

# Hiding in broad daylight: molecular and morphological data reveal a new ocean sunfish species (Tetraodontiformes: Molidae) that has eluded recognition

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The taxonomy of the ocean sunfishes (Molidae) has a complicated history. Currently, three genera and four species are recognized, including two in the genus *Mola* (*M. mola* and *M. ramsayi*). In 2009, a genetic study revealed a potential third species, *Mola* species C, in Southeast Australian waters. Concentrating on this region, we obtained samples and morphological data from 27 *Mola* sp. C specimens, genetically confirmed the existence of this species (mtDNA D-loop and cytochrome *c* oxidase 1), and established its morphology across a size spectrum of 50–242 cm total length. *Mola* sp. C is diagnosed by clavus meristics [15–17 fin rays (13–15 principal, 2 minor), 5–7 ossicles, paraxial ossicles separate], clavus morphology (prominent smooth band back-fold, rounded clavus edge with an indent), and body scale morphology (raised conical midpoints, non-branching). This species does not develop a protruding snout, or swollen dorso- or ventrolateral ridges. Body proportions remain similar with growth. A review of the historic literature revealed that *Mola* sp. C is a new, hitherto undescribed species, *M. tecta*, which we describe and diagnose, and that it is the first proposed addition to the genus *Mola* in 125 years. Its core distribution is likely in the temperate waters of the Southern Hemisphere.

ADDITIONAL KEYWORDS: Australia – CO1 mtDNA – D-loop – morphology – morphometrics – New Zealand – phylogenetics – southern hemisphere – taxonomy.

## INTRODUCTION

The taxonomy of the ocean sunfishes (Molidae Bonaparte, 1832) has a long and complicated history dating back more than 250 years, when *Mola mola* (Linnaeus, 1758) (originally *Tetraodon mola*) was first placed within the Linnaean classification system. Over the following century, numerous putative new species were described, typically based on single specimens,

ranging in life history stages from pre-juveniles (e.g. Koelreuter, 1766; Pallas, 1770; Mitchill, 1828) to large adults (e.g. Ranzani, 1839; Giglioli, 1883; Philippi, 1892). The taxonomy quickly became complex due to limited clarity on intraspecific morphological variation, ontogenetic changes and the potential for sexual dimorphism. This confusion was further compounded by the difficulty in preserving and storing sub-adult and adult specimens. Many specimens were reduced to mounted skins with varying degrees of accuracy in the reproduction of morphology (e.g. Philippi, 1892; Harting, 1865). Furthermore, opinions differed as to the correct systematic position of these unusual looking

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fishes, so species were re-grouped and moved between existing and new taxonomic groups, generating a large number of synonyms. Together with spelling deviations, the number of names in the literature for the Molidae soared (e.g. Fraser-Brunner, 1951) and by the turn of the 19th century, the cumulative number of nominal genera and species had surpassed 19 and 50, respectively (Parenti, 2003; Eschmeyer, Fricke & van der Laan, 2017). Comparative reviews of the taxonomy were (and still are) difficult due to descriptions and drawings with limited detail and lack of accuracy (e.g. Linnaeus, 1758; Guilding in Swainson, 1839; Ayres, 1859), the logistics associated with handling, preserving and storing the very large adults (e.g. Steenstrup & Lütken, 1898; Matsuura, 2015), and the lack of retention or later loss of holotypes (Parenti, 2003; Eschmeyer et al., 2017).

During the 20th century, a general consensus emerged that only a small number of species of sunfish existed. A landmark review of the Molidae by Fraser-Brunner (1951) synonymized the family to just five species in three genera: *Ranzania* Nardo, 1840, *Masturus* Gill, 1884 and *Mola* Koelreuter, 1766. He proposed two species in the genus *Mola*: *M. mola* and *M. ramsayi* (Giglioli, 1883), still recognized by major taxonomic authorities today (e.g. Bailly, 2015; Eschmeyer et al., 2017). Fraser-Brunner (1951) suggested that *M. mola* had a wide distribution in the world's oceans, but was replaced by *M. ramsayi* in the Southern Pacific, with sympatric distributions around Australia.

In 2009, Yoshita et al., using phylogenetic analysis based on D-loop sequences and accompanying morphological data, identified two clades of *Mola* occurring sympatrically off Japan. They termed them *Mola* group A and B (hereafter termed *Mola* sp. A and *Mola* sp. B), and tentatively linked them to *M. ramsayi* and *M. mola*, respectively, based on matching morphology with Fraser-Brunner (1951). However, one morphological discrepancy between *Mola* sp. A and *M. ramsayi* could not be resolved: a smooth clavus band (termed 'band of reduced denticles' by Fraser-Brunner, 1951) was present on *Mola* sp. A (Yoshita et al., 2009), whereas *M. ramsayi* was described by Fraser-Brunner (1951), and several subsequent authors, as lacking a smooth band (e.g. Heemstra, 1986; Glover, 1994; Hutchins, 2001; Bray, 2008; Thys et al., 2013). While further research is needed to formally resolve this discrepancy, here we follow Yoshita et al. (2009), and Matsuura (2015) in tentatively linking *Mola* sp. A to *M. ramsayi*, on the grounds that the smooth band was probably overlooked on the *M. ramsayi* holotype, an oversight subsequently repeated in the literature. Previous and recent findings show that *Mola* specimens from New South Wales in Australia, the type locality of *M. ramsayi*, indeed cluster with *Mola* sp. A (Yoshita et al., 2009; M. Nyegaard, unpublished data). We also follow Yoshita et al. (2009) in linking *Mola* sp. B to *M. mola*,

but recognizing further research is needed to resolve the nomenclature of what appears to be an Atlantic and Pacific clade (Ahuir-Baraja, Yamanoue & Kubicek, 2017; Sawai et al., 2017).

In addition to the *Mola* sp. A and *Mola* sp. B clades, Yoshita et al. (2009) also found evidence of a third *Mola* species (*Mola* sp. C), based on the D-loop sequence of one specimen from New South Wales in Australia, and the partial D-loop sequences of two specimens from South Africa. The latter two specimens were originally from a genetic study by Bass et al. (2005), who interpreted them as a *M. ramsayi* Atlantic group (see Sawai et al., 2017). As no morphological information was collected in either study, the taxonomic status of *Mola* sp. C remained unresolved.

Given the need to formally link genetic clades with nomenclature, BLAST searches of ocean sunfish DNA sequences through the Barcode of Life Data Systems (BOLD; [www.boldsystems.org](http://www.boldsystems.org)) present some pitfalls. Over 100 Molidae mtDNA cytochrome *c* oxidase 1 (*COI*) sequences are, as of March 2017, lodged with BOLD, forming four BINs: *Ranzania laevis* (Pennant, 1776) (comprising the majority of the Molidae sequences), *Masturus lanceolatus* (Liénard, 1840) and two separate clusters of *M. mola*. Currently, no *COI* sequences labelled *M. ramsayi* (or *Mola* spp. A, B or C) are available; however, blasting a *Mola* sp. A *COI* sequence returns a small number of very high similarity scores, pointing to potential mislabelled sequences. This is not surprising, given *Mola* sp. A has been mistaken for *Mola* sp. B in various parts of the world (Sagara et al., 2005; Yoshita et al., 2009; Thys et al., 2013; Sawai et al., 2017). In light of recent genetic and taxonomic findings, a review of available Molidae *COI* sequences would therefore be useful, including to verify the existence of *Mola* sp. C as a separate species.

During a recent large-scale Molidae biopsy survey around Australia and New Zealand, we found a subset of individuals among our material, nesting genetically within the *Mola* sp. C D-loop clade of Yoshita et al. (2009). The aim of this study is to formally describe *Mola* sp. C, and this was achieved by first verifying the existence of the clade through analysis of the *COI* locus, comparing our specimens to Molidae sequences available online. After establishing the common morphological characteristics of genetically verified *Mola* sp. C specimens, we reviewed museum material across Australia and New Zealand to locate any *Mola* sp. C specimens held in collections. Based on both fresh and preserved specimens, we describe the morphology of *Mola* sp. C across a size spectrum of 50–242 cm total length (TL). We compare the morphology to the original descriptions of the synonyms of *M. mola* and *M. ramsayi* to establish whether *Mola* sp. C has been described previously. On the basis of both genetics and morphology, we conclude that *Mola* sp. C is a new *Mola* species, which we describe herein.

## MATERIAL AND METHODS

### SPECIMEN COLLECTION

A large-scale, non-lethal Molidae biopsy-sampling program was undertaken in 2013–2015 in the Australian and New Zealand tuna and billfish long-line fisheries, where sunfish are occasionally caught as by-catch. From 2013 onwards, museums across Australia and New Zealand kept us informed of local sunfish strandings; we obtained photographs, measurements and genetic samples opportunistically, with the help of local residents, fisheries department and museum staff, as well as attending strandings ourselves where possible. To acquire specimens for closer examination, we euthanized three small *Mola* sp. C from the New Zealand long-line fishery and prepared one of these as holotype at the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ).

### REVIEW OF MUSEUM SPECIMENS

The Molidae collections at the natural history museums in Australia and New Zealand were reviewed to identify specimens with morphological features akin to *Mola* sp. C. The Melbourne (NMV), Perth (WAM), Auckland (AIM), Otago (OMNZ) and Wellington (NMNZ) museum collections were inspected in person, while material from the Adelaide (SAMA), Darwin (NTM), Hobart (TMAG), Sydney (AMS), Queensland (QM), Christchurch (CMC) and Whanganui (WRM) museums were inspected via photographs and descriptions provided by museum staff [institutional codes follow Sabaj (2016), except OMNZ and WRM]. From accessible material, we identified a small number of specimens and casts with similar characteristics to our genetically confirmed *Mola* sp. C specimens, and morphometric and morphological data were obtained from these. Tissue samples appropriate for genetic analysis were generally not available from museum specimens (but see Table 1).

### MOLECULAR SEQUENCING

Tissue samples were fixed in RNALater or 95% ethanol. We used a lithium chloride and chloroform salting out method (Gemmell & Akiyama, 1996) for DNA extraction. The mitochondrial D-loop and *COI* loci were amplified using MolaA and MolaB primers (Yoshita *et al.*, 2009), and universal fish primers F1 (Ward *et al.*, 2005), respectively. We used Bioline Biotaq polymerase enzyme for the polymerase chain reaction (PCR) with each reaction consisting of 0.2 µL Taq polymerase, 2 µL 10× buffer, 0.8 µL MgCl<sub>2</sub>, 0.4 µL dNTP (2.5 mM each), 0.8 µL primers, 13.8 µL water and 1 µL template (10 ng/µL). The 20 µL reaction mixtures were subjected to an initial denaturation of 94 °C for 60 s,

followed by 25 cycles of 94 °C for 30 s, 58 °C for 40 s and 72 °C for 60 s. The PCR products were purified using the PALL AcroPrep96 filter plate 30 kDa kit prior to Sanger sequencing in forward and reverse using an ABI Big Dye Terminator v.3.1 cycle sequencing kit. Sequencing products were run on an ABI 3730xl DNA Analyzer through the Genetic Analysis Service at Otago University, New Zealand. All sequences were uploaded to NCBI with accession numbers provided in Supporting Information, Table S1.

### PHYLOGENETIC ANALYSIS

D-loop sequences were assembled in McVector v.14.5.3, and pooled with *Mola* spp. D-loop sequences from Yoshita *et al.* (2009) (North and Southwest Pacific), Ahuir-Baraja *et al.* (2017) (Mediterranean) and Sawai *et al.* (2017) (Indian Ocean), available from the National Center for Biotechnology Information (NCBI). *COI* sequences were pooled with publicly available Molidae *COI* sequences from NCBI and BOLD (Supporting Information, Table S2). D-loop and *COI* sequences from one *Mola* sp. B (261 cm TL) and four *Mola* sp. A (24, 58, 120 and 120 cm TL, all with smooth clavus bands) from New Zealand were included as controls, and to confirm the *Mola* sp. A clade in the *COI* analysis. To avoid a large number of indels in the alignment, which can be problematic in phylogenetic inference (Warnow, 2012), we used *Ma. lanceolatus* as the outgroup in the D-loop analysis, rather than the more divergent *R. laevis*, which was the outgroup for the *COI* analyses. For both loci, the pooled sequences were aligned with ClustalW implemented in MacVector v.14.5.3, using the default settings. The alignments, with a small number of scattered indels for the D-loop, were checked and trimmed.

For both loci, phylogenetic relationships were inferred using maximum likelihood (ML), Bayesian and maximum parsimony (MP) methods, as described below. The most appropriate model of sequence evolution was selected based on the corrected Akaike and Bayesian Information Criteria (AICc and BIC), calculated in jModelTest v.2.1.10 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012), using the likelihood scores of 88 candidate models with 11 substitution schemes. This included models with equal/unequal base frequencies (+F), with/without a proportion of invariable sites (+I) and with/without rate variation among sites (+G) (four rate categories). We used an ML-optimized base tree, and a Subtree-Pruning-Regrafting (SPR) tree topology search. The AICc and BIC gave similar results for the D-loop, with HKY85 (Hasegawa, Kishino & Yano, 1985) +I+G the best fitting model by BIC, and second best fit by AICc. For *COI*, HKY+G was the best fitting model based on both BIC and AICc.

