

Review of the round herrings of the genus *Etrumeus* (Clupeidae: Dussumieriinae) of Africa, with descriptions of two new species

by

Joseph D. DIBATTISTA* (1), John E. RANDALL (2) & Brian W. BOWEN (1)

ABSTRACT. - A review of the round herrings of the genus *Etrumeus* from Africa is presented based on morphological and molecular evidence. *Etrumeus golanii* is described from the northern Red Sea (and also an immigrant to the Mediterranean), and *Etrumeus wongratanai* is described from the east coast of Africa, from Durban to northeastern Somalia. The species described herein are characterized by reciprocally monophyletic mitochondrial DNA cytochrome *b* sequences ($d = 3.30\%$), indicating a long period of separation (ca. 1.65 million years). *Etrumeus golanii* and *E. wongratanai* were formerly identified as the northwestern Atlantic species of the genus, *E. sadina* (regarded as a senior synonym of *E. teres*), from which they are modally distinct in having 47-51 and 43-47 gill-rakers respectively, versus 48-54. *E. wongratanai* and *E. whiteheadi* from South Africa are sympatric near Durban, but are distinct based on mtDNA sequence divergence ($d = 19.0\%$), the number of vertebrae (52 or 53 for *E. wongratanai* versus 50), and gill-raker count (51-56 for *E. whiteheadi* versus 43-47).

RÉSUMÉ. - Revue des shadines rondes africaines du genre *Etrumeus* (Clupeidae : Dussumieriinae) et description de deux nouvelles espèces.

Une revue des shadines rondes africaines du genre *Etrumeus* est présentée en se fondant sur des considérations morphologiques et moléculaires. *Etrumeus golanii* est décrite du nord de la mer Rouge (et aussi immigrante en Méditerranée), et *Etrumeus wongratanai* de la côte est de l'Afrique, de Durban jusqu'au nord-est de la Somalie. Les espèces décrites sont caractérisées par des séquences du cytochrome *b* réciproquement monophylétiques ($d = 3,30\%$), indiquant une longue période de séparation (ca. 1,65 million d'années). *Etrumeus golanii* et *E. wongratanai* étaient antérieurement identifiées comme appartenant à l'espèce de l'Atlantique nord-ouest, *E. sadina* (considérée comme synonyme junior de *E. teres*) mais s'en distinguent par des valeurs modales du nombre de branchiospines respectivement de 47-51 et 43-47 versus 48-54. *E. wongratanai* et *E. whiteheadi* d'Afrique du Sud sont sympatriques près de Durban mais se distinguent sur la base de leur divergence dans leurs séquences *cytb* ($d = 19,0\%$), le nombre de leurs vertèbres (52 ou 53 pour *E. wongratanai* versus 50) et celui des branchiospines (51-56 pour *E. whiteheadi* versus 43-47).

Key words. - Clupeidae - Dussumieriinae - Round herrings - *Etrumeus* - Africa - New species.

The round herring genus *Etrumeus* was revised by Whitehead (1963). He classified it, along with *Dussumieria*, in the family Dussumieriidae, now regarded as a subfamily of the Clupeidae, a group that includes the herrings and sardines (Grande, 1985; Nelson, 2006). Dussumieriinae also includes *Spratelloides*, *Jenkinsia*, and possibly *Sundasalanx* (Grande, 1985; Siebert, 1987), but molecular evidence suggests that the subfamily may not be monophyletic (Lavoué *et al.*, 2007; Li and Orti, 2007). Morphologically, the Dussumieriinae is distinctive in lacking scutes ventrally on the rounded abdomen, except for one flat W-shaped scute that nearly surrounds the pelvic-fin base (Grande, 1985).

Whitehead (1963) recognized only one species of *Etrumeus* worldwide, *Etrumeus teres* (DeKay, 1842), type locality New York, with five junior synonyms. Noting variation in body depth, number of dorsal-fin rays, and number

of gill-rakers of *E. teres* from different regions, Whitehead wrote that "there are five principal populations of *Etrumeus* in temperate seas: North American Atlantic, North American Pacific, and on the coasts of Japan, of South Africa, and of southern Australia. In addition, there appears to be a population in the Red Sea, which has colonized parts of the eastern Mediterranean; another population in the region of the Galapagos Islands; and a population near Hawaii".

Wongratana (1983) briefly described 24 new species of clupeid fishes, one of which he described as *Etrumeus whiteheadi*. It is found in southern Africa from Walvis Bay, Namibia to Durban, KwaZulu-Natal, where it is sympatric with *E. teres*. He distinguished it from *E. teres* mainly in having more gill-rakers and "the pelvic-fin base only just below or before the last dorsal-fin ray", compared to about a third eye diameter posterior to the last dorsal-fin ray. He

(1) Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, P.O. Box 1346, Kāne'ohe, HI 96744, USA. [bbowen@hawaii.edu]

(2) Bishop Museum, 1525 Bernice St., Honolulu, HI 96817-2704, USA [jackr@hawaii.rr.com]

* Corresponding author [joseph99@hawaii.edu]

added that the distributions of the two species may overlap at Cape Town, noting that Matsubara and Iwai (1959) identified two specimens from this port as *Etrumeus micropus* (type locality Japan), which Whitehead (1963) listed among the synonyms of *E. teres*. Whitehead and Wongratana in Fischer and Bianchi (1984) illustrated *E. teres* and recorded it on their distribution map for the northern Red Sea, Gulf of Aden, and South Africa, mentioning that it is a dominant species in the Gulf of Suez. Whitehead and Wongratana in Smith and Heemstra (1986) also prepared brief accounts of *E. teres* and *E. whiteheadi*, including drawings of an adult of each and the developing young of the latter. They reported *E. teres* north to Mozambique. *E. teres* and *E. whiteheadi* are of economic importance in South Africa's multi-species, purse-seine fishery (De Oliveira and Butterworth, 2004).

Other round herrings found off the coast of Africa include *Spratelloides delicatulus* (Bennett, 1832) and *Spratelloides gracilis* (Temminck & Schlegel, 1846), both small (maximum 105 mm SL) in comparison to *Etrumeus*, which exceeds 200 mm in standard length. *Dussumieria acuta* (Valenciennes, 1847) is also found throughout the Indo-Pacific and possibly the coast of Somalia. Similarly, the Indo-Pacific *Dussumieria elopsoides* (Bleeker, 1849) has been reported from the Gulf of Suez to the western Indian Ocean (and possibly Madagascar). The genus *Etrumeus* is distinguished from *Spratelloides* and *Dussumieria* by having 11–16 branchiostegal rays (6–7 in *Spratelloides* and 14–20 in *Dussumieria*), by the adipose eyelid completely covering the eye (only anteriorly and posteriorly on the eye in *Spratelloides* and *Dussumieria*), and by the pelvic fins inserted below or posterior to the vertical at the rear base of the dorsal fin (anterior to that vertical in *Spratelloides* and *Dussumieria*).

