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FULL PAPER

Redescription of the bump-head sunfish *Mola alexandrini* (Ranzani 1839), senior synonym of *Mola ramsayi* (Giglioli 1883), with designation of a neotype for *Mola mola* (Linnaeus 1758) (Tetraodontiformes: Molidae)

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Abstract The genus *Mola* of ocean sunfishes (family Molidae) is currently composed of three species: *Mola mola* (Linnaeus 1758), *Mola ramsayi* (Giglioli 1883), and *Mola tecta* Nyegaard et al. 2017. For a comprehensive revision of the genus, both literature survey and morphological investigations of Molidae were conducted. We found *Mola alexandrini* (Ranzani 1839) to be synonymous with *M. ramsayi* and we herein redescribe *M. alexandrini* based on the rediscovered dried holotype and 21 other fresh and preserved specimens. *Mola alexandrini* can be distinguished from other species of *Mola* by the following combination of characters in adults: head profile with bump; chin with bump; body scales rectangular; clavus rounded, supported by 14–24 (mode 17) clavus fin rays and 8–15 (12) ossicles on the rear margin. A neotype of *M. mola* is designated for comparison with *M. alexandrini*, as these two species have long been confused.

Keywords Morphology · Neotype · Ocean sunfish · Redescription · Synonymy

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Introduction

Species of the genus *Mola* (family Molidae; Tetraodontiformes) are highly derived, large-sized bony fishes characterized by an orbicular and strongly compressed body, attaining more than 3 m total length (TL) and 2,000 kg, with members widely distributed in the open ocean of tropical and temperate seas (Pope et al. 2010; Yamanoue and Sawai 2012). They completely lack a caudal fin, which is replaced by a broad rudder-like lobe called the clavus (Fraser-Brunner 1951; Nakae and Sasaki 2006). Ocean sunfishes have attracted interest for centuries because of their unique shape and large size, and they are described and illustrated in old literature dating from at least the 16th century (cf. Rondelet 1554; Salviani 1554). The published literature on species of *Mola* is extensive and exceeds 1,000 works; nonetheless, numerous aspects of morphology of *Mola* and biology remain mysterious (Fraser-Brunner 1951; Yamanoue and Sawai 2012; Matsuura 2015). Taxonomic confusion remains within the Molidae (56 nominal species, including unavailable names: Eschmeyer et al. 2017), with 34 nominal species in *Mola* alone. Unfortunately, most type specimens of the nominal species are lost (Parenti 2003; Eschmeyer et al. 2017).

The first comprehensive review of the Molidae, by Fraser-Brunner (1951), recognized five species in three genera: *Masturus lanceolatus* (Liénard 1840), *Masturus oxyuropterus* (Bleeker 1873), *Mola mola* (Linnaeus 1758), *Mola ramsayi* (Giglioli 1883), and *Ranzania laevis* (Pennant 1776). Fraser-Brunner (1951) proposed that the genus *Mola* is characterized by having ossicles along the rear margin of the clavus and that *Mola mola* and *Mola ramsayi* are distinguishable from each other using the following features: 1) number of clavus fin rays (16 in *Mola ramsayi* vs. 12 in *Mola mola*); 2) number of clavus ossicles (12 in *Mola ramsayi* vs. 8 or 9 in *Mola mola*); 3) size of the clavus ossicles (broader than the space between them in *Mola ramsayi* vs. narrower than the space between them in *Mola mola*); 4) shape of the clavus margin (not wavy in *Mola ramsayi* vs. wavy or lobed with age in *Mola mola*); 5) clavus ossicles on the paraxial rays ["paraxial ossicles" (PO) in Fraser-Brunner 1951] (these ossicles are separate and smaller than the other ossicles in *Mola ramsayi* vs. these ossicles are united to form a single ossicle and are larger than the other ossicles in *Mola mola*); and 6) presence or absence of a band of reduced denticles along the base of the clavus from the dorsal to anal fins ["naked area of reduced denticles" (NA) in Fraser-Brunner 1951; called a 'smooth band' in this study] (absent in *Mola ramsayi* vs. present in *Mola mola*). In addition, Fraser-Brunner (1951) postulated that *Mola mola* is widely distributed in the world's oceans, while *Mola ramsayi* is distributed only in the South Pacific (New Zealand, Australia and Chile).

Presently, the morphology-based classification of Fraser-Brunner (1951) is generally accepted, yet recent studies of molecular phylogeny have suggested different opinions on the classification of species. Bass et al. (2005) found four clades in *Mola* (namely: *Mola mola* Atlantic group, *Mola mola* Pacific group, *Mola ramsayi* Atlantic group, and *Mola ramsayi* Pacific group) based on partial D-loop sequences of mitochondrial DNA (mtDNA), although the morphological characters were not examined. Yoshita et al. (2009) analyzed both partial and complete D-loop sequences and proposed that *Mola* contains at least three species, which the authors temporarily assigned to *Mola* sp. A, *Mola* sp. B, and *Mola* sp. C. To date, although subclades (or subgroups) were found in *Mola* sp. A and *Mola* sp. B, the three clades have been regarded as representing separate species (Yamanoue and Sawai 2012; Ahuir-Baraja et al. 2017; Sawai et al. 2017a; Nyegaard et al. 2017).

