled by lighter color (ocelli?), with numerous smaller spots over disc and pelvic fins. However, this identification is very remote, as the paralectotype of *T. fuscomaculata* is from the coast of Mozambique and the similarities in coloration are not convincing. *Torpedo suessi* would still be a valid species even if it were conspecific with the paralectotype of *T. fuscomaculata*.

Comments on Other Nominal Species of the Subgenus *Torpedo*

The original descriptions of *Narcacion polleni* Bleeker, 1866 and *Torpedo zugmayeri* Engelhardt, 1912, and the examination of the holotype of the former species, clearly indicate (on the basis of dorsal coloration) that they cannot be used for our new species. These nominal species have been relatively neglected in the literature, and their taxonomic status has never been critically examined.

The holotype of *T. polleni* (fig. 17) does not have a uniform dorsal coloration as in *T. adenensis*. Described originally from Réunion (not figured), *T. polleni* was distinguished by Bleeker from both *T. panthera* and *T. fuscomaculata* (*T. sinuspersici* was overlooked) on the basis of its teeth, shape of disc and fins, and dorsal color. The dorsal coloration was originally described as having a blackish-violet background, with off-white, white, and irregular pearllike spots that coalesce into a strong and varied marbled pattern. The holotype has faded considerably in color, and the background is now brown or orange-brown, but traces of creamy spots that appear to fuse into rosettes (giving it a vermiculate or marbled appearance) are still evident over the disc. The dorsal, caudal, and pelvic fins, along with the edges of the disc, the eye, nasoral regions, and the dorsal snout area, are poorly preserved in the holotype. Garman (1913) mistakenly cites this species as being described from Madagascar.

There are only three possible interpretations concerning *T. polleni* in our view: it is a junior synonym of *T. panthera*, a junior synonym of *T. sinuspersici*, or it is a valid species (it is not a junior synonym of *T. fuscomaculata*). The first of these is the most improbable outcome, as *T. panthera* does not occur off islands in the southwestern Indian Ocean or along the eastern African coast, as far as we can discern, and the dorsal vermiculate pattern of *T. polleni* is more similar to the coloration of *T. sinuspersici* than to *T. panthera*. Bigelow and Schroeder (1953) synonymized this species with *T. panthera*, but they did not examine its type specimen. We tentatively regard *T. polleni* as a synonym of *T. sinuspersici* on the basis of the similarity in coloration, fully realizing that it may eventually prove to be a valid species (*T. sinuspersici* has not been reported from Réunion, Mauritius or the surrounding islands).

Torpedo zugmayeri was described by Engelhardt (1912) from a single 330 mm TL female specimen (not figured) from off Gwadar (southwestern Pakistan; fig. 8). This specimen apparently no longer exists (the same fate of other of Engelhardt's types originally in Munich). Engelhardt (1912) described its coloration as bright brown dorsally with blackish mottles or a blackish-marbled pattern, and ventrally yellowish-white with brown-stained disc edges. This darkly mottled or spotted color pattern clearly distinguishes this nominal species from *T. adenensis* as well as from *T. panthera*. Bigelow and Schroeder (1953) placed *T. zugmayeri* in the synonymy of *T. panthera*, but without elaborating, and overlooking the clear distinctions in coloration present in the original description. It could be either a junior synonym of *T. fuscomaculata*, because of the described similarities in dorsal color (therefore extending its range considerably), a junior synonym of *T. sinuspersici*, or a valid species. *Torpedo fuscomaculata* has not been recorded from the northern Arabian Sea, and its occurrence there is not probable. There is no mention of any light-colored dorsal markings in the original description of *T. zugmayeri*, which is in strong contrast to *T. sinuspersici* (however, see below). In our view this species is either a synonym of *T. sinuspersici* (leaving open the issue regarding the lack of mention of white spots or vermiculations in the original description) or valid, but material from off western Pakistan is needed. Engelhardt (1912) compared his new species only to *T. marmorata*.

The accounts of Blegvad (1944) and Kuronuma and Abe (1986) from the Persian Gulf described a species (misidentified as *T. panthera*) that is brownish with darker irregular spots. Both accounts were based on freshly captured specimens and do not mention white, cream-colored, or lighter spots, mottles, or vermiculations indicative of *T. sinuspersici*, originally described from the Persian Gulf. Belgvad (1944: 44) even included *T. zugmayeri* as a synonym of *T. panthera* (the first citation that we could find of this species after its original description), noting however the differences in coloration between his specimens and Rüppell's (1835) account of *T. panthera* from the Red Sea. Blegvad's depiction (1944: pl. III, fig. 1; an adult male 350 mm TL) shows a specimen that slightly resembles *T. sinuspersici*, with some lightly colored blotches, but this is inconclusive. If *T. zugmayeri* is indeed a valid species, then perhaps these two accounts are the first to record it subsequently, extending its range to the Persian Gulf.