Whitehead (1985) published an annotated and illustrated catalogue of the clupeoid fishes of the world (four families, 80 genera, and more than 300 species), collectively forming more than one-fourth of the world fish catch. He provided a distribution map that shows nine separate populations of *E. teres*: Japan and Taiwan, southern Australia, the entire east coast of Africa and eastern Mediterranean, North America from the Bay of Fundy to the Gulf of Mexico, the northern coast of South America from Colombia to the Guianas, California and Baja California, Galapagos Islands, Peru, and the Hawaiian Islands. In South America he found no specimens south of the Guianas and Peru, none for the eastern Atlantic, and none in the western Pacific between Taiwan and New South Wales, Australia. The only tropical areas with records of *Etrumeus* are northern South America and the east coast of Africa. He wrote, "Electrophoretic studies on proteins may well point to differences between the various populations that will justify separation of subspecies or even species". Such isolation may be reinforced by the dependence of *Etrumeus* larvae on near shore estuaries or coastal embayments for spawning and development (Watson and Leis, 1974).

We do not agree with Whitehead (1963) in the use of the species name *E. teres* for the western North Atlantic species. We follow Jordan and Evermann (1896: 420) and especially Hildebrand (1963: 263) in his thorough treatment of the clupeoids in regarding *Etrumeus sadina* (Mitchill, 1814), also with a type locality of New York, as the valid name of the species (hence *E. teres* is a junior synonym). In reference to Mitchill's description in 1814, Hildebrand highlighted that the form was, "neat, tapering, and slender", and that "the belly was not at all serrate but quite smooth". This does not apply to any other clupeoid known to inhabit the northwestern Atlantic.

In the present paper, we document three species of *Etrumeus* for the east coast of Africa: *E. whiteheadi*, and two new species, both formerly identified as *E. teres*, one from Durban to northeastern Somalia (although specimens are lacking north of Durban to Kenya), and one from the northern Red Sea and eastern Mediterranean Sea. *E. sadina* is here restricted to the northwestern Atlantic from the Bay of Fundy to the Gulf of Mexico. In addition, we extend the range of *E. whiteheadi* north on the Atlantic coast of Africa to Angola.

MATERIAL AND METHODS

Fresh *Etrumeus* specimens were obtained from the Gulf of Suez (N = 2) and South Africa (N = 4). Type specimens of the new species have been deposited in the Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); the Natural History Museum, London (BMNH); Hebrew University of Jerusalem (HUJ); South African Institute for Aquatic Biodiversity, Grahamstown (SAIAB); and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Loans were obtained of additional museum specimens identified as *E. teres* from the BMNH; California Academy of Sciences, San Francisco (CAS); Florida Natural History Museum of the University of Florida, Gainesville (UF); HUJ; Museum of Comparative Zoology of Harvard University, Cambridge (MCZ); Royal Ontario Museum, Toronto (ROM); SAIAB; and the USNM.

Measurements given for specimens are in terms of standard length (SL) and head length (HL). Snout length is measured from the anterior point of the upper lip to the bony edge of the orbit. Body depth is the greatest depth, and body width the greatest width. Orbit diameter is the greatest diameter, and interorbital width is measured vertically over the centre of the eye. Caudal-peduncle depth is the least depth; caudal-peduncle length is measured horizontally from the rear base of the anal fin to the caudal-fin base. Predorsal, preanal, and prepelvic lengths are taken from the upper lip to the origin of the respective fins. Lengths of fin rays are measured from where they emerge from the contour of the body.

Table I. - Upper and lower gill-raker counts of African species of *Etrumeus* and *Etrumeus sadina*.

	Upper limb							Lower limb												
	12	13	14	15	16	17	18	29	30	31	32	33	34	35	36	37	38	39	40	
<i>E. golanii</i>		5	14	3								3	7	7	5					
<i>E. sadina</i>		1	15	10	3								4	6	9	7	2	1		
<i>E. whiteheadi</i>			4	4	8	7	1								3	8	5	7	1	
<i>E. wongratanai</i>	9	17	5					3	5	14	8	1								

Table II. - Total gill-raker counts of species of African *Etrumeus* and *Etrumeus sadina*.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
<i>E. golanii</i>							5	5	8	3	1					
<i>E. sadina</i>								3	6	4	9	4	2	1		
<i>E. whiteheadi</i>											3	2	7	4	3	5
<i>E. wongratanai</i>			4	9	11	3	4									

Counts were made of the pectoral-fin rays on both sides of nearly all specimens (N = 75). Dorsal- and anal-fin ray counts were made in only a few specimens (N = 15) in order to avoid damaging the fins. The last dorsal-fin and anal-fin rays are branched at the base and were counted as one.

Scale counts were possible on only a few specimens because the scales of *Etrumeus* are very deciduous. Most

scales are missing from the majority of specimens, and the scale pockets are not clearly defined. Scales in longitudinal series were counted from the most anterior scale above the upper end of the gill opening to the base of the caudal fin; transverse scales were counted in an oblique row from the origin of the pelvic fin to the base of the dorsal fin.

Accurate gill-raker counts required the careful removal of the first gill arch. The gill-raker counts include rudiments; the raker at the angle is contained in the lower-limb count (Tabs I, II).

Morphometric data were taken from seven specimens of *Etrumeus golanii*, 104.5-208 mm SL, and seven specimens of *Etrumeus wongratanai*, 117-177.5 mm SL, as percentages of the SL (Tabs III, IV). Measurements in the description are given as proportions of SL or HL (except body width, which is related to body depth). Proportional measurements in the text are given as ranges (in parentheses) and rounded to the nearest 0.05; the number preceding the given range represents the holotype.

Table III. - Proportional measurements for type specimens of *Etrumeus golanii* as percentages of the standard length.

	Holotype	Paratypes					
	HUJ 18422	HUJ 5903	AMS 33822	AMS 33822	HUJ 15842	HUJ 15842	HUJ 17000
Standard length (mm)	208.0	104.5	132.0	143.0	155.0	180.5	194.0
Body depth	20.0	16.8	16.3	17.5	16.5	18.3	20.1
Body width	16.3	13.4	14.4	12.6	13.2	14.7	14.9
Head length	24.0	25.4	26.1	25.5	24.2	23.8	23.5
Snout length	6.0	6.7	6.4	5.9	6.5	5.8	5.9
Orbit diameter	8.2	10.0	10.2	9.4	9.4	8.3	8.3
Interorbital width	5.3	6.2	5.3	5.6	5.5	5.3	4.9
Upper-jaw length	7.9	9.1	9.1	9.1	8.4	7.8	8.5
Caudal-peduncle depth	6.5	7.7	7.2	6.6	6.8	6.6	6.2
Caudal-peduncle length	11.1	11.5	11.0	10.1	11.0	11.1	10.3
Predorsal length	45.7	45.0	43.9	46.2	45.2	44.0	44.8
Preanal length	82.2	83.7	87.1	82.9	83.9	87.8	85.1
Prepectoral length	25.2	26.8	27.3	28.0	26.5	25.8	25.5
Prepelvic length	63.9	65.1	67.4	65.0	66.5	67.9	65.7
Dorsal-fin base	15.6	13.4	14.8	13.6	14.8	14.4	14.4
Longest dorsal ray	Broken	Broken	17.4	16.8	16.1	15.0	14.4
Anal-fin base	5.3	6.7	6.1	5.9	5.5	5.5	5.7
Longest anal ray	5.0	4.8	5.3	5.2	4.5	4.2	5.2
Caudal-fin length	Broken	Broken	Broken	Broken	18.7	17.5	17.8
Caudal concavity	10.8	12.0	9.5	9.4	10.3	10.0	10.3
Pectoral-fin length	14.4	15.3	16.7	16.1	15.5	15.2	14.4
Pelvic-fin length	7.5	8.6	9.5	9.1	7.4	7.8	7.2

Counts of the gill-rakers of *E. sadina* from the eastern coast of the United States are provided for comparison with specimens from Africa formerly identified as *E. teres*. The gill-rakers were counted on specimens as small as 58 mm SL, with no indication of an increase in number with growth. Vertebral counts were taken from X-rays.