**Table 1.** *Mola tecta* sp. nov. holotype (in bold), paratypes and other material examined as part of this study

Specimen	TL (cm)	Data source	Front profile	Clavus shape	Smooth band back-fold	Pectoral fin rays	Dorsal/anal fin rays	Principal clavus fin rays <sup>a</sup>	Minor clavus fin rays	Clavus ossicles <sup>a</sup>	Paraxial ossicles	Scale shape
NMNZ P.005890	49.9	M:m,x	Tapered	Rounded, indented	Present (faint)	12	17/17	15 (7/8)	2	0	Separate	Rounded
AIM MA29864	51.1	M:m,x	Tapered	Rounded, faint indented	Present (faint)	13	19/18	13 (6/7)	2	3 (1/2)	Separate	Rounded
NMNZ P.033995	57.2	M:m,x	Tapered	Rounded, indented	Present	12	18/17	14 (6/8)	2	2 (1/1)	Separate	Rounded
NMNZ P.001418	60.2	M:m,x	Tapered	Rounded, faint indented	Not visible	12	18/17	13 (5/8)	2	2 (0/2)	Separate	Rounded
G06	62	F:g,p	–	Rounded, indented	Present	–	–	–	–	–	–	–
NMNZ P.002980	64.6	M:m	Tapered	Rounded, indented	Present (faint)	11	18/17	–	–	3 (1/2)	Separate	Rounded
NZ18	65	F:g,m,d	Tapered	Rounded, indented	Present	–	–	14 (7/7)	2	6 (3/3)	Separate	Rounded
NMNZ P.006126	64.8	M:m,x	Tapered	Rounded, indented	Present	11	18/17	15 (7/8)	2	5 (2/3)	Separate	Rounded
NZ19	69	F:g,m,d	Tapered	Rounded, indented	Present <sup>b</sup>	–	–	19 (9/10) <sup>b</sup>	3–4 <sup>b</sup>	8 (3/5) <sup>b</sup>	Separate	Rounded
NMNZ P.034217	69.8	M:m,x	Tapered	Rounded, indented	Present	13	18/16	15 (7/8)	2	7 (3/4)	Separate	Rounded
OMNZ VT3249	78	C:m	Tapered	Rounded, indented	Present	–	–	–	–	–	–	Rounded
NMV A26565-001	78.5	F:p; M:m	Tapered	Rounded, indented	Present	–	–	15 (7/8)	–	6 (3/3)	Separate	Rounded
NMNZ P.034187	79.7	M:m,x	Tapered	Rounded, indented	Present	12	19/18	13 (6/7)	2	5 (2/3)	Separate	Rounded
NZ17	81	F:g,m	Tapered	Rounded, indented	Present	–	–	14 (6/8)	2	5 (2/3)	Separate	Rounded
SAMA F7542	Ca. 90	M:g,p	Tapered	Rounded, indented	Present	–	–	–	–	–	–	Rounded
NMV A18725	90.5	M:m	Tapered	Rounded, indented	Present	–	–	–	–	6 (2/4)	Separate	Rounded
NZ07	100	F:g,p	Tapered	Rounded, indented	Present	–	–	–	–	–	–	–

Table 1. Continued

Specimen	TL (cm)	Data source	Front profile	Clavus shape	Smooth band back-fold	Pectoral fin rays	Dorsal/anal fin rays	Principal clavus fin rays <sup>a</sup>	Minor clavus fin rays	Clavus ossicles <sup>a</sup>	Paraxial ossicles	Scale shape
<b>NMNZ P-057679</b>	<b>101.1</b>	<b>F:g,m,x; M:m</b>	<b>Tapered</b>	<b>Rounded, indented</b>	<b>Present</b>	<b>11</b>	<b>18/17</b>	<b>15 (7/8)</b>	<b>2</b>	<b>7 (3/4)</b>	<b>Separate</b>	<b>Rounded</b>
AIM MA30933	102	C:m,p	Tapered	Rounded, no indent <sup>c</sup>	Present	-	-	-	-	-	-	-
TMAG D3912	150	F:g,p	-	Rounded, indented	Present	-	-	-	-	-	-	-
NZ08	151	F:g,p	Tapered	Rounded, indented	Present	-	-	-	-	-	-	-
NZ12	155	F:g,m	Tapered	Rounded, indented	Present	12	-	13 (6/7)	2	6 (2/4)	Separate	Rounded
OMNZ X2017.19	169	F:g,m,p,d	Tapered	Rounded, indented	Present	-	-	-	-	-	-	Rounded
NZ14	170	F:g,p	-	Rounded, indented	Present	-	-	-	-	-	-	-
NZ09	193	F:g,p	Tapered	Rounded, indented	Present	-	-	-	-	-	-	-
NZ01	212	F:g,m,p	Tapered	Rounded, indented	Present	11	-	-	-	-	-	-
OMNZ VT3248	242	C:m	Tapered	Rounded, indented	Present	12	-	-	-	-	-	Rounded

All specimens: head bump absent; chin bump absent; snout absent; short dorso-lateral ridge present.  
 TL, total length; C, cast from fresh specimen; F, fresh specimen; M, museum specimen; d, digestive tract content; g, genetic sample; m, morphometric measurements; p, specimen examined from photographs; x, x-ray.  
<sup>a</sup>Dorsally/ventrally of the smooth band back-fold.  
<sup>b</sup>Abnormal clavus, see text for details.  
<sup>c</sup>Indented likely lost during cast preparation.

### Maximum likelihood

ML analysis was done in phyML (Guindon & Gascuel, 2003), implemented through the online T-REX server (Boc, Diallo & Makarenkov, 2012) under the HKY model for both loci. The base frequencies were optimized, and the transition/transversion ratio, gamma shape (in four substitution rate categories) and the proportion of invariable sites (in the D-loop analysis) were estimated by the software. The tree topology was optimized with the 'Best' setting [best of SPR and nearest-neighbour interchange (NNI)] from five random BioNJ start trees, and nodal support assessed by bootstrap from 1000 pseudo-replicates.

### Bayesian analysis

Posterior probabilities (PP) for the Bayesian analyses were estimated in MrBayes (Ronquist *et al.*, 2012) under the HKY model, with rate variation among sites (in four categories) for both loci, and with a proportion of invariable sites for the D-loop analysis. We used default priors and settings. Two concurrent analyses were run, each with four Markov chains (three heated and one cold) of 10 000 000 (D-loop) and 2 000 000 (*CO1*) generations, with the chains sampled every 1000 generations. For both loci, convergence between the two concurrent analyses was confirmed by checking that the SD of split frequencies had decreased below 0.01, and that the effective sample size was above 200 after a burn-in of 30% (Tracer v.1.6; Rambaut *et al.*, 2014).

### MP analysis

For both loci, MP analyses were conducted in Mega v.7 (Kumar, Stecher & Tamura, 2016), including all sites, with an SPR search algorithm (level 1) and five random starting trees. Nodal support was estimated using 1000 bootstrap pseudo-replicates.

### EXTERNAL MORPHOLOGY

The following external characters were assessed whenever possible: (1) body proportions: presence or absence of a 'head bump' (Yoshita *et al.*, 2009; Sawai *et al.*, 2017), and 'chin bump' (Sawai *et al.*, 2017); (2) lateral shape of the head profile: presence or absence of a protruding snout ('forward-projecting snout' in Fraser-Brunner, 1951); (3) frontal profile: presence or absence of swollen 'dorsolateral and ventrolateral ridges' on the body (Barnard, 1935); (4) clavus shape: rounded or lobed/wavy (Fraser-Brunner, 1951; Yoshita *et al.*, 2009; Sawai *et al.*, 2015), with the clavus being the 'movable lobe at the hind margin of the body' (Fraser-Brunner, 1951); and (5) smooth band: present or absent, defined as the 'band of reduced denticles

[termed 'scales' herein] between dorsal and anal fins' (Fraser-Brunner, 1951).

### CLAVUS AND FIN MERISTICS

We examined the clavus on a subset of fresh and preserved specimens (Table 1). The number of clavus ossicles was established by touch on fresh specimens, and by touch and from X-rays, when available, on museum specimens. The number of clavus fin rays, and state of paraxial ossicles (Fraser-Brunner, 1951), was established in fresh specimens after the clavus was cut off along the posterior margin of the smooth band, and dried for several days. The dorsal, anal and clavus fin ray numbers, and the state of the paraxial ossicles, were determined on museum specimens from X-rays.

### SKIN STRUCTURE

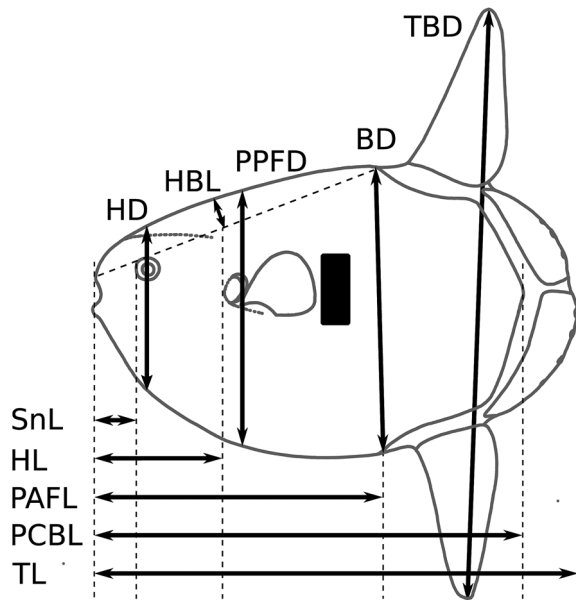
The body scales of the sunfishes are modified into small spines or denticles (Cleland, 1862; Tyler, 1980; Gauldie, 1992) and differ between genera in the family Molidae (Katayama & Matsuura, 2016), as well as between species in the genus *Mola* (Cadenat, 1959; Gauldie, 1992; Sawai *et al.*, 2015; Sawai, 2016b). We examined the scale morphology on the body and clavus on a subset of fresh, preserved and museum cast specimens (Table 1) directly, and through a binocular microscope. A small piece of skin was sampled from two fresh specimens (NZ12 and NZ17) posteriorly of the pectoral fin (Fig. 1), dried and compared with reference skin samples from *Mola* sp. A and *Mola* sp. B (E. Sawai, unpublished data).

### MORPHOMETRIC MEASUREMENTS

External morphometric measurements follow Yoshita *et al.* (2009) and a subset of Sawai (2016a) (Fig. 1) and were obtained from fresh and preserved specimens, as well as museum casts (made from fresh specimens), whenever possible (Table 1). The holotype was measured both fresh and after the preservation process in formalin and isopropyl alcohol. We pooled measurements from fresh and preserved specimens, as potential shrinkage from isopropyl alcohol storage is unlikely to significantly affect the dimensions of preserved specimens (Larochelle *et al.*, 2016). The measurements were calculated as a percentage of TL and plotted against TL to assess potential change in body shape with size.

### ADDITIONAL INVESTIGATIONS

The digestive tract content of three specimens (Table 1) was investigated by emptying the content into a vessel, separating prey items by hand from the



**Figure 1.** Morphometric measurements following Yoshita *et al.* (2009) and a subset of Sawai (2016a). Body depth (BD), head bump length (HBL), head depth (HD), head length (HL), pre-anal fin length (PAFL), pre-clavus band length (PCBL), pre-pectoral fin depth (PPFD), snout length (SnL), total body depth (TBD), total length (TL). Black box indicates region of skin sampling.

heavy parasite load and washing prey items in a 600- $\mu$ m mesh sieve, as needed, for identification under a binocular microscope.

#### REVIEW OF HISTORICAL RECORDS

To establish whether *Mola* sp. C was among previously described *Mola* species, we reviewed the original descriptions of *M. mola* and *M. ramsayi*, and all nominal Molidae species now considered synonyms of *M. ramsayi* or *M. mola*, or regarded as *nomen nudum* by Fraser-Brunner (1951), Parenti (2003) and/or Eschmeyer *et al.* (2017). In total, 37 species descriptions were reviewed, along with relevant, associated literature (Table 2).

## RESULTS

#### PHYLOGENETIC RELATIONSHIP

Details of new *Mola* D-loop sequences (NCBI accession numbers MF158131–MF158149) are provided in Supporting Information, Table S1. The trimmed alignment of Molidae D-loop sequences (new and from the literature) comprised 816 characters, with 187 parsimony informative sites. The phylogenetic trees inferred by ML, MP and Bayesian methods displayed similar

topographies, with no differences in the relationships of the major lineages. As expected, they resembled those of Yoshita *et al.* (2009), Ahuir-Baraja *et al.* (2017) and Sawai *et al.* (2017) with three major clades: *Mola* spp. A, B and C. Our five control sequences from New Zealand nested within the *Mola* sp. A ( $n = 4$ ) and *Mola* sp. B ( $n = 1$ ) clades, respectively, while the remaining 14 sequences clustered with the *Mola* sp. C sequence of Yoshita *et al.* (2009) (Fig. 2). The monophyly of each *Mola* clade was well supported with branch supports of 100% in ML, 1.0 in PP and 100% in MP for each group. The nodal support for the *Mola* sp. A and *Mola* sp. C grouping had moderate support (62% in ML and 71% in MP), with the bootstrap results at times placing *Mola* sp. A and *Mola* sp. B as sister clades.

Details of new *CO1* *Mola* sequences (NCBI accession numbers MF158115–MF158130), and sequences downloaded from BOLD and NCBI, are provided in Supporting Information, Tables S1 and S2. The trimmed alignment of the *CO1* sequences comprised 627 characters, with 124 parsimony informative sites. Five main clades were produced, each with robust node support of 99–100% in ML, 0.95–1.0 in PP and 91–100% in MP (Fig. 3). Three clades corresponded to the sequence taxon labels in NCBI/BOLD (i.e. *R. laevis*, *Ma. lanceolatus* and *M. mola*), while a fourth clade comprised our new *Mola* sp. C sequences, ailing with a BOLD sequence labelled ‘Tetraodontiformes’ (AMS174-08), originating from museum specimen AMS I.41536, registered in OZCAM (2017) as *M. mola*. However, the D-loop from this specimen was included in Yoshita *et al.* (2009) as sample NNSW-1, that is *Mola* sp. C. The fifth clade comprised our four *Mola* sp. A sequences from New Zealand, and one *Ma. lanceolatus* and two *M. mola* sequences from NCBI/BOLD. These latter three sequences were probably mislabelled for the following reasons: (1) The ‘*Ma. lanceolatus*’ sequence KU945271, from specimen ASIZP0806237 (Chang *et al.*, 2017), was originally identified as *M. mola* in the Fish Database of Taiwan (<http://fishdb.sinica.edu.tw>), indicating potential sample or specimen identification uncertainties; (2) ‘*M. mola*’ sequence AP006238 is the *CO1* locus from the ‘*M. mola*’ mitogenome (Yamanoue *et al.*, 2004), re-identified as *Mola* sp. A (sample OI-1) by Yoshita *et al.* (2009); and (3) The ‘*M. mola*’ sequence HQ167728 originated from a Mediterranean specimen, identified at the time by its 100% similarity with the *CO1* locus of the ‘*M. mola*’ mitogenome AP006238, and a lack of *M. ramsayi* records from the area (E. Keskin, Ankara University, personal communication, July 2014). However, mitogenome AP006238 was from *Mola* sp. A (see above), and *Mola* sp. A has since been recorded in the Mediterranean (Ahuir-Baraja *et al.*, 2017). We conclude that the mixed cluster in Fig. 3 is an artefact of sequence mislabelling, rather than an indication of fundamental problems with the *Mola* phylogeny. As