Yoshita et al. (2009) proposed that adult *Mola* sp. A and *Mola* sp. B are distinguishable using the following five characters (Fig. 1): 1) number of clavus fin rays (14–17 in *Mola* sp. A vs. 10–13 in *Mola* sp. B); 2) number of clavus ossicles (8–15 in *Mola* sp. A vs. 8 or 9 in *Mola* sp. B); 3) shape of the clavus margin [not wavy in *Mola* sp. A vs. wavy or lobed in *Mola* sp. B (although not wavy in small specimens of *Mola* sp. B)]; 4) presence or absence of a head bump (present in

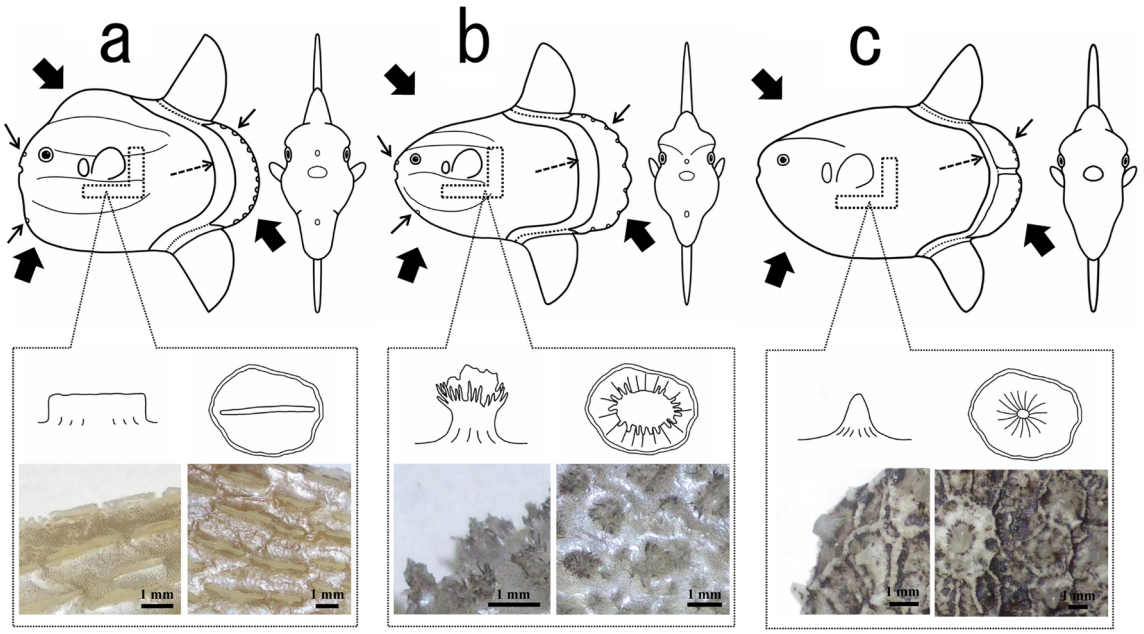

Fig. 1 Generalized body forms (side and front view) and body scale morphology of adult *Mola alexandrini*, *Mola mola*, and *Mola tecta*. **a** *M. alexandrini* [= *Mola* sp. A sensu Yoshita et al. (2009)], **b** *M. mola* [= *Mola* sp. B sensu Yoshita et al. (2009)], **c** *M. tecta* [= *Mola* sp. C sensu Yoshita et al. (2009)]. *Large arrows* indicate points of morphological differences (shape of head, clavus, and chin). *Small arrows* indicate ossicles (on snout, chin, and clavus). *Broken arrows* indicate the smooth band. Broken squares indicate scales on the middle region of the body (left, transverse view; right, upper view; photographs of dried skin). For further details, see 'Materials and methods'

Mola sp. A vs. absent in *Mola* sp. B); and 5) proportion of the body length to body depth (the anterior part of *Mola* sp. A is larger than *Mola* sp. B). Further studies have provided two additional diagnostic characters: shape of the body scales (called denticles in Fraser-Brunner 1951) [rectangular (line shaped when viewed from above) in *Mola* sp. A vs. conical with branching tips (dot shaped when viewed from above) in *Mola* sp. B] (Sawai et al. 2015b; Sawai 2016b; Sawai and Yamanoue 2016b) and presence or absence of a chin bump (present in *Mola* sp. A vs. absent in *Mola* sp. B) (Sawai et al. 2017a) (Fig. 1).

Nyegaard et al. (2017) recently described *Mola* sp. C sensu Yoshita et al. (2009) as *Mola tecta*, based on the holotype and 11 paratypes collected from New Zealand and Australia, and included a review of original descriptions of the genus. *Mola tecta* (>65 cm TL) is distinguishable by the following combination of 11 characters: 1) 15–17 clavus fin rays; 2) 5–7 clavus ossicles; 3) anterior profile laterally tapered (no swollen dorso-lateral and ventro-lateral ridges on body); 4) head profile rounded (without protruding snout); 5) no head bump; 6) no chin bump; 7) smooth band present at base of clavus from the dorsal to anal fins; 8) smooth band with a 'back-fold'; 9) clavus rounded with an indent; 10) ossicles on paraxial fin rays separate; and 11) body scales conical and without branching tips (simple and dot shaped when viewed from above) (Nyegaard et al. 2017). Nyegaard et al. (2017) also suggested that *Mola* sp. A and *Mola* sp. B proposed by Yoshita et al. (2009) presumably apply to *Mola ramsayi* and *Mola mola*, respectively. Although they did not conduct a detailed review about the scientific names of *Mola* sp. A and *Mola* sp. B, they confirmed that the three genetically identified species in *Mola* proposed by Yoshita et al. (2009) are distinct species based on morphology.

The present study aimed to resolve the nomenclatural status of the remaining two genetically identified species (i.e. *Mola* sp. A and *Mola* sp. B), based on both molecular and morphological investigation, by examining the available type material and revaluating the diagnostic characters proposed by previous studies (i.e. Fraser-Brunner 1951; Yoshita et al. 2009; Sawai et al. 2015b; Nyegaard et al. 2017).

Materials and methods

Morphological data were collected from 30 specimens of *Mola*: 14 fresh or preserved specimens of *Mola alexandrini*, plus the holotypes of *Orthragoriscus alexandrini* (mounted skin) and *Orthragoriscus ramsayi* (mounted skin); and 13 fresh or preserved specimens of *Mola mola*, plus the holotype of *Ozodura orsini* (mounted skin). Some data were obtained from photographs, and data from previous studies were also included (i.e. Yoshita et al. 2009; Sawai et al. 2009, 2015b, 2017a; Yamanoue et al. 2010; Sawai 2016a; Ahuir-Baraja et al. 2017; Nyegaard et al. 2017).