To complement morphological comparisons, a total of 38 tissue samples from African *Etrumeus* were included for genetic analysis: 13 from the Gulf of Suez including paratype BPBM 41058 (RS/Eter63 and RS/Eter64 on Fig. 4), three from Antalya, Turkey, and 22 from Durban, South Africa including holotype SAIAB 98808 (SA/Eter62 on Fig. 4), and paratypes BPBM 41057 (SA/Eter39 on Fig. 4), SAIAB 98809 (SA/Eter61 on Fig. 4), and USNM 400909 (SA/Eter61 on Fig. 4). Tissue samples from 10 specimens of *E. whiteheadi*, also collected from South Africa but on the Agulhas Bank, and four previously published *E. whiteheadi* mitochondrial (mtDNA) cytochrome b (cyt b) sequences (Hout Bay, South Africa; GenBank Accession Numbers, EU552567-EU552568 and EU552590-

EU552591; Wilson *et al.*, 2008) were included for comparison. Similarly, nine previously published *cyt b* sequences of *E. sadina* from the Gulf of Mexico, USA (GenBank Accession Numbers: JN029799 [Randall and DiBattista, 2012] and EU552621 [Wilson *et al.*, 2008]) further supplemented genetic analyses.

Total genomic DNA was extracted from each sample using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). A 677 base pair (bp) segment of the *cyt b* gene was amplified using a heavy-strand (5'-GTGACTT-GAAAACCACCGTTG-3'; Song *et al.*, 1998) and light-strand primer (5'-AATAGGAAGTATCATTCG-GGTTTGATG-3'; Taberlet *et al.*, 1992). Polymerase chain reaction (PCR) mixes contained BioMix Red (Bioline Inc., Springfield, NJ, USA), 0.26 μM of each primer, and 5 to 50 ng template DNA in a 15 μl total volume. PCR cycling parameters were as follows: initial 95°C denaturation for 10 min followed by 35 cycles of 94°C for 30 s, 50°C for 45 s, and 72°C for 45 s, with a final elongation step of 72°C for 10 min. All PCR products were then cleaned by incubating with exonuclease I and shrimp alkaline phosphatase (ExoSAP; USB, Cleveland, OH, USA), sequenced in both the forward and reverse directions with fluorescently labelled dye terminators following manufacturer's protocols (BigDye, Applied Biosystems Inc., Foster City, CA, USA), and analysed using an ABI 3130XL Genetic Analyzer (Applied Biosystems) at the Hawaii Institute of Marine Biology EPSCoR Sequencing Facility. The sequences were aligned, edited, and truncated to a common length using Geneious Pro 4.8.4 (Drummond *et al.*, 2009). Representative mtDNA *cyt b* haplotypes were deposited in GenBank (Accession Numbers: JQ914281-JQ914308). jModelTest 1.0.1 (Posada, 2008; but also see Guindon and Gascuel, 2003) was used to determine the best nucleotide substitution model under Akaike information criterion (AIC); the TVM + I + G model (Posada, 2003) was here selected for phylogenetic inference with a gamma estimate of 0.95.

Neighbour-joining distance and maximum-likelihood tree-building methods were applied using PAUP* 4.0 (Swofford, 2000), in addition to MrBayes (Ronquist and Huelsen-

Table IV. - Proportional measurements for type specimens of *Etrumeus wongratanai* as percentages of the standard length.

	Holotype	Paratypes					
	SAIAB 98808	BMNH 1903.2.6	BMNH 1903.2.6	BMNH 1903.2.6	SAIAB 98809	USNM 400909	BPBM 41057
Standard length (mm)	167.0	117.0	122.0	132.5	140.5	168.0	177.5
Body depth	19.8	20.5	18.4	18.5	20.6	19.0	19.4
Body width	13.8	14.5	14.3	14.3	14.2	12.5	14.1
Head length	24.0	26.5	27.0	26.4	25.6	23.8	24.2
Snout length	6.0	6.4	7.4	6.8	5.7	6.0	6.8
Orbit diameter	8.7	9.4	9.8	9.1	9.3	8.6	8.5
Interorbital width	5.7	5.1	5.3	5.7	6.05	5.7	5.6
Upper-jaw length	8.7	9.4	9.8	9.1	9.3	8.6	8.7
Caudal-peduncle depth	7.2	6.8	7.0	7.2	7.8	7.1	6.8
Caudal-peduncle length	10.2	10.7	11.5	10.6	11.4	9.8	10.1
Predorsal length	45.5	46.6	48.4	47.2	45.2	45.8	45.6
Preanal length	84.4	89.7	85.2	84.9	84.0	83.3	86.8
Prepectoral length	26.9	28.6	28.7	27.9	26.3	25.9	27.0
Prepelvic length	67.1	70.9	67.6	65.7	67.6	66.1	67.0
Dorsal-fin base	15.6	15.0	15.2	14.7	14.9	13.7	15.2
Longest dorsal ray	16.8	17.9	16.4	17.4	17.1	16.1	17.2
Anal-fin base	5.1	5.1	5.7	5.7	5.3	4.8	5.0
Longest anal ray	Broken	Broken	Broken	Broken	Broken	Broken	4.5
Caudal-fin length	Broken	19.7	18.9	Broken	19.9	Broken	Broken
Caudal concavity	Broken	12.0	11.5	Broken	9.3	8.9	Broken
Pectoral-fin length	15.6	17.1	17.6	16.6	17.1	14.9	15.8
Pelvic-fin length	8.4	9.4	9.0	8.7	7.5	7.1	7.9

beck, 2003) Bayesian Markov Chain Monte Carlo (MCMC) coalescent approach implemented in Geneious Pro. The Bayesian MCMC search strategy consisted of the default four heated, 1 million step chains with an initial burn-in of 100,000 steps. A single Atlantic Herring (*Clupea harengus*) DNA sequence (Genbank accession no. HQ413291) was used to root the tree. Support for the tree topology was evaluated by bootstrapping over 1000 replicates; only nodes with bootstrap values >50% were considered significant.

RESULTS

Genus *Etrumeus* Bleeker

Etrumeus Bleeker, 1853: 48 (type species, *Clupea micropus* Temminck & Schlegel 1846, by monotypy).

Perkinsia Eigenmann, 1891: 153 (type species, *Perkinsia othonops* Eigenmann = *Etrumeus acuminatus* Gilbert).

Halecula Jordan, 1925: 41 (type species, *Halecula acuminata*), invalid; preoccupied by *Halecula* Facciola 1891.

Parahalecula Fowler, 1958: 5 (replacement name for *Halecula*).



Figure 1. - Holotype of *Etrumeus golanii*, HUJ 18422, 208 mm, Limassol, Cyprus (Photo D. Golani).