**Table 2.** Nominal species listed as *Mola* sp. or *nomen nudum* by Fraser-Brunner (1951) (F), Parenti (2003) (P) and Eschmeyer et al. (2017) (E), with assessment against the *Mola tecta* sp. nov. morphological characteristics described in the text

Assessment of nominal species against the <i>Mola tecta</i> morphological characteristics	Species identity by taxonomic authorities
<p><b><i>Tetraodon mola</i> Linnaeus, 1758: 334. Type locality: Mediterraneo</b>  <b>[Mediterranean Sea]. No types known.</b> Valid species, no citation. Literature source [Artedi, 1738: 61, 83; Bianchi, 1746: 297; Gronovius, 1754: 55 (No. 125)]. Bianchi (1746) and Gronovius (1754) indicated <i>Ranzania laevis</i>, but Artedi (1738) indicated <i>Mola</i> sp. Identification through use of name (see text).</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Mola aculeata</i> Koelreuter, 1766: 337, Pl. 8 (figs 2, 3). Type locality: not known. No types known.</b> Original source: two pre-juvenile specimens from the collection at the Imperial Academy of Sciences in St. Petersburg. Improbable candidate for <i>M. tecta</i> as specimens were highly unlikely to be from the temperature Southern Hemisphere due to the limited exploration of these waters at the time of reporting. Attempts to find the specimens as part of this study were unsuccessful.</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Diodon mola</i> Pallas, 1770: 39, Pl. 4 (fig. 7). Type locality: Guinea. No types known.</b> Original source. Unneeded new name (Eschmeyer et al., 2017). Pre-juvenile; unlikely candidate for <i>M. tecta</i> due to tropical type locality.</p>	<i>M. mola</i> (F,P,E)
<p><b>Ostracion mola</b> Forsskål, 1775: xviii. <b>Type locality: Malta.</b> Original source. Name only, not available (Eschmeyer et al., 2017).</p>	<i>nomen nudum</i> (P,E)
<p><b><i>Diodon nummularis</i> Walbaum, 1792: 600. Type locality: not known. No types known.</b> Literature source [Ruysch, 1710: 26 (No. 63), Pl. 3 (fig. 7); Koelreuter, 1766: 337, Pl. 8 (figs 2, 3); Pallas, 1770: 39, Pl. 4 (fig. 7); Gmelin, 1788: 1452<sup>a</sup> (No. 3)]. Ruysch's (1710) description was superficial, based on a pre-juvenile specimen presumably from Indian waters (given as the old Dutch 'Indiaanisch' and Latin 'Indicus'). Gmelin (1788) was based on literature sources, including Pallas [1770: 39, Pl. 4 (fig. 7)], and Gronovius [1754: 55 (No. 125)]. The latter was based on literature sources Artedi (1738: 61) and Jonstonus [1657: Pl. 9 (No. 1)], both describing adult forms of <i>Mola</i> sp. and <i>R. laevis</i>, respectively. <i>Diodon nummularis</i> is an unlikely candidate for <i>M. tecta</i> due to the localities, and confusion of literature sources.</p>	<i>M. mola</i> (P,E)
<p><b><i>Mola rotunda</i> Cuvier, 1798: 324. Type locality: France. No types known.</b> Presumably literature source (unknown). Unneeded new name for <i>T. mola</i> Linnaeus, 1758 (Eschmeyer et al., 2017).</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Orthroragoriscus fasciatus</i> Bloch &amp; Schneider, 1801: 511. Type locality: mari septentrionali ['northern ocean'; presumably the North Sea]. No types known.</b> Literature source (Duhamel du Monceau, 1777: 306, Pl. 23). Illustration apparently of a specimen from Angola, Africa, but presumably sufficiently similar to include as illustration of <i>O. fasciatus</i>. Unlikely candidate for <i>M. tecta</i> due to description and illustration of protruding snout.</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Orthroragoriscus hispidus</i> Bloch &amp; Schneider, 1801: 511. Type locality: not known. No types known.</b> Literature source [Pallas, 1770: 39, Pl. 4 (fig. 7); Gmelin, 1788: 1452]. Pre-juvenile; unlikely candidate (see <i>D. nummularis</i>).</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Cephalus brevis</i> Shaw, 1804: 437, Pl. 175 (top). Type locality: European seas. No types known.</b> Literature source (Willughby, 1686: 151, Pl. I.26; Linnaeus, 1758: 334; Pennant, 1776: 131; Bloch, 1785: 75, Pl. 125). Unneeded new name based on previously described species and literature sources (Eschmeyer et al., 2017). Unlikely candidate for <i>M. tecta</i> due to mention of commonness in the Mediterranean (Bloch, 1785; Pennant, 1776).</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Cephalus pallasianus</i> Shaw, 1804: 440. Type locality: tropical seas. No types known.</b> Literature source [Pallas, 1770: 39, Pl. 4 (fig. 7); Gmelin, 1788: 1452]. Pre-juvenile, unlikely candidate for <i>M. tecta</i> (see <i>D. nummularis</i>).</p>	<i>M. mola</i> (F,P,E)
<p><b><i>Orthragus luna</i> Rafinesque, 1810a: 17. Type locality: Sicilia [Sicily, i.e. Mediterranean Sea]. No types known.</b> Literature source (Linnaeus, 1758: 334). We consider this an unneeded new name for <i>T. mola</i> Linnaeus, 1758.</p>	<i>M. mola</i> (F,P,E)



Table 2. Continued

Assessment of nominal species against the <i>Mola tecta</i> morphological characteristics	Species identity by taxonomic authorities
<b><i>Orthragus commersoni</i> Rafinesque, 1810a: 17. Type locality: not known.</b> Unknown source. Name only, unavailable (Eschmeyer <i>et al.</i> , 2017). Unlikely candidate for <i>M. tecta</i> due to context of Rafinesque (1810a) indicating <i>R. laevis</i> .	<i>R. laevis</i> (F), <i>nomen nudum</i> (P,E)
<b><i>Diplanchias nasus</i> Rafinesque, 1810a: 17. Type locality: Sicilia [Sicily, i.e. Mediterranean Sea]. No types known.</b> Original source. Also in Rafinesque (1810b: 40) as <i>Diplanchias mola</i> (Eschmeyer <i>et al.</i> , 2017). Unlikely candidate for <i>M. tecta</i> due to locality and description of protruding snout.	<i>M. mola</i> (F,P,E)
<b><i>Mola aspera</i> Nardo, 1827a: 26, 35 (No. 26). Type locality: Adriatica [Adriatic Sea]. No types known.</b> Literature source [Gronovius, 1763: 50 (No. 186); Bloch, 1786: 83, Pl. 128; Daubenton, 1787: 240 ('LUNE')]. Fraser-Brunner (1951: 115) and Eschmeyer <i>et al.</i> (2017) treated this as a questionably synonym. Insufficient taxonomic characters for assessment, however unlikely candidate for <i>M. tecta</i> due to locality.	? <i>M. mola</i> (F), <i>M. mola</i> (P,E)
<b><i>Mola hispida</i> Nardo, 1827b: 104. Type locality: Adriatico mari [Adriatic Sea]. No types known.</b> Literature source [Koelreuter, 1766: 337 <sup>b</sup> , Pl. 8 <sup>c</sup> (figs 2, 3); Pallas, 1770: 39, Pl. 4 (fig. 7 <sup>a</sup> ); Gmelin, 1788: 1452]. Subjectively invalid, secondarily preoccupied in <i>Mola</i> by <i>O. hispidus</i> Bloch & Schneider, 1801 (Eschmeyer <i>et al.</i> , 2017). Pre-juvenile, unlikely candidate for <i>M. tecta</i> (see <i>D. nummularis</i> ).	<i>M. mola</i> (F,P,E)
<b><i>Cephalus ortagoriscus</i> Risso, 1826: 173. Type locality: Nice, France, i.e. Mediterranean Sea. No types known.</b> Original source (Risso, 1810: 60) and literature source <sup>e</sup> (Rondelet, 1558: 326; Bloch, 1786: 83, Pl. 128, Cuvier, 1817: 148). Unlikely candidate for <i>M. tecta</i> due to the number of clavus fin rays (18), its commonness in the Mediterranean, and the mention of sexual dimorphism.	<i>M. mola</i> (F,P,E)
<b><i>Diodon carinatus</i> Mitchill, 1828: 264, Pl. 5 (fig. 1). Type locality: Massachusetts, USA. No types known.</b> Original source. Pre-juvenile, unlikely candidate for <i>M. tecta</i> due to type locality.	<i>M. mola</i> (F,P,E)
<b><i>Pedalion gigas</i> Guilding in Swainson, 1838: 199, fig. 33. Type locality: West Indies. No types known.</b> Original source. Unlikely candidate for <i>M. tecta</i> due to wavy clavus on illustration.	<i>M. mola</i> (F,P,E)
<b><i>Molacanthus pallasii</i> Swainson, 1839: 329. Type locality: not known [given as Guinea in Pallas, 1770]. No types known.</b> Literature source [Pallas, 1770: 39, Pl. 4 (fig. 7)]. We consider this an unneeded new name based on previously described species. Pre-juvenile, unlikely candidate for <i>M. tecta</i> (see <i>D. mola</i> ).	<i>M. mola</i> (F,P,E)
<b><i>Tympanomium planci</i> Ranzani, 1839: 74, 76, table. Type locality: mari adriatico [Adriatic Sea]. Holotype (unique): whereabouts unknown.</b> Literature source (Bianchi, 1755: 331). Subjectively invalid, preoccupied in <i>Mola</i> by <i>M. planci</i> Nardo (1827a) (Eschmeyer <i>et al.</i> , 2017). Unlikely candidate for <i>M. tecta</i> due to protruding snout and scalloped clavus.	<i>M. mola</i> (F,P,E)
<b><i>Trematopsis willughbei</i> Ranzani, 1839: 74, table. Type locality: oceano ['ocean'] [given as Mediterraneo, atque etiam in Oceano (Mediterranean and also in the Ocean) in Willughby, 1686]. Holotype (unique): not found at MZUB.</b> Literature source (Willughby, 1686: 151, Pl. I.26), based on original source. We consider the validity of the species doubtful, as it was based on four holes in a rectangle on top of the head (Willughby, 1686), likely from external damage. Unlikely candidate for <i>M. tecta</i> due to locality, description of a rounded clavus without mention of an indentation, and a protruding snout on the included illustration by Salviani (1554: 154).	<i>M. mola</i> (F,P,E)
<b><i>Ozodura orsini</i> Ranzani, 1839: 75, 80, table, Pl. 6 (right). Type locality: mari adriatico [Adriatic Sea]. Holotype (unique): mount on wall at MZUB.</b> Extant at MZUB, no registration number available. Original source. Unlikely candidate for <i>M. tecta</i> due to locality, description and illustration, in particular a rounded clavus without an indentation, and merged paraxial ossicles.	<i>M. mola</i> (F,P,E)

Table 2. Continued

Assessment of nominal species against the <i>Mola tecta</i> morphological characteristics	Species identity by taxonomic authorities
<b><i>Orthroragoriscus retzii</i> Ranzani, 1839: 75, table. Type locality: not known [given as Landscrona (i.e. Øresund between Denmark Sweden) in Retzius, 1785]. No types known.</b> Literature source (Retzius, 1785: 115, Pl. 4; Retzius, 1800: 310 <sup>o</sup> ). Based on Retzius (1785) (Eschmeyer et al., 2017). Unlikely candidate for <i>M. tecta</i> due to location, rough skin and detailed description and illustration of a prominent smooth band without mention of a back-fold.	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus ghini</i> Ranzani, 1839: 75, table. Type locality: mari mediterraneo [Mediterranean Sea]. No types known.</b> Literature source (Salviani, 1554: 154). Unlikely candidate for <i>M. tecta</i> due to protruding snout on illustration (Salviani, 1554: 154).	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus rondeletii</i> Ranzani, 1839: 75, table. Type locality: mari mediterraneo [Mediterranean Sea]. No types known.</b> Literature source (Rondelet, 1554: 424). Lack of taxonomic details precludes assessment, but unlikely candidate for <i>M. tecta</i> due to commonness at the locality.	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus redi</i> Ranzani, 1839: 75, table. Type locality: mari mediterraneo [Mediterranean Sea]. No types known.</b> Literature source (Redi, 1684: 166). Vague description; lack of taxonomic details precludes assessment. Unlikely candidate for <i>M. tecta</i> due to commonness at the locality.	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus alexandrini</i> Ranzani, 1839: 75, 78, table, Pl. 6 (left). Type locality: mari adriatico [Adriatic Sea]. No known types.</b> Original source. Unlikely candidate for <i>M. tecta</i> due to description and illustration of large head bump and rounded clavus without indentation.	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus blochii</i> Ranzani, 1839: 76, table. Type locality: mari oceano [‘ocean sea’, possibly Atlantic]. No types known.</b> Literature source [Bloch, 1786: 83, Pl. 128; Bonnaterre, 1788: 54, Pl. 17 (fig. 54); Shaw, 1804: 437, Pl. 175 (top)]. Unlikely candidate for <i>M. tecta</i> due to description of rough skin, and mention of commonness at the locality.	<i>M. mola</i> (F,P,E)
<b><i>Orthroragoriscus elegans</i> Ranzani, 1839: 76, table. Type locality: mari atlantico [Atlantic Sea]. No types known.</b> Literature source (Bloch & Schneider, 1801: 511, Pl. 97). Parenti (2003: 3) and Eschmeyer et al. (2017) synonymized <i>O. elegans</i> with <i>M. mola</i> . However, <i>O. elegans</i> was based on <i>O. oblongus</i> in Bloch & Schneider (1801: 511, Pl. 97), which is considered a synonym of <i>R. laevis</i> by Parenti (2003: 4) and Eschmeyer et al. (2017). Unlikely candidate for <i>M. tecta</i> as the illustration in Bloch & Schneider (1801: Pl. 97) is clearly <i>R. laevis</i> .	<i>R. laevis</i> (F), <i>M. mola</i> (P,E)
<b><i>Pallasia pallasii</i> Nardo, 1840: 112. Type locality: not known [given as Guinea in Pallas, 1770].</b> Literature source [Pallas, 1770: 39, Pl. 4 (fig. 7)]. <i>Pallasina pallasii</i> [sic] in Fraser-Brunner (1951: 110, 115), name deviation discussed in Parenti (2003: 6) and Eschmeyer et al. (2017). Unneeded new name based on previously described species. Pre-juvenile; unlikely candidate for <i>M. tecta</i> (see <i>D. mola</i> ).	<i>M. mola</i> (F), <i>nomen nudum</i> (P,E)
<b><i>Orthroragoriscus lunaris</i> Gronow in Gray, 1854: 165. Type locality: Mediterranean Sea. No types known.</b> Literature source <sup>e</sup> [Boussuet, 1558: 179; Gronovius, 1763: 50 (No. 185); Linnaeus, 1766: 412 (gen. 137, No 7); Bianchi, 1755: 331; Borlase, 1758: 268, Pl. 26 (fig. 7); Klein, 1742: 23 (No. 31)]. This author probably meant to describe a <i>Mola</i> species but confused the characteristics and references of <i>R. laevis</i> and <i>Mola</i> sp., precluding assessment.	<i>R. laevis</i> (F), <i>M. mola</i> (P,E)
<b><i>Orthroragoriscus analis</i> Ayres, 1859: 31, fig. 5 (p. 54). Type locality: Santa Barbara Channel, California, USA. Holotype (unique): CAS (lost in 1906).</b> The holotype was unregistered, and lost along with all records in an earth quake and subsequent fire (D. Catalina, California Academy of Sciences, personal communication, April 2017). Original source. Specimen with damaged dorsal and anal fins (Günther, 1870: 319). Description rudimentary, illustration extremely crude, precludes identification below genus level. Unlikely candidate for <i>M. tecta</i> based on locality.	<i>M. mola</i> (F,P,E)