Counts generally follow the methods of Yoshita et al. (2009). Fin rays were macroscopically counted when discernible externally, and those of some specimens were confirmed by dissection or from X-rays. Fin rays of the dorsal + clavus + anal complex (D + C + A fin rays) were counted following Gudger (1937). Ossicles were counted by feeling along the rear margin of the clavus (Fig. 1; see also Sawai et al. 2015b: fig. 1, right).

Measurements were according to Yoshita et al. (2009: fig. 2) and included total length (TL), head bump length (HBL), pre-clavus band length (PCBL), body depth (BD), and total body depth (TBD). Measurements were made with a tape measure, ruler, or calipers to the nearest 0.1 cm. For comparison of the morphometrics of *M. alexandrini* and *M. mola*, the specimens examined were divided into large (>180 cm TL, presumably adult stage) and small (<70 cm TL, presumably young stage) since the body proportions of molids significantly change with age (see Table 1). Unfortunately, moderately sized specimens (70–180 cm TL) were not obtained. Assessment of the developmental stages was based on descriptions of the external morphology provided by Iwai (2005). In Iwai (2005), the young or adolescent stage is defined as the transition period from juvenile to adult where the morphological characteristics of the fish body are developing and thus the morphological characteristics of the species first appear, yet the relative body proportions are different from the final adult form.

Morphological observations here generally follow Fraser-Brunner (1951), Yoshita et al. (2009), Sawai (2016b), Sawai et al. (2017a), and Nyegaard et al. (2017) (see Table 2). Specifically, the following external assessments were made: establishing the shape of the clavus margin as either wavy (i.e. lobed or scalloped), rounded, or rounded with an indent (Fig. 1; see also Yoshita et al. 2009: fig. 5; Nyegaard et al. 2017: fig. 5); ascertaining the presence or absence of a smooth band at the base of the clavus between the dorsal and anal fins (Fig. 1; see also Fraser-Brunner 1951: figs. 13, 14, 16, 17), the presence or absence of a head bump (Fig. 1; see also Sawai et al. 2015b: fig. 2), the presence or absence of a chin bump (Fig. 1; see also Sawai et al. 2017a: fig. 4), and the presence or absence of a smooth band back-fold (Fig. 1; see also Nyegaard et al. 2017: fig. 5). Furthermore, the shape of the body scales on the middle region of the body was observed both macroscopically and microscopically to discern the shape of the scales as rectangular (line shaped when viewed from above), conical with branching tips (dot shaped when viewed from above), or conical without branching tips (simple and dot shaped when viewed from above) (Fig. 1; see also Sawai 2016b: figs. 2–4; Nyegaard et al. 2017: fig. 9). In this study, paraxial fin rays were defined as the pair of fin

Table 1 Measurements for *Mola alexandrini* and *M. mola*

	M. alexandrini				*M. mola*		
	Holotype: MZUB (unnumbered)[a]	BMNH 1883.11.29.22[a]	Other small specimens (means)	Other large specimens (means)[b]	Neotype: MZUB (unnumbered)[a]	Other small specimens (means)[b]	Other large specimens (means)[b]
Total length (cm)	190.0	229.1	29.3–51.5, *n* = 6	181.3–269.0, *n* = 5	59.7	28.2–70.1, *n* = 19	193.7–277.0, *n* = 10
Head bump length (% TL)	18.6[c]	11.0[c]	9.9–14.2 (11.4), *n* = 5	7.7–16.0 (10.6), *n* = 5	8.7[c]	8.8–12.2 (10.4), *n* = 11	5.2–10.9 (7.5), *n* = 10
Pre-clavus band length (% TL)	76.3	81.2	82.9–87.5 (84.9), *n* = 6	80.3–83.1 (81.9), *n* = 5	85.4	82.2–89.5 (85.4), *n* = 19	74.9–81.3 (77.5), *n* = 10
Body depth (% TL)	65.3	57.4	67.8–72.7 (69.6), *n* = 6	56.3–62.8 (59.6), *n* = 5	50.3	63.0–76.4 (70.6), *n* = 18	45.7–58.6 (52.1), *n* = 10
Total body depth (% TL)	broken	broken	150.5–160.0 (154.6), *n* = 4	112.9–155.8 (129.0), *n* = 5	broken	138.3–156.0 (145.9), *n* = 12	109.4–122.8 (117.0), *n* = 8

[a]Mounted specimens

[b]Including data from Yoshita et al. (2009)

[c]Data was taken from measurement of photograph on the screen, when we could not directly measure

rays in the middle of the clavus, nearest to the end of the vertebral column (see also Fraser-Brunner 1951).

Institutional abbreviations follow Fricke and Eschmeyer (2017), with the addition of the following: Ibaraki Nature Museum, Ibaraki, Japan (INM); Ibaraki Prefectural Oarai Aquarium, Ibaraki, Japan (OA); Kitakyushu Museum of Natural History and Human History, Fukuoka, Japan (KMNH); Oman Marine Science and Fisheries Centre, Muscat, Sultanate of Oman (OMMSFC); and Sea and Life Museum, Tottori, Japan (SLM).

The type specimens in MZUB, holotype of *M. alexandrini*, MZUB (unnumbered), and neotype of *M. mola*, MZUB (unnumbered), have a special position in the oldest collections and could not have a unique number ID by museum rule (Bruno Sabelli, personal communication). However, their location is particular in special well-identified positions with appropiate label as type (ICZN 1999, Art. Recommendation 72D–72F).

Mola alexandrini (Ranzani 1839)

(Japanese name: Ushi-manbo; New English name: Bump-head sunfish) [Figs. 1a, 2, 3a, c (left), 4, 5a, 6a–d, 7; Tables 1–2; Electronic Supplementary Material (ESM) Table S1]

Orthragoriscus alexandrini Ranzani 1839: 75, foldout table, pl. 6 (left) (type locality: Adriatic Sea); Alessandrini 1839: 359, pls. 31–34; Steenstrup and Lütken 1898: 61.

Orthragoriscus ramsayi Giglioli 1883: 315 (type locality: New South Wales, Australia); Ramsay 1883: 46.