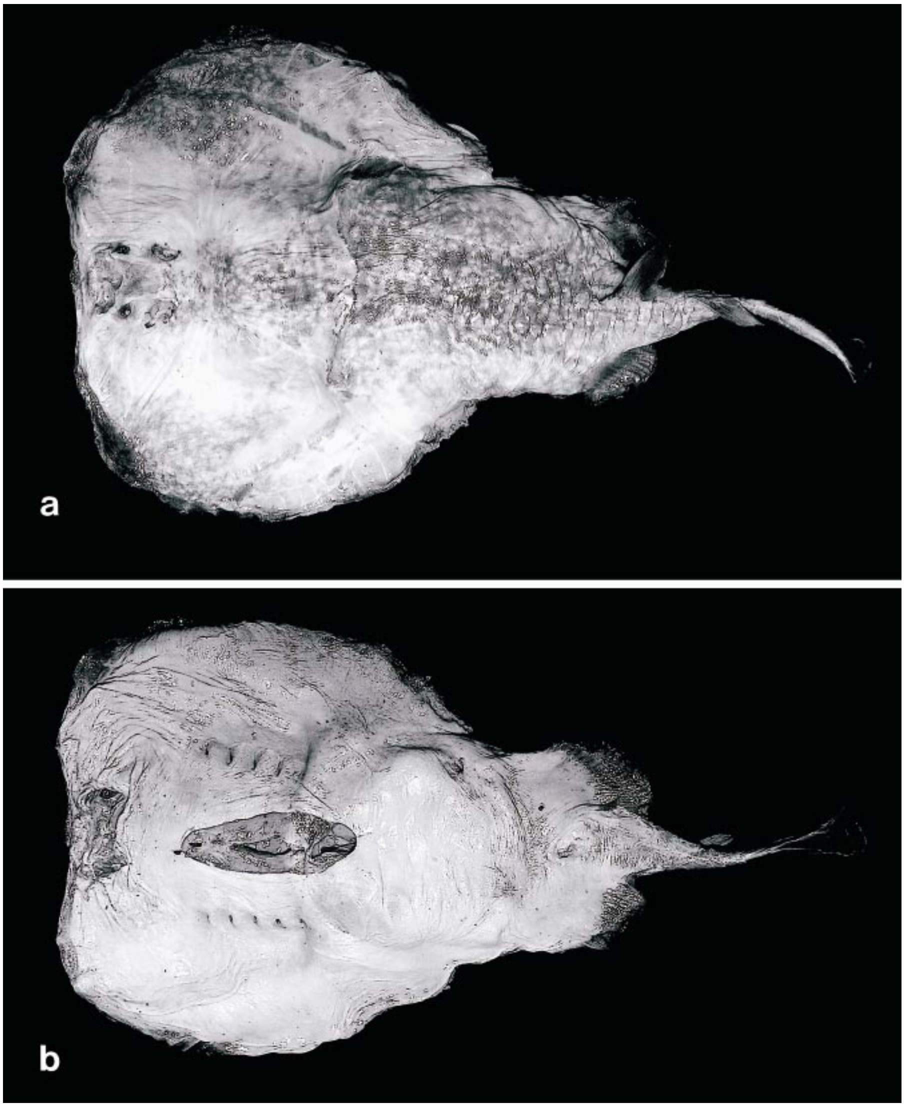

Fig. 17. Dorsal (**a**) and ventral (**b**) views of holotype of *Torpedo polleni* Bleeker, 1866 (RMNH 7424, 300 mm TL female). Note that caudal fin is pointing downward in **b.**

Other valid species of the subgenus *Torpedo* are primarily Mediterranean and west African in distribution and are easily distinguished from *T. adenensis* in coloration, as all present characteristic spots, ocelli, and blotches dorsally. These species are *T. torpedo* (Linnaeus, 1758), *T. marmorata* Risso, 1810, and *T. bauchotae* Cadenat, Capapé, and Desoutter, 1978. *Torpedo andersoni* Bullis, 1962, a species known only from the holotype and paratype from the Bahamas, has reddish spots and blotches over the dorsal disc, tail, and dorsal and caudal fins.

Indo-Pacific Nominal Species of the Subgenus *Tetronarce*

There are few records of species of *Tetronarce* in the Indian Ocean. One species has been reported from South Africa (as *T. nobiliana* Bonaparte, 1835), but it does not extend farther east than Algoa Bay (Compagno et al., 1989; Compagno, 1995). This species is uniformly dark brown, black, or gray dorsally, and may be distinct from true *T. nobiliana* and from another species, possibly new and also of the subgenus *Tetronarce*, that has been recorded from the Mozambique channel (Compagno, 1995). Duhamel (1989) confirmed the occurrence of a *Tetronarce* species from the southern Indian Ocean islands of St. Paul and Amsterdam, tentatively identified as *T. macneilli*. We have also examined a uniform dark brown specimen of *Tetronarce* (ZMUAS 3735) from off southwestern India (previously identified as *T. fairchildi*). None of these occurrences can be confused with *T. adenensis*.

All species of *Torpedo* from the Pacific Ocean, including those from the eastern Pacific, also belong to the subgenus *Tetronarce*. These species are, in the western Pacific (junior synonyms in brackets), *T. fairchildi* Hutton, 1872 [*T. fusca* Parker, 1884], *T. tokionis* (Tanaka, 1908), and *T. macneilli* (Whitley, 1932; a junior synonym of *T. fairchildi*?); and in the eastern Pacific, *T. californica* Ayres, 1855, and *T. tremens* de Buen, 1959 [?*T. peruana* Chirichigno, 1963,?*T. microdiscus* Parin and Kotylar, 1985,?*T. semipelagica* Parin and Kotylar, 1985]. The species described by Parin and Kotylar (1985) from the eastern Pacific submarine ridge of Sala y Gomez appear to differ only in disc and pelvic fin proportions, characters that are commonly preservational, and they may be synonymous. In fact, distinguishing both species from those occurring off the western coast of South America is not straightforward. The distinctions between *T. fairchildi* and *T. macneilli* from New Zealand and Australia, respectively, and even between *T. tremens* and *T. peruana* from Chile and Peru, respectively, are also in need of evaluation (as are the limits of most species of *Tetronarce*). However, all Indo-Pacific species of *Tetronarce* are drab, dark brown, gray, or blackish-purple dorsally, lacking papillae around the spiracles, and are therefore easily distinguished from *T. adenensis*.

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