Table 2. Continued

Assessment of nominal species against the <i>Mola tecta</i> morphological characteristics	Species identity by taxonomic authorities
<b><i>Aledon storeri</i> Castelnau, 1861: 76. Type locality: not known [given as Boston Bay, Massachusetts, USA. in Storer, 1839]. No types known.</b> Literature source [Storer, 1839: 515, Pl. 3 (fig. 1)]. Storer (1839) based on original source. Unlikely candidate for <i>M. tecta</i> based on scalloped clavus and a protruding snout.	<i>M. mola</i> (F,P,E)
<b><i>Pedalion capensis</i> Castelnau, 1861: 75. Type locality: la baie delà Table [Table Bay, South Africa]. No types known.</b> Original source. Unlikely candidate for <i>M. tecta</i> due to description of rough skin, protruding snout and scalloped clavus.	<i>M. mola</i> (P,E)
<b><i>Aledon capensis</i> Castelnau, 1861: 75. Type locality: la baie delà Table [Table Bay, South Africa].</b> New combination for <i>P. capensis</i> described by Castelnau in the same paper, placed into new genus <i>Aledon</i> at the end of the article (Eschmeyer <i>et al.</i> , 2017); an unneeded new name.	<i>M. mola</i> (F,P)
<b><i>Orthorogiscus ramsayi</i> Giglioli, 1883: 315. Type locality: New South Wales, Australia. Type BMNH 1883.11.29.22; stuffed skin, poor condition; restored in 2017 (see text).</b> Holotype listed as BMNH 1888.11.29.22 in Eschmeyer (2017). Original source. Unlikely candidate for <i>M. tecta</i> (see text).	<i>M. ramsayi</i> (F,P,E)
<b><i>Orthorogiscus eurypterus</i> Philippi, 1892: 14, Pl. 6 (fig. 1). Type locality: Chañaral, Chile. Mounted skin at MNHNCH, unregistered, not designation as holotype (see text).</b> Original source. Unlikely candidate for <i>M. tecta</i> (see text).	? <i>M. ramsayi</i> (F), <i>M. ramsayi</i> (P,E)

'Original source' means the species description was based on a specimen; 'literature source' means the species description was based on existing literature. Type status from Eschmeyer *et al.* (2017) unless otherwise stated. Museum codes according to Sabaj (2016).

\*Page 1450 in Walbaum (1792), presumably a typographical error.

<sup>b</sup>Page 440 in Nardo (1827b); <sup>c</sup>Pl. 6 in Nardo (1827b); <sup>d</sup>fig. 9 in Nardo (1827b) presumably typographical errors.

<sup>e</sup>We could not resolve referenced work: 'Salv., 55' (possibly Salviani, 1554: 154); 'Will., 16.' (possibly Willughby, 1686: 151. Pl. I.26); 'Lac., 2,364' (possibly Lacépède, 1798: 633).

<sup>f</sup>Page 320 in Ranzani (1839): table.

<sup>g</sup>We could not resolve referenced work: 'Charlet, Onom. Zoic. Pisc. P.9 \$4' [possibly Charleton, 1668: 129 (No. 3)].

such, the *COI* analysis corroborates the D-loop results, with three clear *Mola* species clades, *Mola* sp. B (*M. mola*), *Mola* sp. A (presumably *M. ramsayi*) and *Mola* sp. C, showing the latter two as sister clades.

openings small, oval, in front of pectorals. Lateral lines around eyes (nearly imperceptible). No swim bladder. Darker above, paler or dusky below, often spots and patterns on the sides.

## DESCRIPTION

FAMILY MOLIDAE BONAPARTE, 1832

GENUS *MOLA* KOELREUTER, 1766

*Mola* Koelreuter, 1766. Type specimen *Mola aculeata*, i.e. pre-juvenile form.

*Mola* Cuvier, 1798. Type specimen *Tetraodon mola* Linnaeus, 1758, i.e. adult form.

**Diagnosis:** Genus diagnosis, modified from Parenti (2003): Body ovoid, highly compressed laterally; lacking a true caudal fin; caudal region with a pseudocaudal (clavus), rounded, sometimes slightly crenulated, but without a mid-flap extension. Mouth small; teeth united, fused and beaklike. Fins without spines; dorsal fin posterior, erect, high, short-based, anal fin opposite the same shape. Pelvic fins absent. Skin leathery and thick; scales reduced, rounded base with a single, erect point or rectangular shape; non-imbricated. Gill

## *MOLA MOLA* (LINNAEUS, 1758)

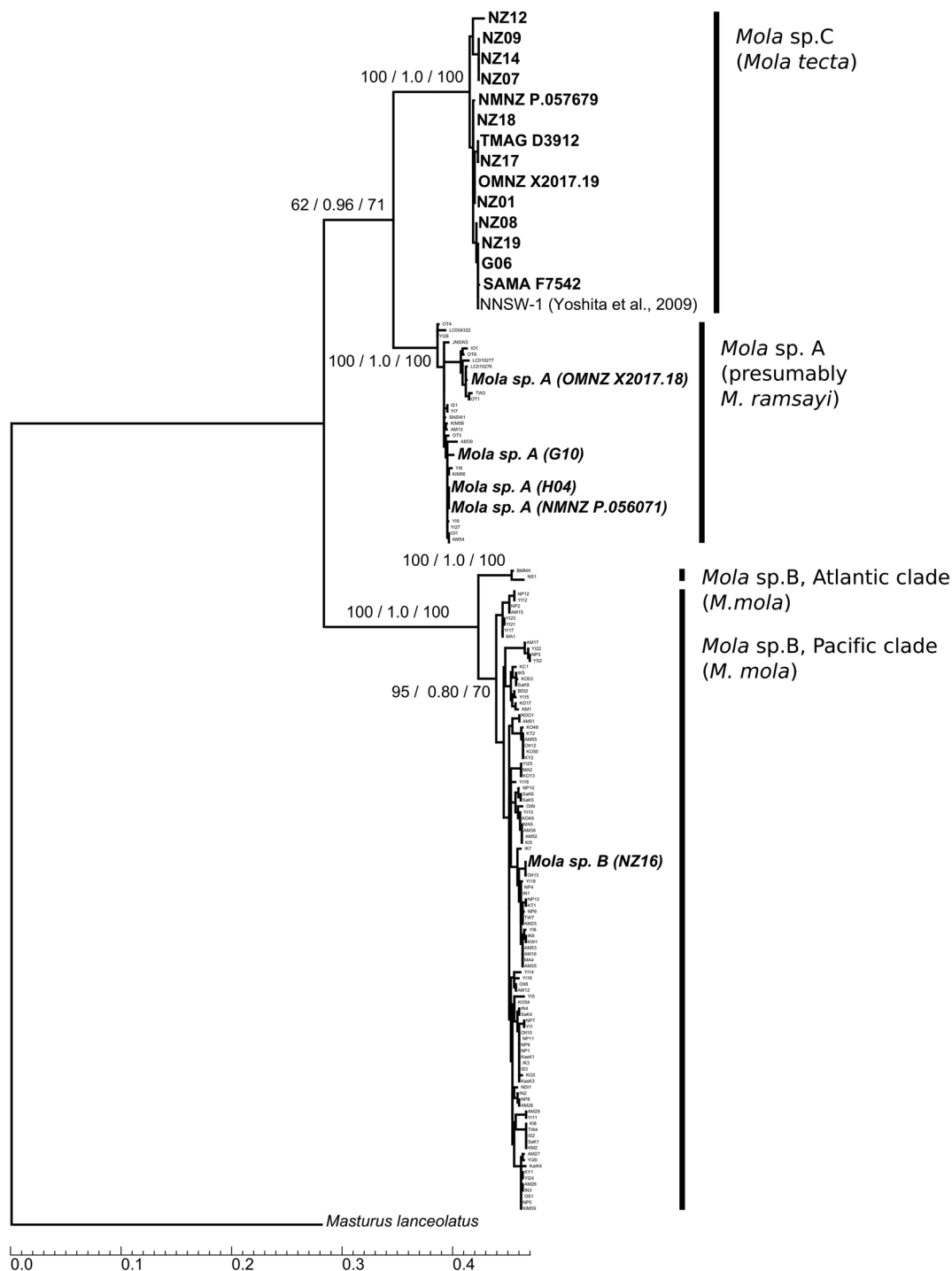
*Mola mola* (Linnaeus, 1758). No known holotype (Parenti, 2003; Eschmeyer *et al.*, 2017)

**Distribution:** Currently thought to be widely distributed in all the world's oceans except for the polar seas, however may be relatively uncommon in some areas (e.g. around Australia and New Zealand).

## *MOLA RAMSAYI* (GIGLIOLI, 1883)

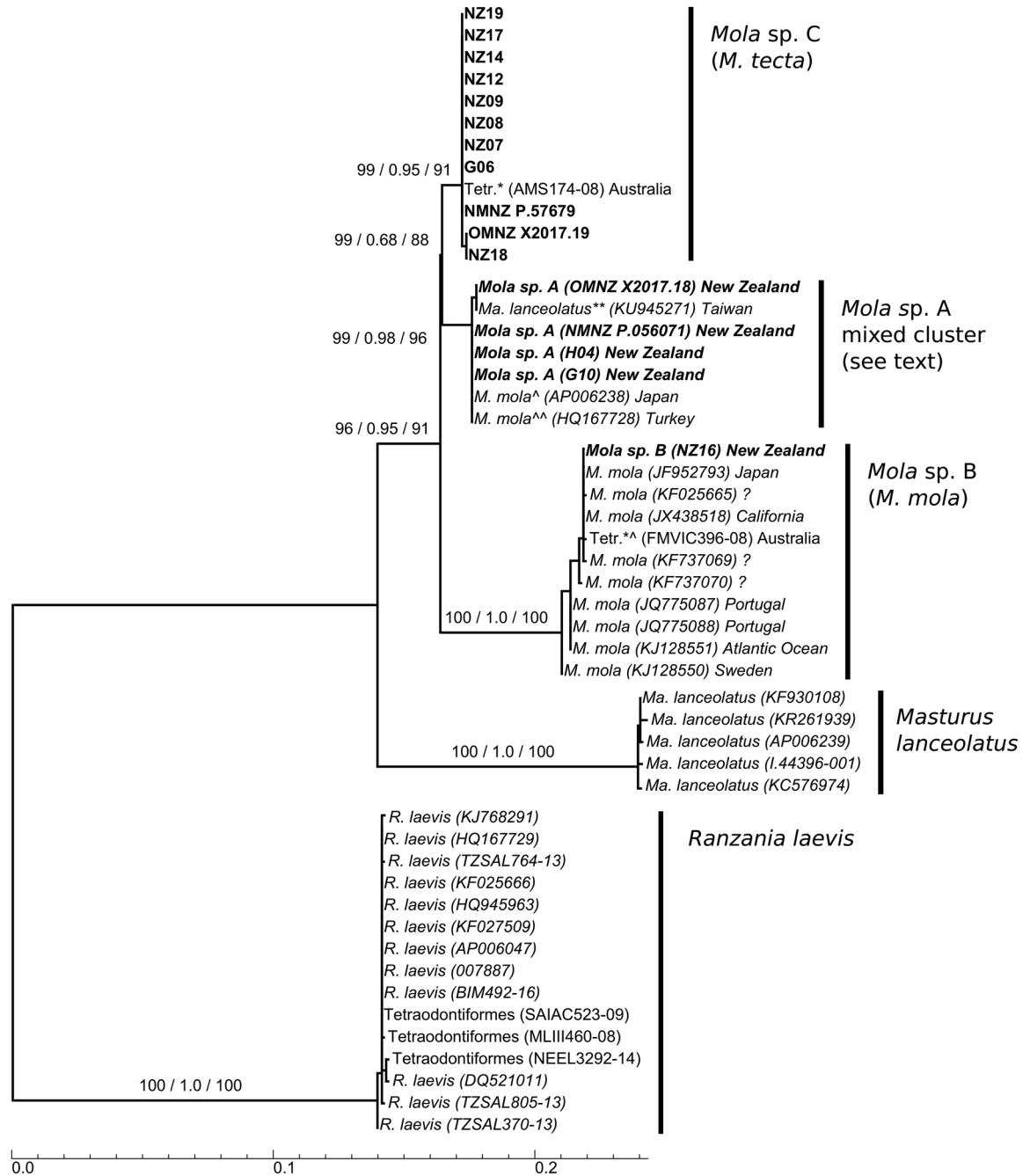
*Mola ramsayi* (Giglioli, 1883). Holotype: BMNH 1883.11.29.22

**Distribution:** Previously thought to be restricted to the South Pacific (Fraser-Brunner, 1951), however if *Mola* sp. A is shown to belong to *M. ramsayi*, the distribution is much wider than previously thought, including the Pacific and Indian oceans in both hemispheres, as well as the Mediterranean and probably also the European seas.