Orthagoriscus mola: Williams 1893: 110, pl. 8A; Parker 1897: 627; Wilton and Brown 1908: 5, pl. 4, fig. 7.

Orthagoriscus alessandrini: Steenstrup and Lütken 1898: 20 (misspelling of *O. alexandrini*).

Ozodura alessandrinii: Steenstrup and Lütken 1898: 21 (misspelling of *O. alexandrini*).

Orthagoriscus alexandrinii: Steenstrup and Lütken 1898: 34, fig. 15 (misspelling of *O. alexandrini*).

Mola mola (not of Linnaeus): Waite 1913: 223 (in part), pl. 9; Waite 1921: 198 (in part), fig. 332; Waite 1923: 230, unnumbered fig. on p. 231; Phillipps 1926: 171 (in part), fig. 2; Gudger 1928: 257 (in part), unnumbered figs. on pp. 258–259, 261; Barnard 1935: 654 (in part), figs. 5a–b; Smith 1950: 422 (in part), pl. 95, fig. 1213; Smith 1965: 422 (in part), pl. 95, fig. 1213; Khan 1975: 295, fig. 1; Anderson et al. 1998: 29 (in part), pl. 4, fig. 44; Roach 2003: 1; Yamanoue et al. 2004: 269; Barreiros and Teves 2005: 4 (in part), unnumbered fig. on p. 4; Bass et al. 2005: 405 (in part); Sagara et al. 2005: 35 (in part); Konow et al. 2006: 208, fig. 1a; Nakatsubo et al. 2007a: 259 (in part); Nakatsubo et al. 2007b: 613 (in part); Soichi 2009: 200 (in part), fig. 2B; Pope et al. 2010: 472 (in part), fig. 1; Jawad 2013: 287 (in part), fig. 1; Phillips et al. 2015: 1118 (in part), fig. 1, nos. 2, 6, 13; Pan et al. 2016: 2 (in part), fig. 1a.

Mola ramsayi: Whitley 1931: 126 (in part), pl. 16, figs. 3–4; Fraser-Brunner 1951: 90 (in part), figs. 13–14; Tyler 1980: 377; Last et al. 1983: 521, fig. 33.24; Heemstra 1986: 908, fig. 270.3; Hutchins and Swainston 1986: 114, fig. 686, Appendix I; Al-Ghais 1994: 19, unnumbered figs. on pp. 19, 30; Glover 1994: 917, fig. 809; Hutchins 2001b: 3966, unnumbered fig. on p. 3968; Brito 2003: 77 (in part), fig. 2; Parenti 2003: 3 (in part); Heemstra and Heemstra

Table 2 Morphological characters for *Mola alexandrini*, *M. mola*, and *M. tecta*

	M. alexandrini			*M. mola*		*M. tecta*	
	Holotype: MZUB (unnumbered)[a]	BMNH 1883.11.29.22[a]	Other specimens (means)[b]	Neotype: MZUB (unnumbered)[a]	Other specimens (means)[b]	Holotype: NMNZ P.057679[e]	Other specimens (means)[e]
Total length (cm)	190.0	229.1	29.3–325.0, *n* = 20	59.7	28.2–277.0, *n* = 34	101.1	49.9–242.0, *n* = 25
Counts (means)							
Pectoral fin rays	12	12	11–12 (11.7), *n* = 14	12	10–13 (11.8), *n* = 20	11	11–13 (11.9), *n* = 11
Dorsal fin rays	18	18	16–19 (17.6), *n* = 10	18	18–19 (18.4), *n* = 8	18	17–19 (18.1), *n* = 8
Anal fin rays	17	17	15–17 (16.5), *n* = 10	16	17–18 (17.4), *n* = 8	17	16–18 (17.1), *n* = 8
Clavus fin rays	Uncountable	Uncountable	14–24 (17.3), *n* = 12	13	11–14 (12.3), *n* = 15	17	15–17 (15.9), *n* = 10
D+C+A fin rays	-	-	48–57 (52.0), *n* = 10	47	47–50 (48.5), *n* = 8	52	50–52 (51.3), *n* = 7
Ossicles on clavus	11–13	12	0–15 (10.3), *n* = 15 [8–15 (11.8), *n* = 10, >60 cm TL][c,d]	7	0–9 (6.4), *n* = 23 [8–9 (8.6), *n* = 14, >60 cm TL][d]	7	0–7 (4.3), *n* = 13 [5–7 (5.8), *n* = 8, >65 cm TL (final number)]
Morphological observations							
Shape of clavus edge	Round	Round	Round, *n* = 20	Round	Wavy (>126.4 cm TL), *n* = 14	Rounded with an indent	Rounded with an indent, *n* = 24; deformed, *n* = 1
Smooth band	Present	Present	Present, *n* = 20	Present	Present, *n* = 34	Present	Present, *n* = 25
Smooth band back-fold	Absent	Absent	Absent, *n* = 19; present, *n* = 1	Absent	Absent, *n* = 34	Present	Present, *n* = 24; not visible, *n* = 1
Head bump	Present	Present	Present (>162.5 cm TL), *n* = 12	Absent	Absent, *n* = 34	Absent	Absent, *n* = 25
Shape of body scale	Rectangular	Rectangular	Rectangular (>162.5 cm TL), *n* = 11	Conical	Conical with branching of tip (>109.9 cm TL), *n* = 14	Conical without branching of tip	Conical without branching of tip, *n* = 17
Chin bump	Present	Present	Present (>135.0 cm TL), *n* = 13	Absent	Absent, *n* = 34	Absent	Absent, *n* = 25

D+C+A dorsal+clavus+anal

[a]Mounted specimens

[b]Including data from Yoshita et al. (2009), Sawai et al. (2009, 2015b, 2017a), Yamanoue et al. (2010), Sawai (2016a), and Ahuir-Baraja et al. (2017)

[c]For specimens with a range (e.g. 11–13 ossicles), the lower number was used

[d]Ossicles of *M. mola* reached the final number (Sawai, unpublished data)

[e]Data from Nyegaard et al. (2017), but an abnormal specimen (NZ19) was removed in present paper