Diagnosis

Dorsal-fin rays 17-22; anal-fin rays 9-13; pectoral-fin rays 14-17 (rarely 14 or 17); pelvic-fin rays 8 or 9; scales thin and deciduous (most missing in preserved specimens), about 48-56 in longitudinal series; no scutes ventrally on abdomen, except one large W-shaped scute around pelvic-fin base; gill-rakers long and numerous, 41-56 on first gill arch; branchiostegal rays 14-16; vertebrae 48-56; body elongate and only slightly compressed; snout pointed; mouth terminal or lower jaw slightly projecting; minute teeth on jaws, vomer, palatines, pterygoids, and tongue; a single supramaxilla about half length of maxilla and tapering anteriorly; eye large; transparent adipose tissue completely covering eye (no vertical slit over pupil); origin of dorsal fin closer to front of snout than base of caudal fin; caudal fin forked; paired fins ventral, their base broadly shielded ventrally by large scales, each fin with a long axillary process; origin of pelvic fins below or posterior to rear base of dorsal fin; anal fin small, origin nearer base of caudal fin than origin of pelvic fins.

Etrumeus golanii DiBattista, Randall & Bowen sp. nov.

(Fig. 1; Tabs I, II, III)

Etrumeus teres Fowler and Steinitz, 1956: 261 (Eilat, Red Sea).

Etrumeus teres Whitehead (in part), 1963: 321, Fig. (Red Sea & Mediterranean Sea).

Etrumeus teres Whitehead and Wongratana (in part), 1983 in Fischer and Bianchi, 1984: Fig. (northern Red Sea).

Etrumeus teres Whitehead and Wongratana (in part) in Smith and Heemstra, 1986: 200, Fig. 54.1 (Mozambique border to Durban).

Etrumeus teres Whitehead (in part), 1985: 31, Fig. (northern Red Sea and Mediterranean Sea).

Etrumeus teres Fischer *et al.*, 1987: 1058, Fig. (eastern Mediterranean Sea)

Etrumeus teres Başusta *et al.*, 1997: 6 (İskenderun, Turkey).

Etrumeus teres Yılmaz and Hoşsucu, 2003: 438 (Antalya, Turkey).

Etrumeus teres Golani, 2000: 2 (Limassol, Cyprus).

Etrumeus teres Corsini *et al.*, 2005: 19 (Rhodes Island, Greece).

Etrumeus teres Kallianiotis and Lekkas, 2005: 30 (Cyclades, Greece).

Etrumeus teres Falautano *et al.*, 2006: 1 (Lampedousa, Italy).

Etrumeus teres Kasapidis *et al.*, 2007: 410, Fig. 1 (Malia Bay to Chania Bay, Greece).

Etrumeus teres Zenetos *et al.*, 2007: 1 (Hydra Island, Greece).

Etrumeus teres Yarmaz *et al.*, 2010: 1 (Dikili Strait, Turkey).

Material examined

Holotype. - HUJ 18422, 208 mm, Limassol, Republic of Cyprus, D. Golani, trammel net, 50 m, from fisherman, 22 Jul. 1999.

Paratypes. - HUJ 5903, 4: 95-105 mm, Eilat, Israel, 12 May 1972; AMS 33822-006, 2: 132-143 mm, south of Bluff Point Beacon, 20 m, hook and line or purse seine, Gubal Island, Egypt (27°40'N, 33°49'E), J. Paxton, 25 Jan. 1993; HUJ 15842, 2: 155-180.5 mm, Haifa Bay, Israel, O. Sonin, 16 Dec. 1991; HUJ 17000, 1: 194 mm, Haifa Bay, Israel, O. Sonin, 22 Jul. 1992; BPBM 41058, 2: 148.5-150 mm, Gulf of Suez, Egypt, S. Mehanna, Oct. 2010.

Nontype material

Jaffa, Israel, HUJ 19924, 2: 148-153 mm; Haifa Bay, Israel, HUJ 17758, 3: 178-212 mm.

Diagnosis

A species of *Etrumeus* with dorsal-fin rays 19-22; anal-fin rays 10 or 11; gill-rakers 13-15 + 33-36 (total 47-51); vertebrae 52 or 53; origin of pelvic fins about one-third eye diameter posterior to a vertical at rear end of dorsal fin base; colour in alcohol: centre of scales on dorsal half of body blackish, the edges pale grey (pale edges progressively narrower posteriorly); ventral half of body abruptly silvery white; colour when fresh: iridescent blue-green dorsally on body, dark pigmentation as in alcohol preserved specimens, shading through bronze to silvery white on abdomen; largest specimen, 208 mm.

Description

Dorsal-fin rays 21 (19-22), the first four unbranched; anal-fin rays 11 (10 or 11), the first three unbranched; principal caudal-fin rays 18; pectoral-fin rays 16 (15-17, usually 16), the first unbranched; pelvic-fin rays 8, the first unbranched, but the last branched to base; longitudinal scale series 53; transverse scale series 11; median predorsal scales 18; gill-rakers 15 + 36 (13-15 + 33-36); branchiostegal rays 15 (one count); vertebrae 53 (52 or 53).

Body moderately elongate, the depth 5.0 (4.85-6.15) in SL; body moderately compressed, the width 1.2 (1.1-1.65) in body depth; head pointed; HL 4.15 (3.8-4.35) in SL; snout length 4.0 (3.75-4.3) in HL; eye large, 2.8 (2.55-2.9) in HL; adipose eyelid covering all of eye; interorbital space flat, except for a median triangular depression with a marginal and median ridge extending from behind premaxilla to a pupil diameter posterior to orbit; interorbital width above centre of orbit 4.55 (4.05-4.95) in HL; caudal-peduncle depth 3.7 (3.3-3.85) in HL; caudal-peduncle length 2.2 (2.15-2.5) in HL.

Mouth terminal or with lower jaw slightly protruding; maxilla forming an angle of about 20° to horizontal axis of body, and reaching a vertical at front edge of orbit, its ventral edge with a row of tiny teeth; premaxillae roughly rectangular in dorsal view at front of jaw, with a few, small, retrorse teeth laterally on inner edge; upper-jaw length 3.0 (2.75-3.1) in HL; tongue subtriangular with a thin fleshy leading edge, the dorsal surface with a thin granular lamella. Nares a low fleshy tubule within a round aperture posterior to lateral end of premaxilla.

Operculum forming a right angle ventroposteriorly; bones of operculum striated; posterior margin of operculum with a row of very small papillae, except in the small slightly convex middle portion. Gill opening extending forward to below anterior edge of orbit; gill-rakers long and slender, the longest at angle, slightly longer than longest gill filament.

Scales cycloid, thin, and deciduous; no lateral line; no scales on head; median predorsal scales extending forward to above posterior edge of preopercle; no scales on fins except posteriorly on anal fin and a broad triangular sheath of scales on caudal fin, full width of fin basally, the apex nearly reaching base of fork in fin.

Dorsal fin slightly anterior to middle of body, the predorsal length 2.20 (2.0-2.3) in SL; first three dorsal-fin rays very slender and closely spaced, the first about a pupil diameter in length, nearly one-half length of second ray; second anal ray about one-half length of third ray; fifth dorsal ray longest (1.4-1.65 in HL); anal fin small, posterior on body, the preanal length 1.20 (1.15-1.25) in SL; last anal ray clearly longest, 4.75 (4.45-6.7) in HL; caudal fin length n/a (4.65-5.75 in SL), and deeply forked, the caudal concavity 2.2 (2.0-2.75) in HL; pectoral fins ventral on body, just behind head, the prepectoral length about equal to HL; pectoral fins broad-

based, separated at base by a large triangular scaly sheath; a large scaled axillary process dorsal to pectoral fin, nearly as long as fin; second pectoral ray longest, 1.7 (1.45-1.65) in HL; small pelvic fins posteriorly on body, the prepelvic length 1.55 (1.45-1.6) in SL, and broadly separated by a scaly flap; second pelvic ray longest, 3.2 (2.7-3.25) in HL.