**Figure 2.** Phylogenetic relationships inferred by maximum likelihood (ML), based on *Mola* mitochondrial D-loop sequences from Yoshita *et al.* (2009), Ahuir-Baraja *et al.* (2017), Sawai *et al.* (2017) and this study (in bold). Numbers above or below internal branches of the major clades of *Mola* sp. A, *Mola* sp. B, and *M. tecta* (*Mola* sp. C) refer to ML bootstrap values (left), Bayesian posterior probabilities (middle) and maximum parsimony bootstrap values (right). Scale bar represents nucleotide substitution.

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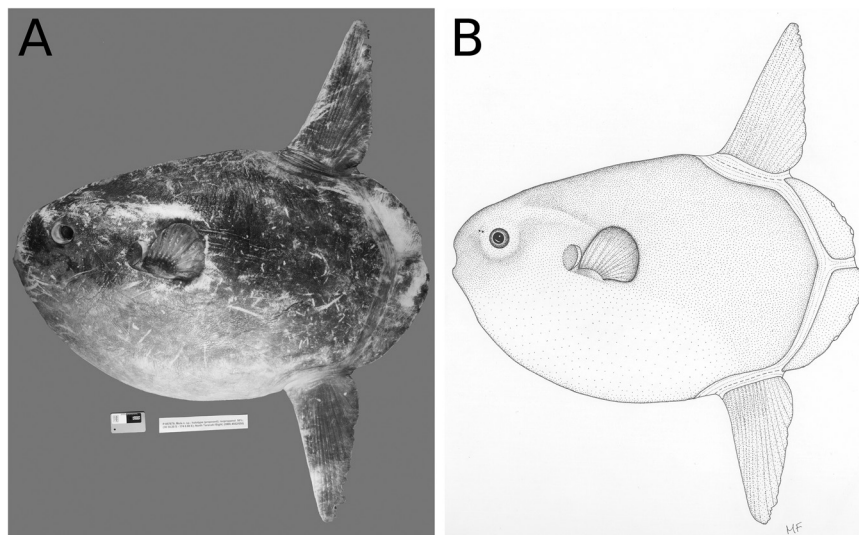
**Figure 3.** Phylogenetic relationships inferred by maximum likelihood (ML), based on Molidae mitochondrial cytochrome *c* oxidase 1 sequences from the Barcode of Life Data Systems, the National Center for Biotechnology Information and this study (in bold). Numbers above or below internal branches of the major species clades refer to ML bootstrap values (left), Bayesian posterior probabilities (middle) and maximum parsimony bootstrap values (right). Scale bar represents nucleotide substitution. \*Lodged as Tetraodontiformes; from specimen AMS I.41536, also NNSW-1 in *Yoshita et al. (2009)*, i.e. *Mola* sp. C. \*\*Probably *Mola* sp. A (see text). ^Sample OI-1 in *Yoshita et al. (2009)*, i.e. *Mola* sp. A. ^^Probably *Mola* sp. A (see text); \*Lodged as Tetraodontiformes, from specimen NMV A25071, *Mola* sp. in *OZCAM (2017)*.

***MOLA TECTA* SP. NOV**

(TABLE 1; FIGS 1–10, 12)

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New English name: Hoodwinker ocean sunfish. New Japanese name: Kakure-manbo

*Orthroriscus mola* (not of Linnaeus) – Lidth de Jeude, 1890: 189–190, Pl. 8.*Mola ramsayi* (not of Giglioli) – Gauldie, 1992: 263–266 [description of skin structure], figs 4–6 – Bass *et al.*, 2005: 405–413 [as ‘Atlantic group’], figs 2, 3, table 1; accession numbers AY940816 and AY940826 (partial D-loop); AY940834 and AY940838 (cyt-b).*Mola* group C Yoshita *et al.*, 2009: 237, NNSW-1 in table 1 and figs 3, 4; Accession number AB439108 (D-loop).*Mola* species C of Yoshita *et al.*, 2009 – Ahuir-Baraja *et al.*, 2017: 1133, table SI, fig. 2 – Sawai *et al.*, 2017: 99–102, figs 1, 2, table 1.***Holotype*: NMNZ P.057679 (Fig. 4)** (fresh measurements: 101.1 cm TL; measurements after fixation: 101.2 cm TL), male, North Taranaki Bight, west coast North Island, New Zealand (38°25.5'S 174°9.0'E), trawl, 78 m, 25 December 2015; coll.: observer Scott Yeoman FV *Ivan Golubets*, OBS 4552/050. Measurements (fresh and after fixation) provided in Supporting Information, Table S3.***Paratypes***: Eleven specimens (49.9–90.5 TL): **AIM MA29864** (51.1 cm TL), female, whole specimen in isopropyl alcohol, Poor Knights Islands, New Zealand (35°29.3'S 173°43.7'E), 8 November 1969; **NMNZ P.001418** (60.2 cm TL), male, whole specimen in isopropyl alcohol, off Hawke's Bay, New Zealand (39°25'S 177°6'E), June 1952; **NMNZ P.002980** (64.6 cm TL), male, whole specimen in isopropyl alcohol, North Rona Bay, Eastbourne, Wellington Harbour, New Zealand (41°16'S 174°55'E), drag net, coll.: Robert Falla, 30 November 1960; **NMNZ P.005890** (49.9 cm TL), female, whole specimen in isopropyl alcohol, off Great Barrier Island, New Zealand (36°5'S 175°35'E), trawl 36–37 m, coll.: C. Gaelic, 25 June 1973; **NMNZ P.006126** (64.8 cm TL), female, whole specimen in isopropyl alcohol, Oriental Bay, Wellington Harbour, New Zealand (41°17.40'S 174°47.587'E), beach cast, 29 June 1955; **NMNZ P.033995** (57.2 cm TL), male, whole specimen in isopropyl alcohol, Bay of Plenty, Opotiki Beach, New Zealand (37°45'S 177°20'E), November 1996; **NMNZ P.034187** (79.7 cm TL), male, whole specimen in isopropyl alcohol, Bay of Plenty, surf at Opotiki, New Zealand (37°45'S 177°20'E), hand, coll.: Andy Glazier; **NMNZ P.034217** (69.8 cm TL), male, whole specimen in isopropyl alcohol, Bay of Plenty, Opotiki Beach, New Zealand (37°44'S 177°20'E), coll.: Andy Glazier, December 1996; **NMV A18725** (90.5 cm TL), whole specimen in isopropyl alcohol, Port Phillip Bay, Victoria (37°52'S 144°49'E), coll.: F. Hadathy & S. Praljak, 28 August 1995; **NMV A26565-001** (78.5

**Figure 4.** *Mola tecta* sp. nov. holotype: NMNZ P.057679, 101.1 cm total length (fresh measurement), male, North Taranaki Bight, west coast North Island, New Zealand (38°25.5'S 174°9.0'E), trawl, 78 m, 25 December 2015, collected by Scot Yeoman, Ministry of Primary Industries, New Zealand. (A) Photographed and (B) illustrated by Carl Struthers and Michelle Freeborn, respectively, Museum of New Zealand Te Papa Tongarewa.

cm TL), whole specimen in isopropyl alcohol, Barwon Heads, Victoria (38°17.4'E 144°27.36'S), coll.: Warren Chapman, 30 April 2009; **SAMA F7542** (c. 90 cm TL), whole specimen in ethanol, Spencer gulf, South Australia (34°47.4'S 138°28.8'E), coll.: J. Verrier, 27 June 1994 [current specimen label indicates 1989, considered an error by collection authority (R. Foster, SAMA, personal communication, February 2017)].

*Other material:* Sixteen specimens (62–242 cm TL): **AIM MA30933** (102 cm TL), cast from fresh specimen, New Zealand; **G06** (62 cm TL), live specimen (not retained), northeast of North Island, New Zealand, (36°30'S 177°45'E), long-line, 8 July 2013; **NZ01** (212 cm TL), fresh specimen (not retained), Otago Harbour, New Zealand (45°49'S 170°37'E), beach cast, 18 February 2015; **NZ07** (100 cm TL), fresh specimen (not retained), Banks Peninsula, New Zealand (43°50'S 172°40'E), beach cast, 30 April 2014; **NZ08** (151 cm TL), fresh specimen (not retained), Banks Peninsula, New Zealand (43°50'S 172°40'E), beach cast, 30 April 2014; **NZ09** (193 cm TL), fresh specimen (not retained), Banks Peninsula, New Zealand (43°50'S 172°40'E), beach cast, 30 April 2014; **NZ12** (155 cm TL), female, fresh specimen (clavus, skin sample retained), Birdling's Flat, Banks Peninsula, New Zealand (43°49'S 172°42'E), beach cast, 10 May 2014; **NZ14** (170 cm TL), fresh specimen (not retained), near Birdling's Flat, Banks Peninsula, New Zealand (43°50'S 172°40'E), beach cast, 14 December 2015; **NZ17** (81 cm TL), male, fresh specimen (clavus, skin sample retained), west of South Island, New Zealand (41°32'S 170°56'E), purse seine, 12 April 2014; **NZ18** (65 cm TL), female, fresh specimen (clavus retained), east of North Island, New Zealand (38°47'S 178°25'E), long-line, 17 May 2014; **NZ19** (69 cm TL), male, fresh specimen (clavus retained), east of North Island, New Zealand (35°9'S 176°3'E), long-line, 10 August 2014; **OMNZ VT3249** (78 cm TL), cast from fresh specimen, Kaka Point, Clutha District, New Zealand, (46°22'S 169°44'E), beach cast, 7 March 1963; **OMNZ VT3248** (242 cm TL), cast from fresh specimen, Otago Harbour, Dunedin, New Zealand (45°49'S 170°38'E), beach cast, 1961; **OMNZ X2017.19** (169 cm TL), female, fresh specimen (not retained), North Taranaki Bight, New Zealand (38°26'S 174°9'E), beach cast, 18 January 2017; **RMNH. PISC.D.2059** (223 cm TL), female, mounted skin, Ameland, Netherlands, beach cast, 13 December 1889; **TMAG D3912** (150 cm TL), fresh specimen (not retained), Lindisfarne, Tasmania, Australia (42°51'S 147°20'E), beach cast, 12 December 2014.

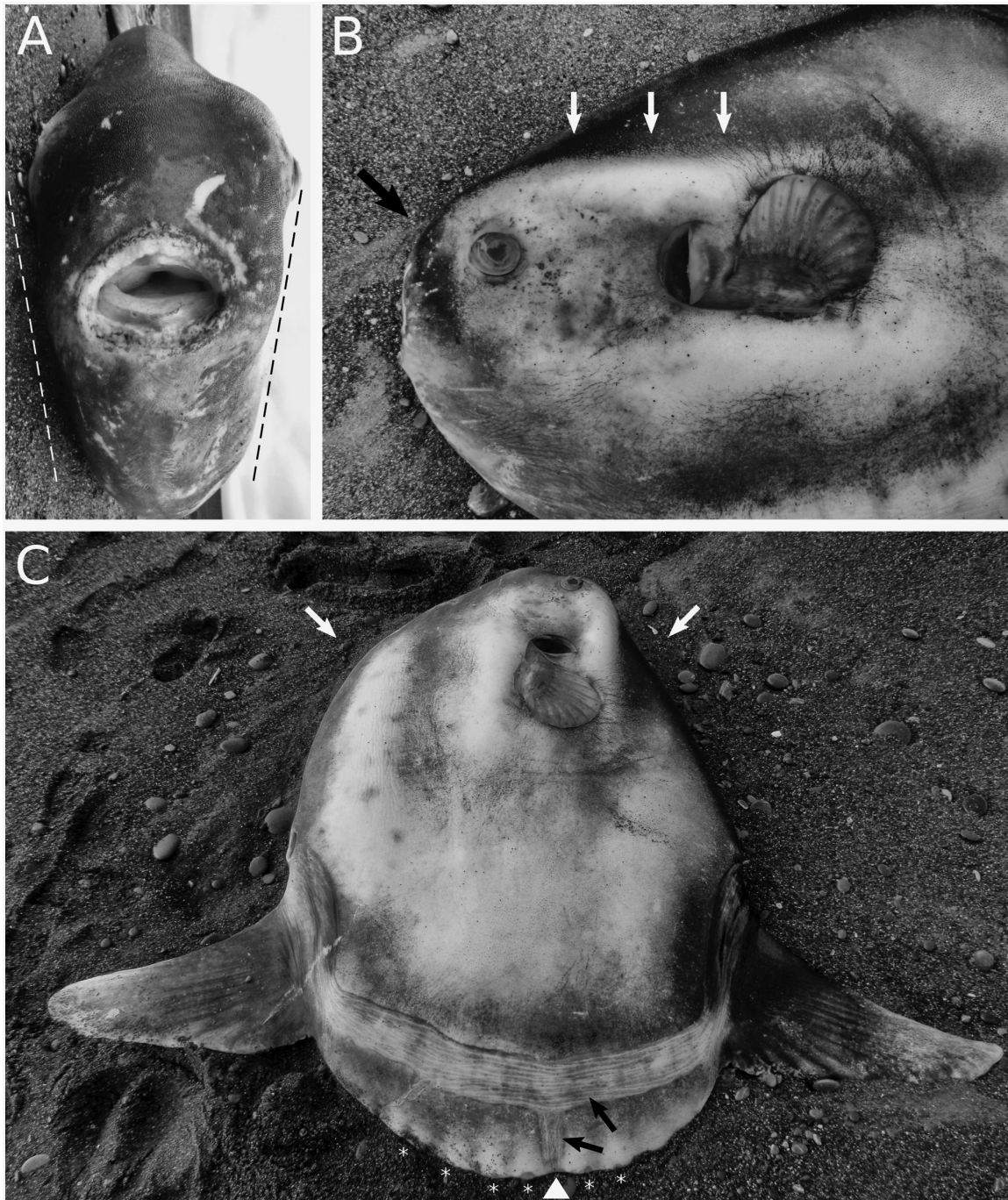
*Diagnosis:* Within the investigated size range (50–242 cm TL), *M. tecta* sp. nov. is diagnosed from others in the genus *Mola* by the following combination of

characters: slender body shape without head bump or chin bump; tapered profile when viewed from the front, with the widest point across the eye area; short dorsolateral ridge to posterior end of pectoral fin; rounded profile without protruding snout. Pronounced smooth band consisting of creased, elastic skin with highly reduced density of body scales; distinctive smooth band back-fold diving the clavus into a smaller upper and larger lower portion. Rounded clavus, slightly crenulated, with an indentation associated with the smooth band back-fold. Usually 11–13 pectoral fin rays, 17–19 dorsal fin rays, 16–18 anal fin rays, 15–17 clavus fin rays (13–15 principal rays, 2 minor rays along the edges of the smooth band back-fold); usually 5–7 separate ossicles on the clavus edge in specimens over 65 cm TL; no ossicles or ossification associated with the smooth band back-fold, ossicles on paraxial fin rays separate, of similar size to the neighbouring clavus ossicles. Body scales with conical, non-branching erect central point of differing sizes.