2004: 458; Bass et al. 2005: 405 (in part); Bray and Hoese 2006: 1937; Mohan et al. 2006: 23, unnumbered fig. on p. 24; Bray 2008: 859, unnumbered fig. on p. 860; Pope et al. 2010: 473 (in part); Jawad et al. 2012: 1, figs. 1–2; Saunders 2012: 133; Kishore et al. 2013: 9, fig. 1; Thys et al. 2013: 1, fig. 1A; Yasemi and Nazari Bejgan 2014: 242, fig. 1; Matsuura 2015: 96, fig. 6; Phillips et al. 2015: 1118, fig. 1, nos. 4a–b; Stewart and Struthers 2015: 1745 (in part), fig. 250.2; Thys et al. 2016: 1, fig. 2; Matsuura 2017: 87, figs. 13-3, 15-1, unnumbered figs. on p. 95; Thys et al. 2017: 1, fig. 3.

Fig. 2 Holotype of *Orthragoriscus ramsayi* (junior synonym of *Mola alexandrini*) deposited in BMNH. BMNH 1883.11.29.22, 229.1 cm TL (mounted skin), Darling Harbour, New South Wales, Australia. *Red square*, 10 cm × 10 cm

Masturus lanceolatus (not of Liénard): Gudger 1937: 375 (in part), pl. 4, fig. 13.

Mola alexandrini: Barnard 1947: 212, pl. 25, fig. 7; Barnard 1948: 402; Smith 1950: 422; Smith 1965: 422.

Pseudomola lassarati Cadenat 1959: 1115, figs. 9–11 (type locality: Vridi, Ivory Coast); Blache et al. 1970: 198, fig. 539; Tyler 1980: 377; Tortonese 1990: 1079.

Mola ramsayi Atlantic group: Bass et al. 2005: 405.

Mola mola group A: Yoshita et al. 2005: 171.

Mola sp. group A: Yoshita et al. 2009: 232, fig. 5 (left).

Mola sp. A: Sawai et al. 2009: 9, fig. 5; Yamanoue et al. 2010: 27; Sawai et al. 2011: 181; Yamanoue and Sawai, 2012: 167, figs. 9.1 (right)–9.2 (left); Hatooka and Hagiwara 2013: 1747, unnumbered fig. on p. 1747 (bottom); Sawai et al. 2014: 127, fig. 1; Sawai et al. 2015a: 201, fig. 1; Sawai et al. 2015b: 65, figs. 1A, 2A–C, 3A; Sawai 2016b: 349, fig. 4; Sawai and Yamanoue 2016a: 54, fig. 1; Sawai and Yamanoue 2016b: 451, figs. 2A, 3A; Ahuir-Baraja et al. 2017: 1133, fig. 1; Sawai et al. 2017a: 99, figs. 3–4; Sawai et al. 2017b: fig. 1; Nyegaard et al. 2017.

?*Mola ramsayi*: Whitley 1931: 127 (in part), text fig. 2, pl. 16, fig. 1; Atria 1967: 3; Villalba and Fernández 1985: 71; Gauldie 1990: 193, fig. 4B; Gauldie 1992: 263, figs. 4–6; Luque and Oliva 1993: 273; Hutchins 2001a: 48; Putra et al. 2015: 545.

Holotype. MZUB (unnumbered), sex unknown, 190.0 cm TL, Adriatic Sea (mounted skin; presumably adult stage).

Other materials examined (*n* = 13). AIM MA30934, 211.0 cm TL, New Zealand(?) (cast); BMNH 1870.12.27.41, 42.5 cm TL, South Australia(?); BMNH 1883.11.29.22, 229.1 cm TL, New South Wales, Australia (holotype of *Orthragoriscus ramsayi*: mounted skin); INM-1-000568, 280.0 cm TL (measured when fresh), off Hirakata, Ibaraki, Japan (36°51'N, 140°48'E) (sample code KIMo-1 in Sawai et al. 2015b; mounted skin); KMNH VR 100,123, female, 325.0 cm TL (measured when fresh), off Ohse, Ibaraki, Japan (36°34'N, 140°39'E) (sample code OI-1 in Yoshita et al. 2009 and Sawai et al. 2015b; mounted skin); NMNZ P.006345, male, 38.8 cm TL, off Te Kaha, New Zealand (37°39'S, 177° 31'E); NMNZ P.009887, male, 38.5 cm TL, off North Cape, New Zealand (35°13'S, 172° 28'E); NMNZ P.034449, female, 51.5 cm TL, Southern Colville Ridge, New Zealand (36°24'S, 176° 51'E); NMNZ P.036964, female, 45.3 cm TL, off Mahia Peninsula, New Zealand (39°05'S, 178°53'E); NMNZ P.056071, male, 29.3 cm TL, off Raglan Harbour, New Zealand (37°44'S, 174°10'E); OA-Pi-1, 300.0 cm TL (measured when fresh), off Ohse, Ibaraki, Japan (36°34'N, 140°39'E) (sample code OIMo-1 in Sawai et al. 2015b; mounted skin); OMMSFC1085, 91.6 cm TL, coast of Sur, Sultanate of Oman (22°35'N, 59°30'E); OMMSTC1097, 135.0 cm TL, coast of Quriat, Sultanate of Oman (22°16'N, 58°59'E).

Additional specimens not preserved (n = 8). Almsp-1 (sample code in Ahuir-Baraja et al. 2017), female, 240.0 cm TL, Almazora, Spain (39°56'N, 00°03'W); AM-54 (sample code in Yoshita et al. 2009), female, 332.0 cm TL, Aji Island, Miyagi, Japan (38°16'N, 141°28'E); FI-19 (sample code in Yamanoue et al. 2010), female, 265.1 cm TL, Funakoshi Bay, Iwate, Japan (39°23'N, 141°58'E); IO-1 (sample code in Yoshita et al. 2009), female, 181.3 cm TL, Ie Island, Okinawa, Japan (26°45'N, 127°45'E); TaHMo-2 (this study), 162.5 cm TL, off Hualian, Taiwan (24°03'N, 121°37'E); YI-9, 26, 27 (sample code in Yoshita et al. 2009), 3 specimens (3 females), 249.0–269.0 cm TL, Yamada Bay, Iwate, Japan (39°29'N, 142°04'E).