Colour of holotype when fresh as in figure 1. Colour in alcohol: dorsal half of body and postorbital head very dark grey, the edges of scales pale (pale edges narrower posteriorly); ventral half of body abruptly silvery white (pale yellowish where scales intact); head near-black dorsally (except yellowish concave part of interorbital), yellowish ventrally except silvery over subopercle and opercle; tip of snout and lower jaw black; edge of dorsal half of opercle narrowly black; dorsal and caudal fins yellowish with dusky rays; anal and pelvic fins pale yellowish; pectoral fins with blackish rays and pale yellowish membranes, except distally where abruptly pale yellowish.

Etymology

The species is named in honour of Dr. Dani Golani who provided the type specimens, genetic material, and a photograph of the holotype.

Remarks

E. golanii is easily separated from the western North Atlantic *E. sadina* in having 52 or 53 vertebrae, compared to 49 for *E. sadina*, and modally 49 gill-rakers versus 51 for *E. sadina*.

E. golanii is closest morphologically and genetically to *E. wongratanai*, which is described below. It is modally distinct in having 47-51 gill-rakers, compared to 43-47 for *E. wongratanai*, a dark spot on each scale dorsally on the body, and 3.3% genetic differentiation at mtDNA. We were unable to find any consistent difference in proportional measurements of the two species.

Distribution

The opening of the Suez Canal almost 150 years ago connected the Red Sea to the Mediterranean Sea and allowed the introduction of numerous marine species from the Red Sea to the Mediterranean (Golani *et al.*, 2002), and a few in the other direction. *Etrumeus* was first recorded in the Mediterranean Sea from Haifa Bay, Israel in 1961 (Whitehead, 1963). It then spread northwest to Cyprus, the Greek island of Rhodes, and the Aegean Sea (Golani, 2000; Kasapidis *et al.*, 2007; Yarmaz *et al.*, 2010), where it now represents an important commercial resource. The quick succession of records across the Mediterranean is probably not an artifact of increased scientific interest in recent years but realized dispersal patterns, given the extensive fisheries in this region.

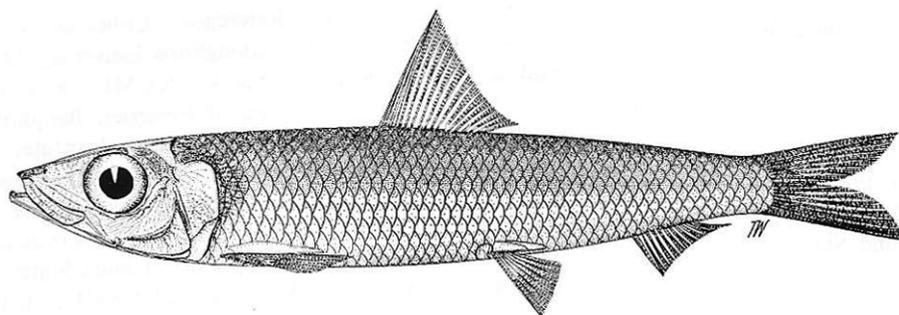


Figure 2. - Holotype of *Etrumeus whiteheadi*, BMNH 1890.6.27.24, 166 mm, Algoa Bay, Port Elizabeth, South Africa (Drawing T. Wongratana).

***Etrumeus whiteheadi* Wongratana**

(Fig. 2; Tabs I, II)

Etrumeus whiteheadi Wongratana, 1983: 387, Fig. 1 (type locality, Algoa Bay, Port Elizabeth, South Africa).

Etrumeus whiteheadi Whitehead & Wongratana in Smith and Heemstra, 1986: 201, Fig. 54.2 (Walvis Bay to Durban).

Material examined

SAIAB 1501, 4: 182-205 mm, Western Cape, South Africa (34°8.0'S, 18°19.0'E), 25 Feb. 1971; SAIAB 11304, 163 mm, Durban, Kwazulu-Natal, South Africa (29°51.0'S, 31°0.0'E); SAIAB 11305, 211 mm, Durban, Kwazulu-Natal, South Africa (29°51.0'S, 31°0.0'E); SAIAB 74676, 4: 154-172 mm, off Thogela River, Kwazulu-Natal, South Africa (29°32.0'S, 31°47.7'E), 18 Aug. 2002; SAIAB 19985, 174 mm, Western Cape, off Cape Hangklip, South Africa (34°24.1'S, 18°7.3'E), 3 Nov. 1983; SAIAB 14955, 7: 130-181 mm, Eastern Cape between Kleinbruk and Swartkops Rivers, South Africa, 1 Aug. 1980; SAIAB 34091, 4: 146-152 mm, Port Elizabeth, South Africa, 4 Nov. 1983; SAIAB 65834, 2: 144-160 mm, Angola (17°15.0'S, 11°40.0'E).

Diagnosis

A species of *Etrumeus* with dorsal-fin rays 18-20; anal-fin rays 12 or 13; pectoral-fin rays 14-17 (rarely 14 or 17); longitudinal scale series 48-51; predorsal scales 15; transverse scales 11; gill-rakers 14-18 + 30-34 (total 51-56); vertebrae 50 (9 counts); pelvic-fin base below or slightly anterior to rear base of dorsal-fin base; blue-green dorsally, silvery ventrally. It reaches a SL of at least 220 mm.

Remarks

This species has the highest total gill-raker count (51-56) of specimens we have examined from 15 different populations of *Etrumeus* (the lowest is from the eastern Pacific, with 41-46; Randall and DiBattista, 2012). The combined ranges of total gill-raker counts for the other two African species are 43-51. Vertebral counts of 50 for *E. whiteheadi* and 52 or 53 for *E. golanii* and *E. wongratana*, and the posterior position of the pelvic fins of the last two species provide complete

separation. The 19% to 20% genetic difference separating *E. whiteheadi* from the other two African species correlates with the strong meristic differences.

E. whiteheadi has been given the common names of South African Round Herring, Cape Round Herring, and Redeye Round Herring. None of these names are appropriate because this species is not the only South African Round Herring, because it ranges far from the Cape of Good Hope, and because red eyes are postmortem eye colour that can be seen in any species of *Etrumeus*. We propose that the patronyms given in the present paper also be used for the common names.

Distribution

The first South African record of *E. whiteheadi* may have been Gilchrist and Thompson (1917) as *E. micropus* (Temminck & Schlegel) from KwaZulu-Natal, but they listed it by name only, without diagnostic data. Barnard (1925) apparently had specimens of both *E. whiteheadi* and *E. wongratana*, in view of his distribution: "Port Elizabeth and Natal coast". Smith (1949) may also have had material of both species. His illustration is closest to *E. whiteheadi* from the position of the pelvic fins and his mention of a length of 15 inches, but his stating, "rarely seen south of Durban" favours *E. wongratana*.

Etrumeus wongratana

DiBattista, Randall & Bowen sp. nov.

(Fig. 3; Tabs I, II, IV)

Etrumeus micropus (non Temminck & Schlegel) Barnard, 1925: 108 (Port Elizabeth and Natal coast).

Etrumeus micropus (non Temminck & Schlegel) Smith, 1949: 88, Fig. 106 (rarely seen south of Durban).

Etrumeus micropus (non Temminck & Schlegel) Matsubara and Iwai, 1959: 3, pl. 1, upper Fig. (Cape Town).