*Description:* Description of the holotype (Fig. 4) followed by a range of paratypes and sample specimens in brackets (see Table 1 for the contribution of data from individual paratypes and sample specimens).

A species of *Mola* with the typical characteristics for the genus, most notably a deep body, highly compressed laterally, truncated, lacking a true caudal fin, near-symmetrical, spineless dorsal and anal fins. Eyes small, round; two small nostrils located in front of eye; mouth small, terminal; teeth fused, beaklike; gill openings small, oval, located in front of the pectoral fins, and covered by a soft gill membrane; gill rakers are concealed under the subcutaneous gelatinous layer; all fins are spineless; caudal fin and pelvic fin absent; pectoral fin small, round, located mid-laterally, fitting into a shallow groove in the side of the body; caudal fin replaced by a clavus, comprised of highly modified elements of the dorsal and anal fins; body covered in thick subcutaneous gelatinous layer except for pectoral, dorsal and anal fins, skin covered in thick mucus, anal opening immediately anterior of anal fin.

No head bump (0), no chin bump (0), no swollen dorsolateral or ventrolateral ridges on body (0); short dorsolateral ridge to posterior end of pectoral fin reflecting the underlying cranio-skeletal structure, front profile tapered (in all investigated specimens) (Figs 5, 6). Lateral profile rounded, without protruding snout (0) or any indications thereof (0) (Fig. 5B). Holotype of typical body dimensions (Fig. 7); *M. tecta* maintains its body proportions with growth, with similar length and depth measurements as percentages of TL across the investigated size spectrum; total body depth (TBD) relative to TL appears to decrease with growth, due



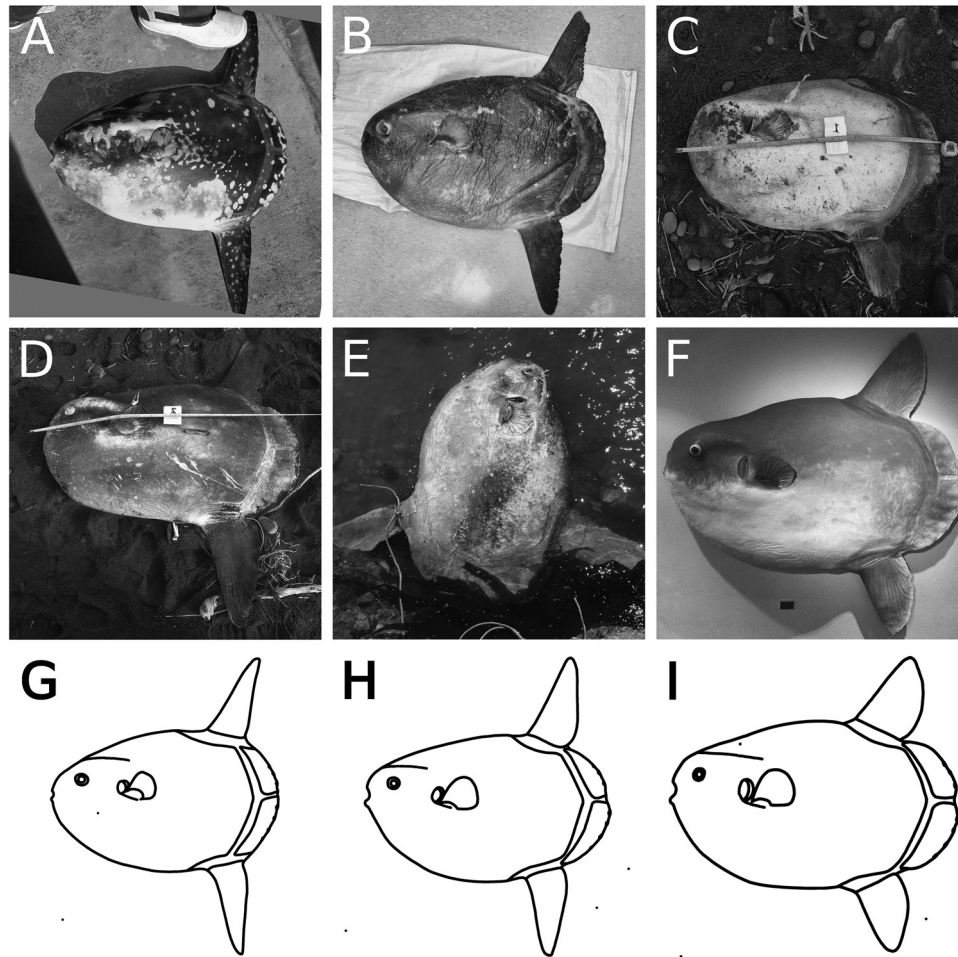
**Figure 5.** *Mola tecta* sp. nov. specimen NZ12, 155 cm total length. (A) Tapered profile (hashed lines) with widest point across the eye area; (B) rounded profile without protruding snout (black arrow); short dorsolateral ridge (white arrows) to pectoral fin; (C) prominent smooth clavus band with back-fold (black arrows), and associated indent (white triangle) on an otherwise rounded clavus edge. White stars indicate ossicles.

to shorter dorsal and anal fins relative to TL in larger specimens (Figs 6, 7A).

Eleven (11–13) pectoral fin rays, 18 (17–18) dorsal and 17 (16–18) anal fin rays, 15 (13–15) regularly spaced principal clavus fin rays, with 7 (5–7) above, and 8 (7–8)

below the smooth band back-fold. An additional 2 (2) minor fin rays embedded along the edges of the smooth band back-fold; minor fin rays and back-fold positioned between the two paraxial fin rays (Fig. 8). Seven (0–7) ossicles: 3 (0–3) above, and 4 (0–4) below the smooth





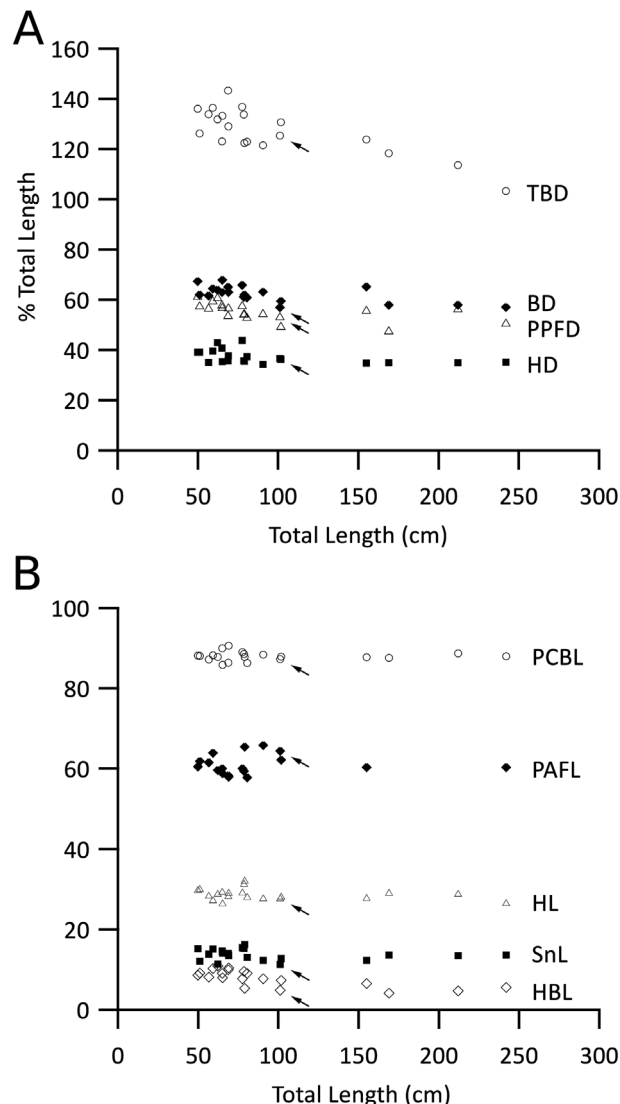
**Figure 6.** Slender body proportions without head bump, chin bump or protruding snout of *Mola tecta* sp. nov. at different total lengths: (A, G) G06: 62 cm; (B) NZ18: 65 cm; (C) NZ07: 100 cm; (D) NZ08: 151 cm; (E) NZ01: 212 cm; (F, I) OMNZ VT3248 242 cm (cast); (H) NMNZ P.057679 (holotype): 101 cm. Photographs by Tom Trnski, Auckland War Memorial Museum (A), Marianne Nyegaard, Murdoch University (B, F), Ken Logan, local resident of Christchurch, New Zealand (C, D), Jean McKinnon, University of Otago (E). Illustrations by Michelle Freeborn, Museum of New Zealand Te Papa Tongarewa (G–I).

band back-fold (Figs 4, 5C), positioned on the crest of slight crenulations on the clavus trailing edge (Fig. 8B,C), adult ossicle number established around 65 cm. Paraxial ossicles separate, situated on either side of the smooth band back-fold (in all investigated specimens) (Fig. 8).

Shape of scales is similar across much of the body and clavus. For comparison with other Molidae, we refer here to the skin on the body posterior of the pectoral fin (Fig. 1). Scales with a raised central point, which is smooth and conical without branching tips (Fig. 9). The scales butt against each other; the boundaries become highly visible in the dried state (not shown). Size of the raised, central point on the body scales vary, with larger scattered between smaller (Fig. 9A, B). Smooth band nearly free of scales (in all investigated specimens); scales only slightly reduced, and of smaller

sizes, on the elastic skin of the smooth band back-fold (density of scales on back-fold varies between individuals). Clavus rounded with an indent at smooth band back-fold (Figs 4, 5C) (back-fold and indent may be less evident in small, preserved specimens due to stiffening of the back-fold during preservation).

Coloration of holotype after defrosting uniform grey, darker dorsally, lighter ventrally (Fig. 4). The colour of live specimens appears grey or dark brown with dusky white, mottled spots and patterns (Fig. 6A; Supporting Information, Fig. S1). Darker dorsally, lighter ventrally. It is not known whether live *M. tecta* can rapidly change the contrast of its skin patterns, as *Mola* sp. A and *Mola* sp. B can (Nyegaard M and Sawai E, personal observation), but we consider it likely. The colour of freshly dead specimens is similar to live specimens, or uniform grey to grey-blue (Figs 5, 6B–E).



**Figure 7.** Morphometric measurements of *Mola tecta* sp. nov. specimens (Table 1), as percentage of total length (TL). (A) Black diamonds: body depth (BD), black squares: head depth (HD), open triangles: pre-pectoral fin depth (PPFD), open circles: total body depth (TBD); (B) open diamonds: head bump length (HBL), open triangles: head length (HL), black diamonds: pre-anal fin length (PAFL), open circles: pre-clavus band length (PCBL), black squares: snout length (SnL). Holotype NMNZ P.057679 morphometrics (fresh) indicated with arrows.

**Etymology:** The species name *tecta* is derived from the Latin *tectus* (disguised, hidden), as this species evaded discovery for nearly three centuries, despite the keen interest among early sunfish taxonomists and the continued attention these curious fish receive. The Japanese name is derived from the species name *tecta*: ‘hidden’ (Kakure), ‘sunfish’ (manbo), while

the English name, ‘Hoodwinker’, pertains to the figurative meaning ‘trickster, deceiving by disguise’, c. 1600.

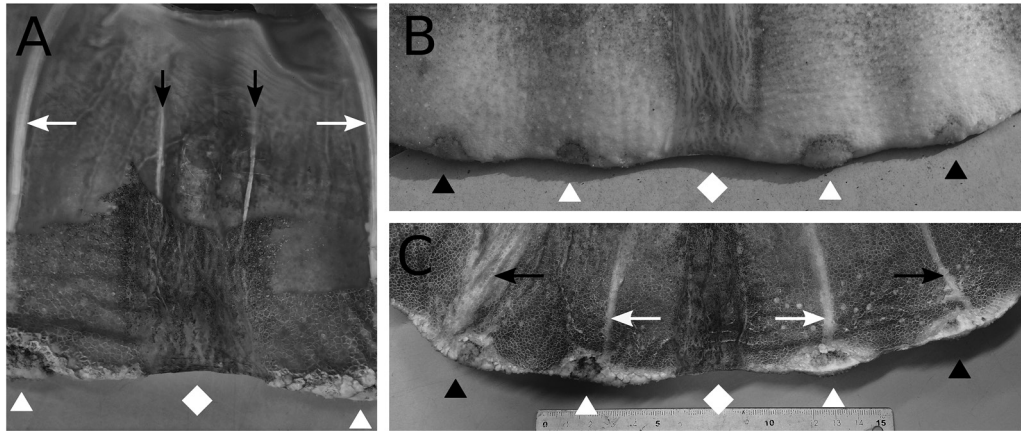
**Habitat and distribution:** *Mola tecta* has been confirmed in the southeast of Australia (New South Wales, South Australia, Tasmania and Victoria) (Yoshita *et al.*, 2009; this study), around New Zealand (this study), and off South Africa (Bass *et al.*, 2005) (Fig. 10). Photographs (e.g. Supporting Information, Fig. S1A) indicates that it also occurs in Chilean waters. This suggests that *M. tecta* is distributed widely in the temperate waters of the Southern Hemisphere, with occasional, but presumably rare, occurrences in the Northern Hemisphere (see below under Broader Molidae literature). Migrations are unknown.

**Biology:** It attains at least 242 cm TL, probably more. It likely exhibits a similar biology to the other *Mola* species whereby feeding takes place during deep dives (e.g. Nakamura, Goto & Sato, 2015; Thys *et al.*, 2016). Digestive tract contents of three specimens (Table 1) consisted of salps (*Thetys vagina* and *Pyrosoma* sp.), and the remains of a nectonic siphonophore, and in one instance, a 3 × 5 mm Styrofoam ball. All dissected specimens were heavily infested with parasites, particularly in the intestines (cestodes) and in the liver (likely larval *Trypanorhynch* cestodes). The shape of the gonads differs between the sexes; the ovary is singular and ball-shaped, the testis are paired, elongated and rod-like and do not appear to frill during maturation. Spawning grounds, eggs, larvae and pre-juveniles are not known.