Diagnosis. *Mola alexandrini* is distinguishable from other species of *Mola* by the following combination of characters: 14–24 (mode 17) clavus fin rays; 8–15 (12) clavus ossicles (specimens >60.0 cm TL); rounded clavus (usually not wavy and without indents); smooth band on clavus without a back-fold; head with high protuberance (bump) (specimens >162.5 cm TL); scales rectangular on middle region of body, shape developing with age (final shape not established on specimens <70.0 cm TL, but established on

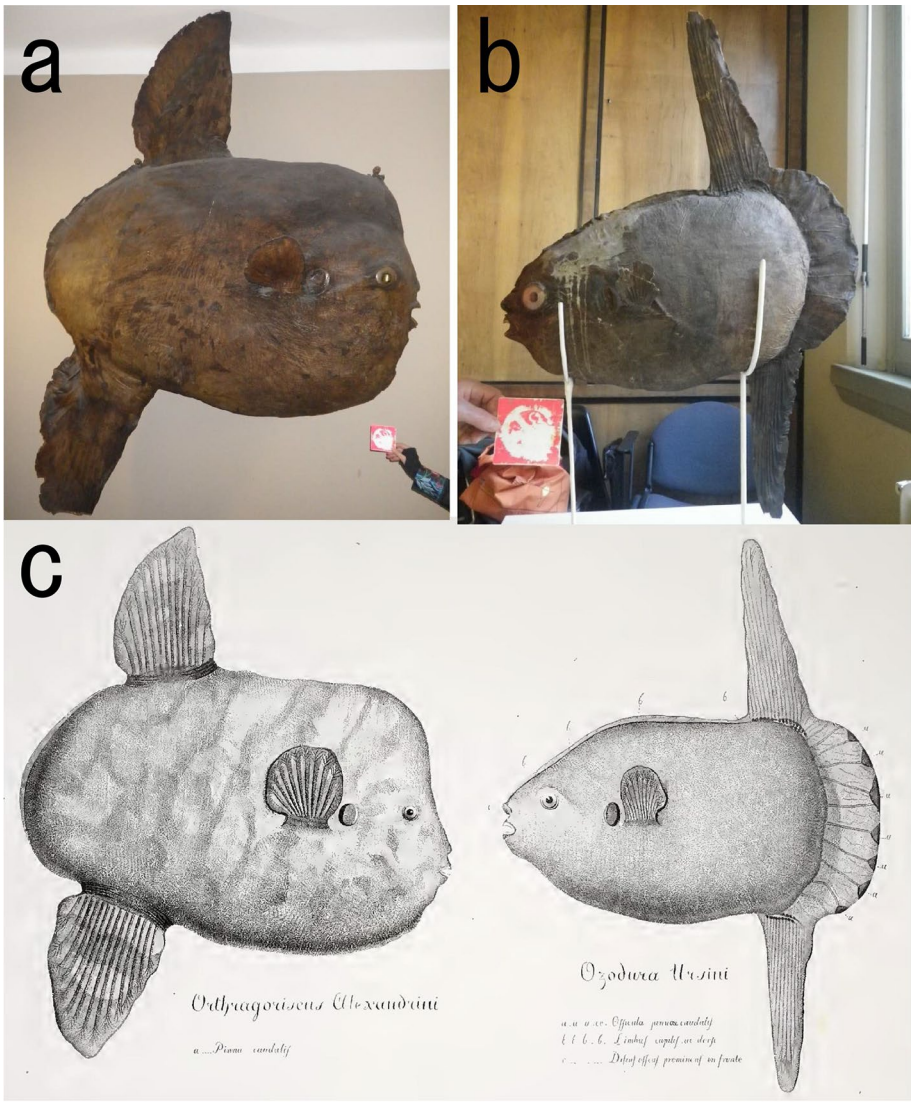

Fig. 3 Type specimens of *Mola alexandrini* and *Mola mola*. **a** Holotype of *M. alexandrini* (holotype of *Orthragoriscus alexandrini*), MZUB (unnumbered), 190.0 cm TL (mounted skin), Adriatic Sea; **b** neotype of *M. mola* (holotype of *Ozodura orsini*), MZUB (unnumbered), 59.7 cm TL (mounted skin), Adriatic Sea; **c** drawing of holotypes of *Orthragoriscus alexandrini* (left) and *Ozodura orsini* (right) from Ranzani (1839). *Red square* 10 cm × 10 cm

specimens >162.5 cm TL); chin with enlarged bump (specimens >135.0 cm TL).

Description. Measurements, counts and observations are shown in Tables 1–2. Body orbicular, deep, and laterally compressed; body surface covered with small rectangular scales (line shaped when viewed from above; Fig. 1a), smooth to the touch; whole body with thick white subcutaneous gelatinous layer, except for pectoral, dorsal and anal fins; mouth small and terminal (snout projecting beyond mouth in some large specimens); teeth in both jaws fused and beak-like; pair of small nostrils in front of eyes; eyes small; gill openings small, oval, located in front of pectoral fins, and covered by soft gill membrane; gill rakers concealed under subcutaneous gelatinous layer; lateral lines present at least on head; many small, white, rounded otoconia instead of otoliths; all fins spineless; caudal fin and pelvic fins absent; pectoral fins small, rounded, located midlaterally and fitting into shallow groove on sides of body; dorsal fin located opposite anal fin, and both fins similarly triangular (fin tips change from acute angle to obtuse angle with age); caudal fin replaced with broad clavus, comprising highly modified elements of the dorsal and anal fins; clavus margin rounded in individuals of all sizes; smooth band at base of clavus between dorsal and anal fins (Fig. 1a), and body scales in smooth band smaller than in surrounding area; urogenital opening immediately in front of anal fin, and anal opening immediately in front of urogenital opening; external differences between the sexes not apparent, but the shape of gonads differs in males and females: ovary single and ball shaped, and testis paired, elongated, and rod-like.