Etrumeus teres (non De Kay) Whitehead (in part), 1963: 321 (South Africa).



Figure 3. - Holotype of *Etrumeus wongratanai*, SAIAB 98808, 167 mm, Durban, South Africa (Photo S. Chater).

Etrumeus teres (non De Kay) Whitehead and Wongratana in Smith & Heemstra, 1986: 200, Fig. 54.1 (Mozambique border to Durban).

Etrumeus teres (non De Kay) Whitehead (in part), 1985: 30, Fig. (Mozambique to South Africa).

Material examined

Holotype. - SAIAB 98808, 167 mm, 26 m, hook and line, Durban beachfront, South Africa (29°48.555'S, 31°04.327'E), S. Chater, Jan. 2010.

Paratypes. - BMNH 1903.2.6., 3: 117-132.5 mm, Kwa-Zulu-Natal, South Africa, J. Quekett, 6 Feb. 1903; BPBM 41057, 1: 177.5 mm, SAIAB 98809, 1: 140.5 mm, and USNM 400909, 1: 168 mm, same collection data as holotype.

Nontype material

SAIAB 5711, 142 mm, Durban, Kwazulu-Natal, South Africa (29°51.0'S, 31°0.0'E); USNM 305934 and USNM 305936, Somalia (11°41'N, 51°22'E and 11°29'N, 51°15'E), 1: 185 mm and 3: 155-165 mm; USNM 301972, Ras Scenaghef, Somalia, 3: 134-174 mm.

Diagnosis

A species of *Etrumeus* with dorsal-fin rays 21 or 22; anal-fin rays 10; pectoral-fin rays 15-17; gill-rakers 12 or 13 + 32 or 33 (total 43-47); vertebrae 52 or 53; origin of pelvic fins about one-third eye diameter posterior to a vertical at rear base of dorsal fin; colour in alcohol: dark purplish grey on dorsal half of body (iridescent blue where scales present), abruptly pale silvery grey on ventral half; a faint dusky blotch posterior to upper third of opercle; colour when fresh: body iridescent blue-green on dorsal half of body, the scale edges of upper two or three rows black, abruptly silvery white ventrally; a semicircular blackish spot posterior to upper third of opercle. The largest specimen examined was 185 mm.

Description

Dorsal-fin rays 21 (21-22), the first four unbranched; anal-fin rays 10, the first three unbranched; principal caudal-

fin rays 18; pectoral-fin rays 16 (15-17), the first unbranched; pelvic-fin rays 8, the first unbranched, but the last branched to base; longitudinal scale series about 55; transverse scale series about 13; median predorsal scales about 17; gill-rakers 13 + 32 (12-14 + 30-34; total 43-47); branchiostegal rays 15 (one count); vertebrae 52 (52 or 53).

Body moderately elongate, the depth 5.05 (4.85-5.40) in SL; body moderately compressed, the width 1.45 (1.3-1.5) in body depth, and broadly rounded ventrally; head acutely pointed, forming an angle of about 50°; HL 4.2 (3.7-4.2) in SL; snout length 4.0 (3.6-4.5) in HL; eye large, 2.75 (2.75-2.9) in HL; adipose eyelid covering all of eye; interorbital space flat, except for a median triangular depression with a marginal and median ridge extending from behind premaxilla to a pupil diameter posterior to orbit; interorbital width above centre of orbit 4.2 (4.2-5.15) in HL; caudal-peduncle depth 3.35 (3.3-3.9) in HL; caudal-peduncle length 2.35 (2.25-2.5) in HL.

Mouth terminal or with lower jaw slightly protruding; maxilla forming an angle of about 20° to horizontal axis of body, and reaching a vertical at front edge of orbit, its ventral edge with a row of tiny teeth; premaxillae roughly rectangular in dorsal view at front of jaw, with a few, small, retrorse teeth laterally on inner edge; upper-jaw length 2.75 (2.75-2.9) in HL; tongue subtriangular with a thin fleshy leading edge, the dorsal surface with a thin granular lamella. Nares a low fleshy tubule within a round aperture posterior to lateral end of premaxilla.

Operculum forming a right angle ventroposteriorly; flange of suborbital covered with finely branching sensory tubules; preopercle with a system of multiple-branching, sensory tubules from a common centroanterior base; very fine papillae variably present on posterior margin of operculum. Gill opening extending forward to below anterior edge of orbit; gill rakers long and slender, the longest at angle, slightly longer than longest gill filament.

Scales cycloid, thin, and deciduous; no lateral line; no scales on head; median predorsal scales extending forward to above posterior margin of preopercle; no scales on fins except last few rays of dorsal and anal fins and a broad triangular sheath of scales on caudal fin, full width of fin basally, the apex nearly reaching base of fork of fin (the broad basal sheath of scales medially on paired fins are not attached to the fins).

Dorsal fin slightly anterior to middle of body, the predorsal length 2.2 (2.05-2.2) in SL; first three dorsal-fin rays very slender and closely spaced, the first about a pupil diameter in length, nearly one-half length of second ray; second anal ray about one-half length of third ray; fifth dorsal ray longest, 1.45 (1.4-1.65) in HL; anal fin small, posterior on body, the preanal length 1.2 (1.0-1.2) in SL; last anal ray clearly longest n/a (5.38 in HL); caudal fin length (5.0-5.3 in SL), and deeply forked, the caudal concavity (2.2-2.8 in HL); pectoral

fins ventral on body, just behind head, the prepectoral length about equal to HL; pectoral fins broad-based, separated at base by a large triangular scaly sheath; a large scaled axillary process dorsal to pectoral fin, nearly as long as fin; second pectoral ray longest, 1.55 (1.5-1.6) in HL; small pelvic fins posteriorly on body, the prepelvic length 1.5 (1.5-1.5) in SL, and broadly separated by a scaly flap; second pelvic ray longest, 2.85 (2.8-3.45) in HL.

Colour of holotype when fresh as in figure 3. Colour of holotype in alcohol dark purplish grey on dorsal half of body (iridescent blue where scales present), abruptly pale silvery grey on ventral half; a faint dusky blotch posterior to upper third of opercle; head blackish dorsally except pale yellowish concave grooves on interorbital and dorsally on basal part of snout; side of snout and eye dull yellow; jaws and supramaxilla brassy except anteriorly where blackish; operculum brassy, becoming silvery on opercle; dorsal, caudal, and pectoral fins dusky yellowish, the dark pigmentation strongest on leading edges, pale distally; pelvic and anal fins pale yellowish.

Remarks

As mentioned, *E. wongratanai* is closely related to *E. golanii*. It is modally distinct in having 43-47 gill-rakers, compared to 47-51 for *E. golanii*, no dark spot on each scale dorsally on the body, and 3.3% genetic differentiation at mtDNA. *E. wongratanai* is readily differentiated from the northwestern Atlantic *E. sadina* by its count of 52 or 53 vertebrae compared to 49 for *E. sadina*, and genetically by 18% mtDNA divergence from *E. sadina* sequences.

We provisionally reclassify the six specimens identified as *E. teres* from southern Madagascar (on loan from USNM) as *E. wongratanai* based on biogeographic considerations, but we defer definitive identification until we can obtain fresh material for molecular analysis. Among the two species known to occupy this region, the vertebral count of 53 for the Madagascar specimens allies them with *E. wongratanai* and not *E. whiteheadi*, which has 50 vertebrae.