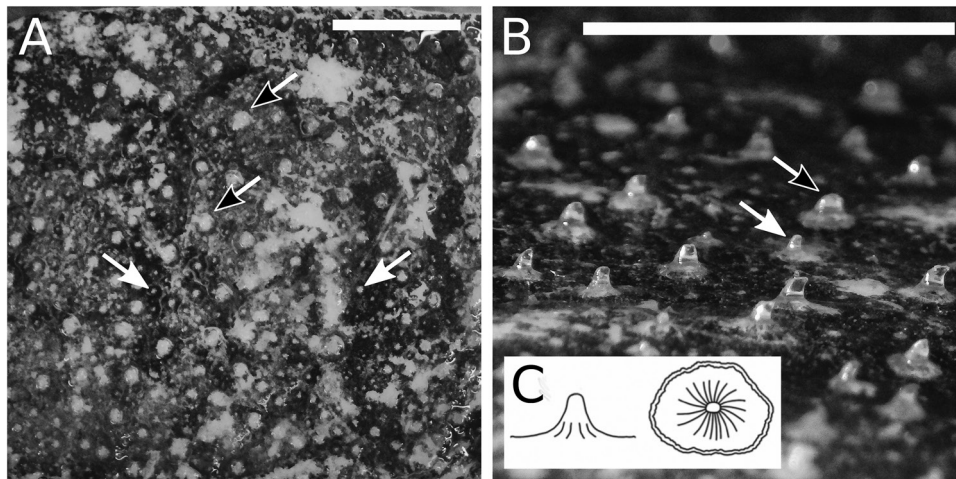
**Remarks:** The clavus fin ray structure of NZ19 (Table 1) appeared abnormal with a secondary, irregular smooth band back-fold present below the main back-fold. Also, in addition to 14 regularly spaced principal fin rays, we found 5 smaller, less rigid and highly irregular fin ray-like structures; 4 of these were set close to each other, bending towards the main back-fold, while the fifth was Y-shaped and associated with the secondary back-fold. Their irregularity and disordered appearance pointed to malformations, which are not uncommon in the other *Mola* species (Sawai *et al.*, 2009). The formation of ossicles (8) also appeared affected.

#### KEY TO THE *MOLA* SPECIES

Fraser-Brunner’s (1951) review included a key to the genus *Mola*, whereby *M. mola* and *M. ramsayi* were distinguished based on six characters: the number of



**Figure 8.** Clavus structures of *Mola tecta* sp. nov. specimen NZ12, 155 cm total length. (A) Dried clavus, left side, skin partially removed: two minor fin rays (black arrows) embedded along the edge of the smooth band back-fold (white diamond) between the paraxial fin rays (white arrows), which bear separate ossicles (white triangles). (B) Fresh and (C) dried state, right side: small ossicles (triangles) on the crests of slight crenulations along the rounded clavus edge; no ossicles or ossification associated with the clavus band back-fold (white diamond); paraxial fin rays (white arrows) each bearing a separate ossicle (white triangles), similar to the ossicles (black triangles) on neighbouring principle fin rays (black arrows).



**Figure 9.** Scales of *Mola tecta* sp. nov. (holotype NMNZ P.057679, fresh state) on the body behind the pectoral fin (see Fig. 1) from (A) a 90 degree angle, and (B) an oblique angle (1 cm scale bars), with conical, non-branching central points, larger (black arrows) scattered among smaller (white arrows) scales. (C) Typical shape of *Mola tecta* sp. nov. body scale: side view (left), and 90 degree angle (right), showing the raised central point on the dermal plate.

clavus fin rays and ossicles, the size of clavus ossicles against the space between them, the clavus shape (lobed or rounded), state of the paraxial ossicles (separate or united) and presence/absence of a smooth band. While research in recent years have added important morphological insights into the sunfishes, the outstanding tasks of formally linking the genetic *Mola* sp. A clade with nomenclature, and clarifying the status of the two *Mola* sp. B clades (Atlantic vs Pacific), currently limit us to an interim update of the Fraser-Brunner (1951)

*Mola* key. Further research is also needed to determine at what size specific characters are established, for example the number of ossicles, wavy clavus, etc. Thus, the interim key below should be applied with caution, in particular to smaller individuals. Characteristics, which we consider to be generally established at 65–70 cm TL, include clavus fin ray numbers, clavus ossicle numbers, state of the paraxial ossicle(s) and the presence of a smooth band back-fold and associated clavus edge indent in *M. tecta*. Also, the scale morphology

appears to be fully developed for *M. tecta*, while further research is needed for the other *Mola* species.

Interim key to the species of adult form *Mola* [modified from Fraser-Brunner (1951)]:

1. Smooth band (pre-clavus) with pronounced back-fold; clavus supported by 15–17 rays [13–15 principal, 2 minor], 5–7 of the principal rays bearing ossicles; ossicles borne on paraxial rays separate, of similar size to neighbouring; clavus edge rounded, with an indent at the smooth band back-fold; without a protruding snout, head bump or chin bump; short dorsolateral ridge to posterior end of pectoral fin; conical body scales of varying sizes, without branching tips, sparsely set.....  
.....*Mola tecta* sp. nov.  
– Smooth band without pronounced back-fold, or with a faint, superficial back-fold; other shape of clavus; 8 or more ossicles.....**2**
2. Smooth band (pre-clavus) subtle, or moderately pronounced; clavus supported by 14–17 rays, 8–15 of which bear ossicles; clavus edge rounded; protruding snout in some individuals; head bump, chin bump, swollen dorso- and ventrolateral ridges in large individuals; body scales with slightly raised rectangular midpoints in horizontal rows.....  
.....*Mola* sp. A (presumably *Mola ramsayi*)  
– Smooth band pronounced; clavus supported by 10–13 rays, 8–9 of which bear ossicles; ossicles invested with cuticle, which grows to form lobes with fish growth, creating a wavy clavus edge; conical body scales with branching tips, densely set; protruding snout in some individuals; without or with moderate head bump; without or with small chin bump; swollen dorso- and ventrolateral ridges in large individuals.....  
.....*Mola* sp. B (presumably *Mola mola*)

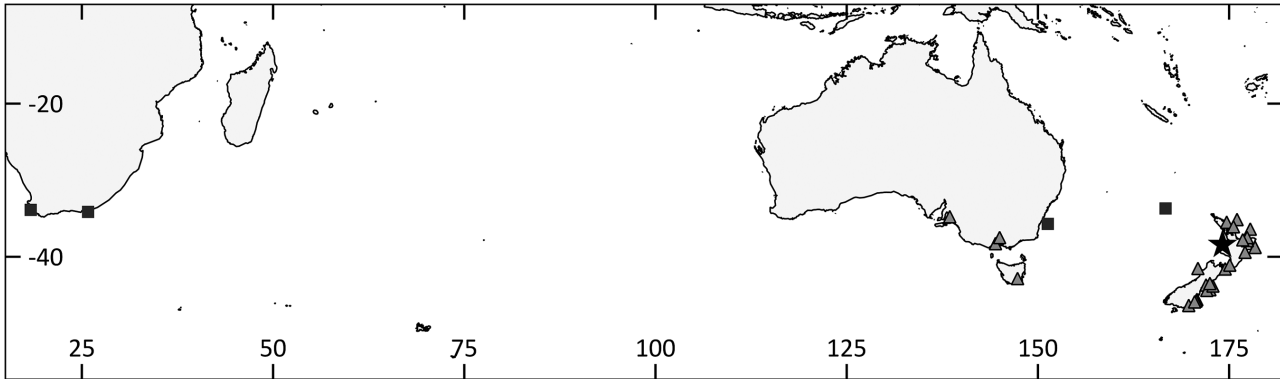
Source information for *Mola* sp. A and *Mola* B morphology: **head bump/chin bump:** Yoshita *et al.* (2009), Matsuura (2015: fig. 6), Sawai *et al.* (2015), Ahuir-Baraja *et al.* (2017), Sawai *et al.* (2017); **protruding snout:** Fraser-Brunner (1951), Sawai E and Nyegaard M (unpublished data); **dorso- and ventrolateral ridges:** Thys *et al.* (2013: fig. 1B), Matsuura (2015: fig. 6), Sawai E and Nyegaard M (unpublished data), **smooth band:** Yoshita *et al.* (2009), Sawai *et al.* (2015), Ahuir-Baraja *et al.* (2017); **smooth band back-folds:** M. Nyegaard and E. Sawai (unpublished data); **clavus fin ray/ossicle counts:** Yoshita *et al.* (2009), Sawai (2016a), Sawai *et al.* (2017); **clavus shape:** Yoshita *et al.* (2009), Matsuura (2015: fig. 6), Ahuir-Baraja *et al.* (2017: fig. 1), Sawai *et al.* (2017); **skin structure:** Gaulide (1992), Sawai *et al.* (2015), Sawai (2016b).

#### REVIEW OF NOMINAL *MOLA* SPECIES

To confirm whether a scientific name consistent with the *M. tecta* characteristics was proposed in the past, we reviewed the original descriptions of nominal *Mola* species and other relevant names (Table 2), as well as associated historical literature. Due to the current uncertainty in regards to linking the genetic clades of *Mola* sp. A and *Mola* sp. B with established nomenclature, we did not attempt to assign species names to the nominal species descriptions, instead, we focused on establishing whether any nominal species description matched *M. tecta*. In support of this evaluation, early Molidae taxonomic history was also reviewed.

The original description of *M. mola* (*T. mola*, type locality in the Mediterranean) was brief, and included references to sunfish descriptions by Artedi (1738: 61, 83), Bianchi (1746: 297) and Gronovius (1754: 55), who in turn referenced various early, often nebulous, sunfish descriptions. Most of these were from the Mediterranean and the European seas, some describing and illustrating what we now recognize as '*Mola* forms' (e.g. Rondelet, 1554: 424; Gessner, 1560: 158, 159; Aldrovandi, 1613: 412), others '*Ranzania* forms' [e.g. Aldrovandi, 1613: 413; Jonstonus, 1657: Pl. 9 (No. 1)]. As Linnaeus referenced both forms, it is not clear which sunfish he intended to describe. Although there is no known extant holotype for *M. mola* (*sensu* Parenti, 2003), we know this species today from the historical application of the name. Linnaeus' *Mola/Ranzania* ambiguity was noted by several authors (e.g. Retzius, 1785; Jacob, 1826; Steenstrup & Lütken, 1898) and caused confusion in early sunfish systematics; however, the name eventually came to mean *M. mola* as described in Fraser-Brunner (1951).

Early sunfish systematics was also influenced by differing opinions on how to resolve the taxonomy, in particular for the comparatively minute pre-juveniles, the elongated '*Ranzania*' shapes, and the many different sizes and shapes of *Mola* specimens. The collective endeavours of many naturalists resulted in numerous proposed classifications, as well as an extensive web of references and synonymies, with several nominal names based on re-grouping of existing species (Table 2). The distinct pre-juveniles were initially viewed as a separate species, or genus, resulting in a number of nominal species names, all later synonymized with *M. mola* (Fraser-Brunner, 1951; Parenti, 2003; Eschmeyer *et al.*, 2017). In our view, the current lack of clarity on *Mola* spp. pre-juvenile morphology and identification precludes a conclusive assignment below genus level. However, these nominal species are improbable candidates for *M. tecta* due to their type localities in the Mediterranean, USA and 'tropical seas' (Table 2). While a small number of pre-juvenile specimen localities are not known, they were unlikely



**Figure 10.** Locations of *Mola tecta* sp. nov.: holotype (black star); paratypes and other examined material (excluding RMNH.PISC.D.2059 from the Dutch Coast) (grey circles); NSW-1 (Yoshita *et al.*, 2009), AY940816, AY940826 (Bass *et al.*, 2005) and one unnamed specimen from Gauldie (1992) (black squares).

to originate from the temperate Southern Hemisphere, as this region was still relatively unexplored by science at the time they were reported (Table 2).

Most of the nominal species names were based on larger ‘typical’ sunfish specimens, with type localities in the Mediterranean and European seas. *Mola mola* was, until comparatively recently, considered the only *Mola* species present here; nevertheless, two records of *Mola* sp. A in the Mediterranean (Ahuir-Baraja *et al.*, 2017; fig. 3) and one record of *M. tecta* from the Dutch coast (see below under Broader Molidae literature) preclude automatic assignment of all the European ocean sunfish names to *M. mola*. However, a careful review of the nominal species descriptions, illustrations and associated literature strongly suggests that *M. tecta* was not among them (Table 2). Of the nominal species in Table 2, three had type localities in the Southern Hemisphere, in areas we believe to be within the core distribution of *M. tecta*, and warrant further discussion.

*Aledon capensis* Castelnau, 1861 was described based on a 100 cm TL specimen caught in Table Bay near Cape Town, South Africa, where one of the *M. tecta* specimens in Bass *et al.* (2005) was also sampled (Fig. 10). However, *A. capensis* was ‘...très-remarquable par une avance en forme de nez, qui se prolonge au-dessus de la bouche’ [...remarkable for a nose shape, extending beyond the mouth], and together with the description of a lobed clavus we conclude in agreement with Fraser-Brunner (1951), Parenti (2003) and Eschmeyer *et al.* (2017) that this specimen was *M. mola* (Table 2).

*Mola ramsayi* (Giglioli, 1883) (originally *Orthogoriscus ramsayi*) was based on a large specimen [244 cm TL according to Whitley (1931)] from New South Wales in Australia, exhibited at the 1883 International Fisheries Exhibition in the UK. Giglioli (1883) examined it and concluded ‘...it differs from our

*O. mola* [= *M. mola*], [and] belongs to the southern hemisphere’ but gave few taxonomic details. The specimen became the name bearing type at the London Natural History Museum (BMNH 1883.11.29.22). As the Yoshita *et al.* (2009) *Mola* sp. C specimen was sampled at the type locality of *M. ramsayi* in New South Wales, and due to the unresolved discrepancy between the morphology of *Mola* sp. A and *M. ramsayi*, the question arises whether *Mola* sp. C could be *M. ramsayi*, and *Mola* sp. A another species altogether? It is an unlikely scenario however; photos of the newly restored *M. ramsayi* holotype (Natural History Museum, London: [www.instagram.com/p/BIzgLphgufI/](https://www.instagram.com/p/BIzgLphgufI/)) clearly show a head bump and chin bump, a lack of, or inconspicuous, smooth band, all inconsistent with the head profile and prominent smooth band of *M. tecta*.