Head bump forming with age, from above eyes to front of dorsal-fin base; chin bump evident with age, from beneath lower jaw to beneath pectoral fins (profile gently curved to bulbous in some large specimens); lateral ridges from head, above and below eyes, to beyond pectoral fins (Fig. 1a),

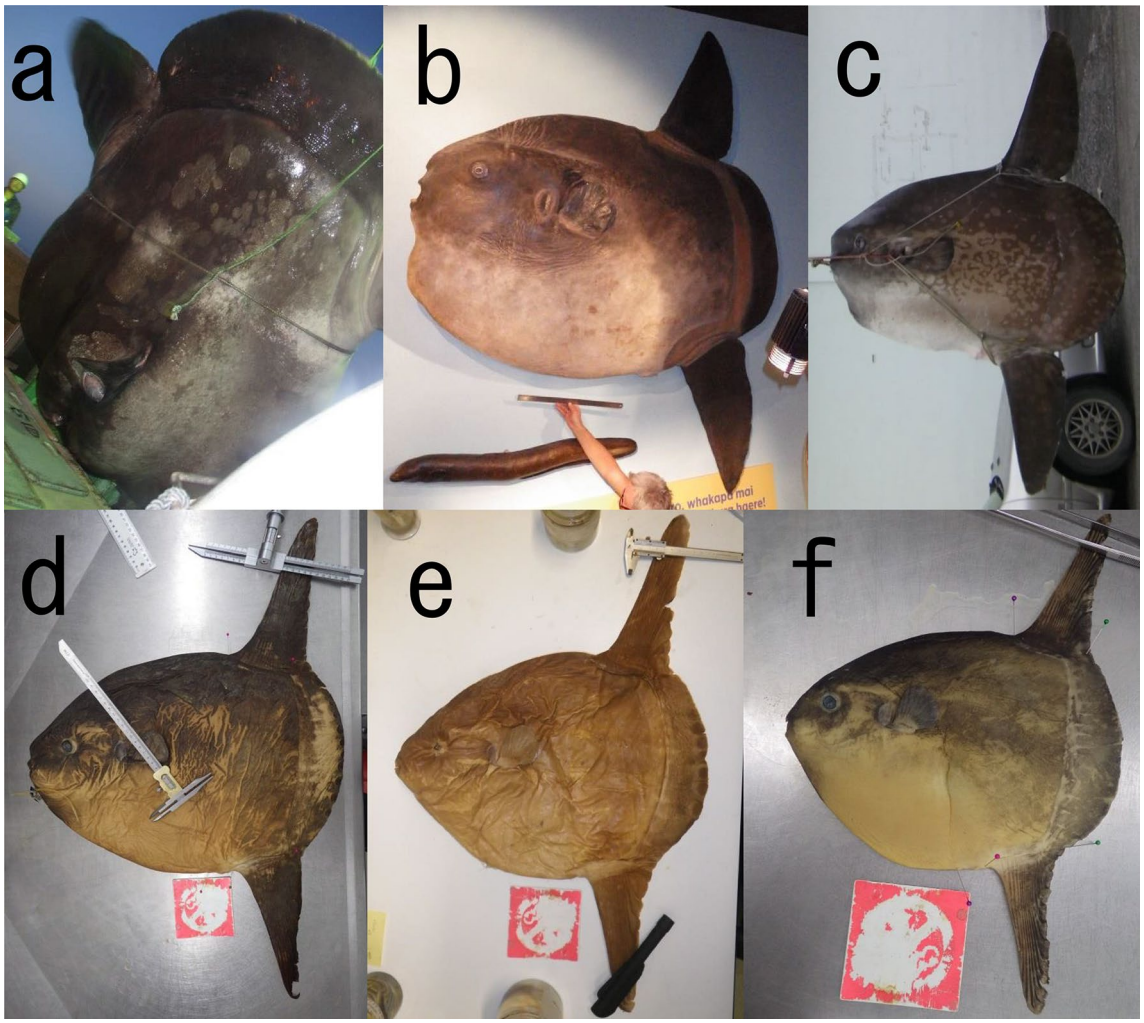

Fig. 4 Specimens of *Mola alexandrini*. **a** AM-54, 332.0 cm TL (photographed by K. Sagara); **b** AIM MA30934, 211.0 cm TL (cast); **c** TaHMo-2, 162.5 cm TL (photographed by Z. T. Lin); **d** NMNZ P.034449, 51.5 cm TL; **e** BMNH 1870.12.27.41, 42.5 cm TL; **f** NMNZ P.056071, 29.3 cm TL. *Red square* 10 cm × 10 cm

developing with age; clavus ossicles, a snout ossicle, and a chin ossicle developing with age (Fig. 1a).

Colour of fresh specimens. When alive or freshly collected, generally gray or dark reddish brown dorsally, dusky white ventrally, all fins gray or dark reddish brown (similar to dorsal region), and many large or small paler spots and irregular pattern over the body (Figs. 4a, c). Body colour of live bump-head sunfish can instantaneously change to dark, pale and spotted pattern.

Colour of preserved specimens. Body reddish brown or yellow, and live body colours, spots, and patterns faded (Fig. 4d–f).

Distribution and ecological notes. *Mola alexandrini* is widely distributed in the world's oceans except for the polar regions (Fig. 5a; ESM Table S1); collected from waters off Japan, Taiwan, Galápagos Islands, New Zealand, Australia, Turkey, Oman, and Spain (Yamanoue et al. 2004, 2010; Bass et al. 2005; Sagara et al. 2005; Yoshita et al. 2005, 2009; Sawai et al. 2009, 2011, 2017a; Yamanoue and Sawai 2012; Thys et al. 2013, Ahuir-Baraja et al. 2017; Nyegaard et al. 2017). *Mola alexandrini* presumably prefers warmer water temperatures than inhabited by *Mola mola*; in waters off the Sanriku coast of Japan, sea surface temperatures during the occurrence of *M. alexandrini* (16.8–25.6°C, average 19.9°C) were on average higher than during the occurrence of *M. mola* (11.5–25.6°C, average 17.7°C) (Sawai et al. 2011).