Distribution

Although we have not examined any specimens between Durban and northeastern Somalia, seventeen specimens from Somalia (Gulf of Aden and off the Horn of Africa) are here identified as *E. wongratanai*. Whitehead (1985) has shown a continuous range of "*E. teres*" in his distribution map for the entire east coast of Africa, but he has given no specific localities between southern Mozambique and northeast Somalia at Cape Gardafui. This may be a real population gap or a region of low population abundance for a species of *Etrumeus* (primarily a temperate genus) given the tropical latitude. The apparent abundance off the Cape and the Gulf of Aden coast of Somalia, still well within the tropical zone, can be explained by the cooler sea owing to upwelling gen-

erated by monsoons.

We have also not examined any specimens of *E. wongratanai* south of Durban, although there are reports of this species occurring as far south as Port St. Johns, Eastern Cape (31°37.859'S, 29°33.378'E; S. Charter, pers. comm.). The identification of two specimens from Cape Town reported by Matsubara and Iwai (1959) as *E. micropus* and re-identified based on their meristic data as *E. teres* (= *E. wongratanai* for South Africa) by Wongratana (1983) might be questioned. In their extensive review of the purse-seine fishery for *E. whiteheadi*, Roel and Armstrong (1991) wrote, "*E. teres* (East Coast or tropical round herring)... is a tropical species which extends only as far south as Natal on the east coast of South Africa (Whitehead and Wongratana, 1986)".

Etymology

The species is named in honour of Dr. Thosaporn Wongratana, in recognition of his extensive systematic research on clupeoid fishes.

Comparative material

Etrumeus sadina, UF 39749, 2: 114-115 mm, ESE of Cape Lookout, North Carolina, USA; ROM 34508, 5: 103-114 mm, Maces Bay, New Brunswick, Canada; UF 38257, 15: 85-105 mm, Alabama, Mobile Bay, USA.

Etrumeus sp., USNM 307970, 6: 145-158 mm Madagascar, south coast.

Genetic analysis

The genetic analysis, based on 61 sequences of mtDNA *cyt b* of *Etrumeus* specimens supports species-level differentiation between *E. whiteheadi*, *E. golanii*, and *E. wongratanai*. All phylogenetic methods converged on a single tree topology, with evolutionary separations between Red Sea (and Mediterranean) and South African individuals (Fig. 4). The analyses confirmed separation between these two groups and *E. whiteheadi* from South Africa or *E. sadina* from the Gulf of Mexico, USA. Bayesian trees converged on the same topology for multiple runs and when the run length was increased. Sequence divergence (*d*) between these clades was based on the corrected average pairwise nucleotide difference (Posada, 2003) from Arlequin vers. 3.1 software, divided by the total number of base pairs in the sequence.

Table V. - Matrix of pairwise sequence divergence (*d*; below diagonal) between African *Etrumeus* clades/species and *Etrumeus sadina* based on the corrected average pairwise nucleotide difference (Posada 2003) from Arlequin 3.1 software.

Clade/Species	1	2	3	4
<i>E. golanii</i> (1)	0.0016			
<i>E. sadina</i> (2)	0.22	0.00		
<i>E. whiteheadi</i> (3)	0.20	0.12	0.0069	
<i>E. wongratanai</i> (4)	0.033	0.18	0.19	0.0027

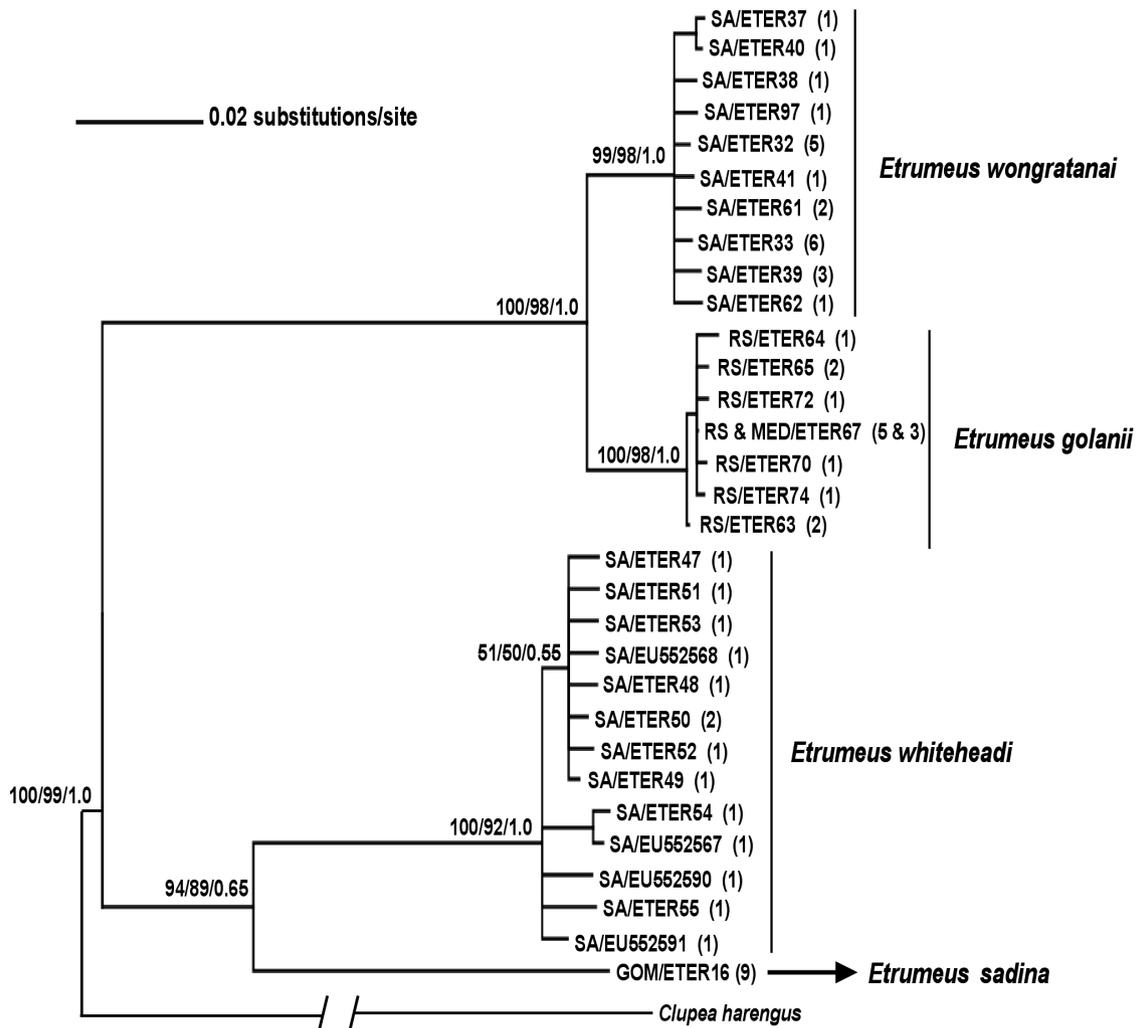


Figure 4. - Phylogeny showing relationships among mtDNA cytochrome *b* haplotypes (677 bp) for *Etrumeus* specimens collected in the Red Sea (RS, *N* = 13), the Mediterranean Sea (MED, *N* = 3), and off the southeast coast of South Africa (SA, *N* = 22). *Etrumeus whiteheadi* (*N* = 10) specimens, also collected from South Africa, were included for comparison. Genetic analyses were further supplemented by the addition of four previously published DNA sequences of *E. whiteheadi* and nine previously published DNA sequences of *Etrumeus sadina* from the Gulf of Mexico, USA. Trees were constructed using neighbor-joining (NJ), maximum-likelihood (ML), and Bayesian (BA) approaches; all phylogenetic methods converged on a single tree topology and so only the NJ tree is presented here. Maximum bootstrap values for NJ and ML methods, as well posterior probabilities from BA analysis are shown above the nodes (NJ/ML/BA). Numbers in parentheses represent the number of specimens for each haplotype, and branch lengths are according to indicated scale. Note that the branch leading to the outgroup species was reduced by 50%.