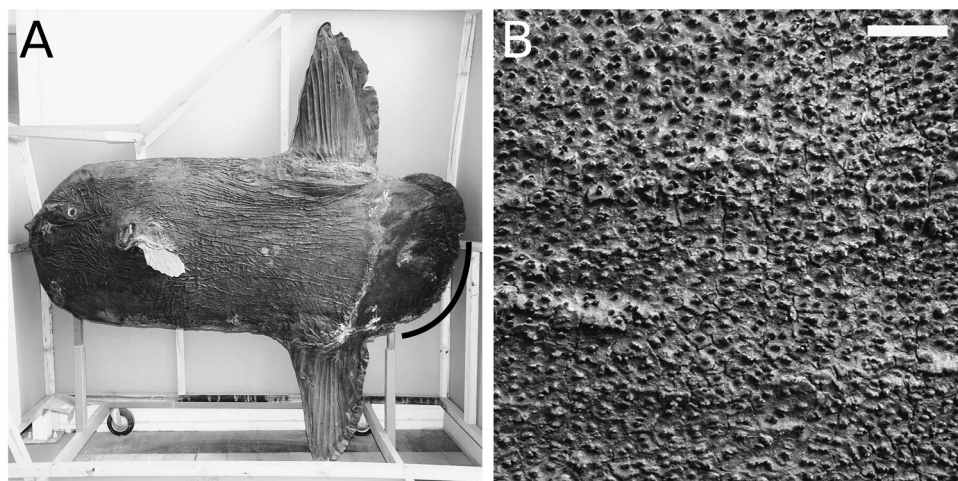
*Orthogoriscus eurypterus* Philippi, 1892 was described as a new species based on a large specimen (222 cm TL, 247 cm TBD), caught on 29 October 1889 off Chanaral in Chile. It was prepared and mounted prior to assessment, which likely rendered it somewhat distorted (Schneider, 1930). The features, which made Philippi believe he had a new species, were ‘...su forma mas alargada’ [the more elongated shape]; ‘...la situacion de las aletas dorsal i anal, mucho ménos atrasada; la dorsal principia casi en la mitad de la longitud del cuerpo’ [the position of the dorsal and anal fins with the dorsal fin sitting almost in the middle of the body]; ‘...la forma mui ancha de ellas’ [the wideness of the fins], and the edge of the clavus, described as ‘...bien redondeado’ [well rounded] and ‘...no ofrece una séria de osificaciones cortantes i separadas, parece mas bien todo osificado’ [not showing a string of individual ossifications but seeming to be ossified in the entire length]. While the TBD:TL ratio of 111% and the wide dorsal and anal fins are consistent with all three *Mola* species (Yoshita *et al.*, 2009; this study), the combination of a rounded clavus

and an elongated body on such a large fish point to it possibly being *M. tecta*. The position of the dorsal and anal fins ‘almost in the middle of the body’ is inconsistent with *M. tecta*, but could be an artefact of preparation and mounting. The ossification of the entire length of the clavus edge, however, is inconsistent with *M. tecta*, and we further note that while Philippi described the presence of a smooth band in detail, he did not make any mention of a back-fold. Phillipi’s specimen is extant at the National Museum in Santiago de Chile (MNHCH) as an unregistered specimen, which was not designated as holotype (Castro A, MNHCH, personal communication, November 2015). We examined this specimen via photographs provided to us by the museum, which confirmed distortion in the specimen and loss of over half the clavus edge (Fig. 11A). However, the skin structure is well preserved, is densely populated with scales (Fig. 11B), resembles the skin of a mounted *Mola* sp. B specimen described by Sawai et al. (2015: fig. 3B) and is dissimilar to that of *M. tecta* with its much wider set scales (Fig. 9). A small stretch of the upper clavus edge of the *O. eurypterus* specimen is preserved (Fig. 11A), and small ossicles are visible, interspersed with stretches of ossified clavus edge. This corresponds to the description by Philippi (1892) and is consistent with the clavus morphology of *M. mola*. We conclude, in line with Andersson’s (1900) careful review of *M. mola* body dimensions, that *O. eurypterus* is ‘...ett mycket stort exemplar af den vanliga *Orthogoriscus mola*’ [a very large specimen of the common *O. mola* (= *M. mola*)], and that the lack of clavus lobes was likely caused by damage during the preservation process. Our conclusion differs from Fraser-Brunner (1951), Parenti (2003) and

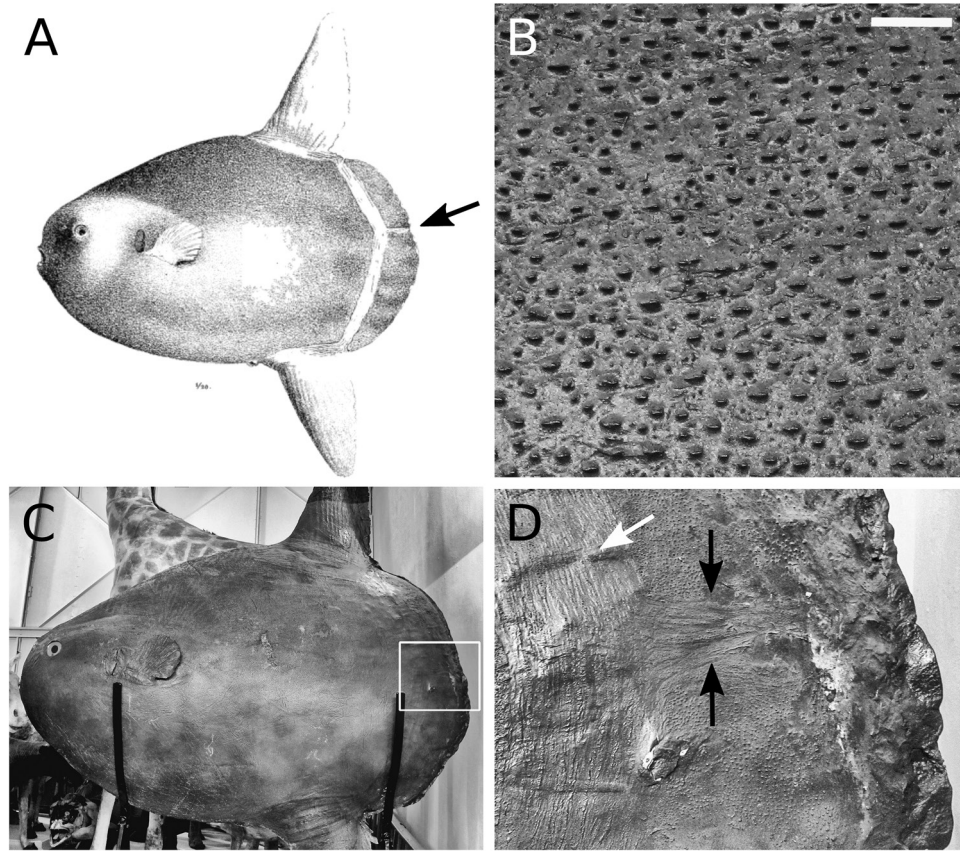
Eschmeyer et al. (2017), who list *O. eurypterus* as a junior synonym of *M. ramsayi* (Table 2).

#### BROADER MOLIDAE LITERATURE

Within the broader Molidae literature, we did not find any specimen descriptions matching *M. tecta*, with the exception of Lidth de Jeude (1890), who described and illustrated a ‘...smooth band parting off backwards’ from the prominent smooth band on a 223-cm-long female sunfish, stranded on the Dutch coast in December 1889. Lidth de Jeude could not find mention of a back-fold elsewhere in the literature, discussed the difficulty of species identification and tentatively settled on *O. mola* (= *M. mola*). His illustration later appeared in Martin & Drewry (1978: fig. 171A) as the female form of *M. mola*, with a comment that the back-fold was probably atypical. Lidth de Jeude’s detailed and to-scale drawing (Fig. 12A) has a strong resemblance to *M. tecta*, and, while the TBD:TL ratio and count of eight ossicles are slightly higher than our findings, his skin structure description is consistent with *M. tecta*. The mounted skin is extant at the Leiden Naturalis Biodiversity Center in the Netherlands (RMNH.PISC.D.2059), and we examined this from photographs sent to us by the museum (Fig. 12B–D); the body shape (Fig. 12C), skin structure (Fig. 12B) and smooth band with a back-fold (Fig. 12D) suggest it is likely *M. tecta*. Juede did not describe his specimen as a new species, and with no other indications of this species in the North East Atlantic, where sunfish sightings and strandings are not infrequent, it probably represents a rare occurrence of *M. tecta* outside the temperate waters of the Southern Hemisphere.



**Figure 11.** Presumed *Mola mola*: (A) mounted skin of *Orthogoriscus eurypterus* (Philippi, 1892) extant at the National History Museum in Santiago de Chile (MNHCH – unregistered, no type status). Black line indicates extent of clavus edge loss; (B) macroscopic skin structure on the body (1 cm scale bar). Photographs by Augusto Tomás Cornejo Castro, MNHCH.



**Figure 12.** Presumed *Mola tecta*: (A) Reproduction from Lidth de Juede (1890) of 223 cm total length female sunfish, stranded on the Dutch coast in 1889, originally identified as *Orthratoriscus mola* (now *M. mola*), showing the smooth band back-fold (black arrow) observed by Lidth de Juede; (B) macroscopic skin structure on the body behind the pectoral fin; (C) whole body view (white box indicates area of back-fold) and (D) smooth band (white arrow) and back-fold (black arrows) on the mounted skin (RMNH.PISC.D.2059), extant at the Naturalis Biodiversity Center, The Netherlands. Photographs: Ronald de Ruiter, RMNH.

## CONCLUSION

Our genetic and morphological analyses support the preliminary findings of Yoshita *et al.* (2009), that *Mola* sp. C is a species distinct from *Mola* sp. A and *Mola* sp. B. We have reviewed the relevant taxonomic literature and conclude that this is a new sunfish species not previously described. Our analysis and review also show that the *CO1* locus, used as the standard DNA barcoding for many taxon, can, like the D-loop, be used to identify individuals of the three *Mola* species.

It seems baffling that such a large fish has gone unnoticed by the scientific community despite the extensive interest in sunfish taxonomy following, and even predating the time of Linnaeus. In addition to the difficulty of studying these fish due to their large adult sizes, the explanation may partly lie in that early research efforts were concerned predominantly with European and American sunfish, and that only three of the many nominal *Mola* species names

(Table 2) were based on specimens from the Southern Hemisphere (i.e. Castalneu, 1861; Giglioli, 1883; Philippi, 1892). By the time sunfish were recorded by the scientific community in Australia in the 1860s (e.g. Royal Society of Tasmania, 1869) and 1870s in New Zealand (e.g. Hutton, 1872, 1873), the Molidae literature was already extensive and complicated, with a general consensus emerging that most of the proposed *Mola* species were probably the same (i.e. Nardo, 1840; Steenstrup & Lütken, 1898). Later, even *M. ramsayi* did not always gain support as a separate species, despite surviving the Fraser-Brunner (1951) review as a ‘Southern Hemisphere species’. McCann (1961), for example, summarized and discussed all New Zealand sunfish stranding records as *M. mola*, without any mention of *M. ramsayi*. In recent years, it has become generally accepted that both *M. mola* and *M. ramsayi* occur around New Zealand and southern Australia (e.g. Gauldie, 1992; Hutchins, 2001; Bray, 2008; Swainston, 2011; Stewart & Struthers, 2015). Preliminary results

from our Molidae biopsy program in Australia and New Zealand suggests that *Mola* sp. B (=presumably *M. mola*) is a relatively rare visitor in those waters, whereas *M. tecta* is relatively common (M. Nyegaard, unpublished data). With few local *M. mola* for comparison, and in light of the long standing taxonomic confusion, *M. tecta* in this region has presumably been mistaken for *M. mola* and/or *M. ramsayi*, allowing it to 'hide in broad daylight'. Its detection constitutes the first proposed addition to the genus in 125 years since [Philippi \(1892\)](#), and 130 years since the last valid *Mola* species, *M. ramsayi* (Giglioli, 1883), was described.

The description herein of *M. tecta* sp. nov. clearly shows it as a separate species of *Mola*, and also highlights areas of further research to establish the degree of natural variation across its growth spectrum, geographical areas and between the sexes, to provide sufficient information for a comprehensive *Mola* identification key to be developed. The taxonomic review also highlights the need to formally link other genetic *Mola* spp. clades with nomenclature, and further describe their morphologies across the large size spectra. This would enhance our ability to differentiate the *Mola* species and thereby better understand their zoogeographies, an important basis for gauging vulnerability to by-catch in fisheries – a potential key threatening process to *M. mola* populations, at least locally ([Jing et al., 2015](#)). Like the other two *Mola* species, the eggs, pre-juveniles and juveniles of *M. tecta* need to be located and verified through molecular methods to describe all life stages. Our results to date are, however, sufficient to conclude that *M. tecta* should be considered a valid species in the genus *Mola*.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Coloration of live *Mola tecta* sp. nov. (A) Swimming near the surface in Reserva Marina Isla Chañaral, Chile, 2015. Still from footage by César Villarroel (<https://vimeo.com/129499857>); (B) stranded and re-floated in Port Phillip Bay, Victoria, 1979. Photograph by Martin Gomon, Museums Victoria, Australia; (C) and (D) caught and released alive from tuna longlines off New Zealand, July 2013. Photographed by fisheries observer Marli Dee, New Zealand Ministry of Primary Industries. (A) and (B) identified from morphology, including a smooth band back-fold (white arrows); (C) and (D) identified genetically (D-loop).

**Table S1.** National Center for Biotechnology Information (NCBI) Accession numbers for mtDNA D-loop and cytochrome *c* oxidase 1 (*COI*) sequences analysed as part of this study. Institutional codes according to Sabaj (2016), except ABTC (Australian Biological Tissue Collection) and OMNZ (Otago Museum).

**Table S2.** Whole or partial Molidae cytochrome *c* oxidase 1 (*COI*) sequences lodged with Barcode of Life Data Systems (BOLD) and/or the National Center for Biotechnology Information, as of 19 March 2017.

**Table S3.** Morphometric measurements of the *Mola tecta* sp. nov. holotype (NMNZ P.057679) after initial freezing and thawing (fresh state), and after preservation (1 month in formalin, followed by 1 month in an isopropyl alcohol stepping process).