We here found that Red Sea (or Mediterranean) and South African clades displayed $d = 0.20-0.22$ and $d = 0.18-0.19$, when compared to *E. whiteheadi* or *E. sadina* sequences, respectively, and $d = 0.033$ when compared to each other (Tab. V). This is in contrast to $d = 0-0.0069$ within clades. Such genetic divergence is consistent with a long period of separation between existing (*ca.* 9 to 11 million years) and newly described species (*ca.* 1.65 million years), based on an approximation for *cyt b* calibration in teleost fishes (2% per million years between lineages; see Bowen *et al.*, 2001; Reece *et al.*, 2010).

KEY TO THE AFRICAN SPECIES OF *ETRUMEUS*

- 1a. Origin of pelvic fins about one-third eye diameter posterior to vertical at rear end of dorsal fin; vertebrae 52 or 53; gill rakers 43-51 2
- 1b. Origin of pelvic fins directly below or slightly anterior to rear end of dorsal fin base; vertebrae 50; gill rakers 51-56; (southern Africa from Durban to southern Angola) *whiteheadi*

- 2a. Gill rakers 47-51; scales on dorsal half of body with a dark grey spot (northern Red Sea and eastern Mediterranean Sea) *golanii* sp. nov.
 2b. Gill rakers 43-47; scales dorsally on body without a dark spot (KwaZulu-Natal to northeastern Somalia).
 *wongratanai* sp. nov.

DISCUSSION

The taxonomy of herrings and anchovies (Order Clupeiformes) has been recently revised from the highest ranks (DiDario and Schaffer, 2002; DiDario, 2009) to the lowest taxonomic designations, which are characterized by species distinguishable by genetics and distributions, with only subtle differences in morphology (Bowen and Grant, 1997; Grant and Bowen, 2006). Indeed, Whitehead (1985) commented that the only distinguishing character for sardine (*Sardinops*) species (apart from genetics) was that they inhabited different regions of the world, but he endorsed the taxonomy explicitly based on this geographic isolation. Much the same can be said for *Etrumeus*.

The round herring is the most important commercial species in the Gulf of Suez purse-seine fishery, contributing about 25% of the total production in this region (Sanders and Kedidi, 1984). A stock assessment of “*E. teres*” in the Gulf of Suez, where the annual sea temperature varies from 20°C to 25°C, indicates that the fishery then involved 84 vessels (Sanders and Kedidi, 1984). The largest annual landing (1979-1980) was 6449 metric tons, dropping to 2076 metric tons in 1981-1982, indicating overexploitation. The authors wrote, “The quantities landed from immediately adjacent to the Gulf were negligible...none were caught from the grounds off southern Egypt”. The fishery is seasonal, generally from October or November through May, and takes place at night, involving the prior concentration of fish by light attraction. Fishing operations cease during an approximate 10-day period each month when the moon is full. Two carangid fishes, *Trachurus indicus* and *Decapterus maruadsi*, are also caught with *E. golanii*, but they contribute less than 10% of the total catch. Spawning takes place from January through May, and the young recruit to the fishery between seasons, reaching an average total length of 8.2 cm at age one. Sexual maturity is attained a few months before age two.

Roel and Armstrong (1991) published on the status of the fishery for *E. whiteheadi* in South Africa, which differs from *E. golanii* in being regarded as underexploited, despite 80 purse-seiners operating in 1989 with a total annual catch of up to 685,000 tons. The main target species of the purse-seine fishery are the South African Pilchard (*Sardinella ocellatus*) and the South African Anchovy (now *Engraulis encra-*

sicolus). *E. whiteheadi* is often found in mixed schools with these two, more commercially important, clupeoid fishes.

Roel and Armstrong (1991) also reviewed what is known of the biology of *E. whiteheadi*. As in other species of the genus, there is diel vertical migration of adults and subadults to coincide with the migration of the zooplankton. During daylight hours, the fish congregate about 15-20 m above the seabed at a depth of 100-400 m (individuals smaller than 11 cm are usually found in less than 100 m). The fish begin to migrate toward the surface a few hours before sunset, feeding mainly on euphausiids and copepods (Wallace-Fincham, 1987). At daybreak they coalesce into schools and begin their descent. Their large eyes probably facilitate their vertical migrations to track zooplankton sources each night. From a study of otoliths, Geldenhuys (1978) reported that only 50% were mature at age 3 and a SL of 17 cm, and all were mature at age 5 and a SL of 22 cm; young fish were found throughout the year. Roel and Melo (1990) reported peak spawning from August to October.

We now present additional justification for *E. golanii* and *E. wongratanai* being treated as distinct species. First, despite modest morphological differentiation between these populations (*i.e.*, gill-rakers and scale markings), we observed a 3.3 % difference at the mtDNA *cyt b* gene and a phylogeny that indicates reciprocally monophyletic lineages (Fig. 4). Although it is still not possible to define a clear cut-off value for genetic divergence at *cyt b* that would be applicable across all teleosts, this level of genetic differentiation is comparable to differences observed between recognized pairs of geminate species of shore fish separated more than three million years ago by the rise of the isthmus of Panama ($d = 0.033$ to 0.048 ; Lessios, 2008).

Second, *E. golanii* is isolated in the northern Red Sea from *E. wongratanai* that ranges north to the eastern Gulf of Aden off Somalia, a distance of more than 1,700 km. Pleistocene glaciations over the past two million years severely restricted movement between these two bodies of water owing to the shallow sill at the Strait of Bab el Mandab (Siddall *et al.*, 2003). The higher sea temperature south of the Gulfs of Suez and Aqaba in the Red Sea is an effective contemporary barrier to dispersal. The turbidity of the southern portion of the Red Sea is an additional barrier that likely reinforces geographic separation of these two new species.

Third, morphological homogeneity with deep genetic differentiation are also known from other members of the ancient “lower” teleosts. For example, the bonefishes (*Albula* sp.) included a single pantropical species (*A. vulpes* in Whitehead 1986), with highly conserved morphology and ecology across its range. Subsequent genetic investigations revealed eight deeply divergent (and sometimes sympatric) mtDNA lineages (Bowen *et al.*, 2007), which are now receiving taxonomic recognition (Hidaka *et al.*, 2008; Pfeiler *et al.*, 2011). Indeed, *Albula* specimens from distant locations

are often indistinguishable based on conventional, external morphological traits. Stabilizing selection in the homogeneous habitat occupied by bonefishes (*i.e.*, tropical sand flats) is thought to promote the retention of highly conserved morphology despite overlapping species distributions and highly dispersive leptocephalus larvae. The fact that we see a similar pattern in the round herring indicates that *Etrumeus* may also experience stabilizing selection in response to their homogeneous habitat in the open ocean, although further study of this and other cryptic fauna is needed to confirm this hypothesis.

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