Remarks. A large mounted specimen, exhibited on a wall at MZUB, appears identical to the figure in the original description of *Orthragoriscus alexandrini* by Ranzani (1839). Also, two of the characters used in the original description [i.e. "*in parte postica fere ovatum*" (= the posterior part is almost oval) and "*fronte altissima prominenti*" (= forehead projected high)] are consistent with our observations of the holotype (Fig. 3a; Table 2). In addition, the total length of

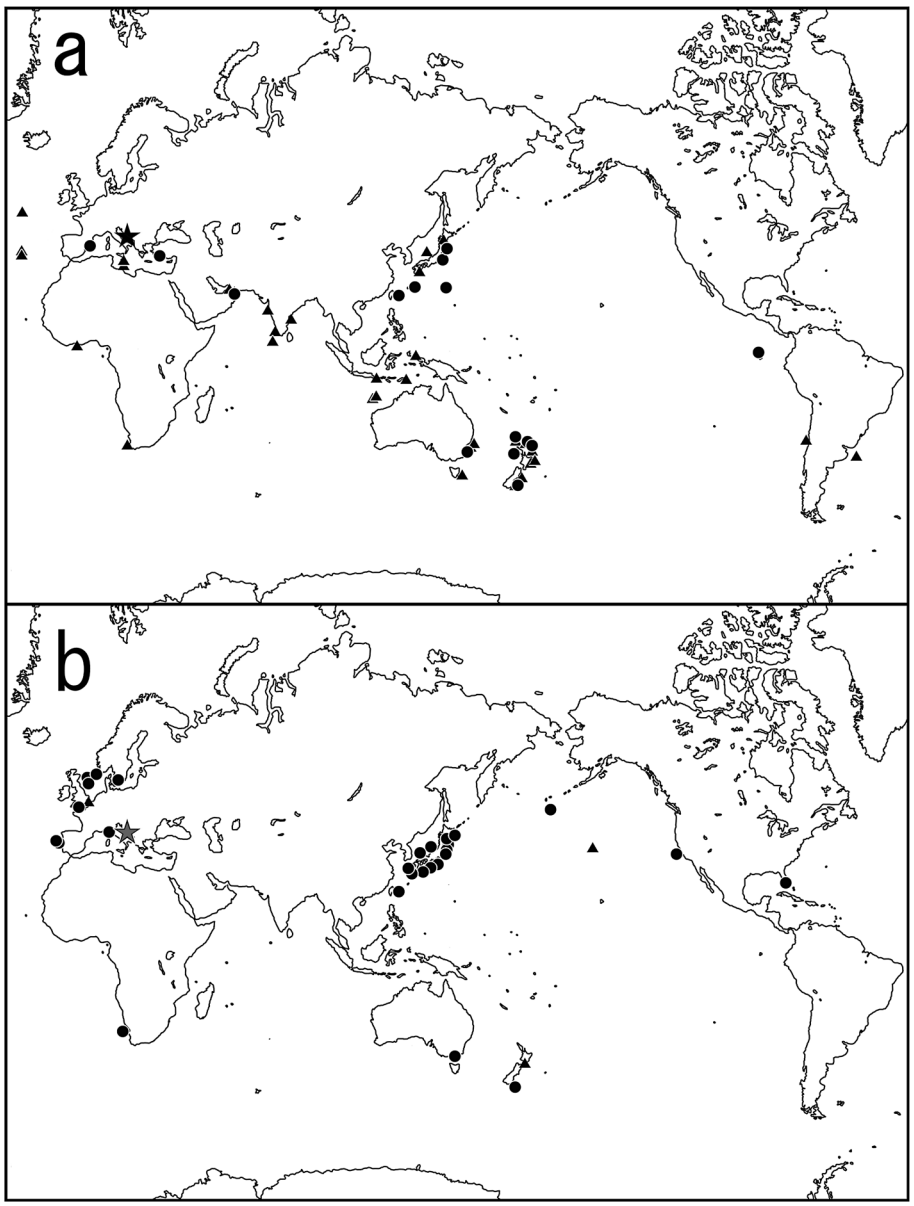

Fig. 5 Distribution of *Mola* as confirmed by this study and from the literature (ESM Table S1). **a** *Mola alexandrini*; **b** *Mola mola*. *Star* type locality (black, holotype; gray, neotype), *circles* records of genetically identified specimens, *triangles* records of morphologically identified specimens

the whole specimen was given as "6. 2. 3" in the original description (Ranzani 1839), which can be interpreted as 6 feet, 2 inches, 3 lines, which is equivalent to 189 cm in English units (metric units), and is very near our measurement of 190.0 cm TL for the holotype. Furthermore, because the original description of *O. alexandrini* appeared in a journal published by the University of Bologna, the mounted specimen can be regarded as the legitimate holotype of this species.

In Fraser-Brunner's (1951) comprehensive review of the Molidae, *M. alexandrini* was regarded as a junior synonym of *M. mola*, and this synonymization was later accepted by both Parenti (2003) and Eschmeyer et al. (2017). However, Fraser-Brunner (1951) examined the holotype of *Orthragoriscus ramsayi*, but not the holotype of *O. alexandrini*. Since he believed the former species was distributed only in the South Pacific, he appears to have automatically treated specimens found in the Northern Hemisphere as *M. mola*. Furthermore, the holotype of *O. ramsayi* only possesses two of the six key characters of *Mola ramsayi* (i.e. a rounded clavus and 12 ossicles) that were proposed by Fraser-Brunner (1951) (Table 2), and two other characters (16 clavus fin rays, and the ossicles on the paraxial rays are separate and smaller than the other ossicles) were not observed on the specimen, likely owing to the thickness of the skin. Regarding the remaining specimen, BMNH 1883.11.29.22, the clavus fin rays and state of the paraxial ossicles are not visible. Thus, we consider it likely that Fraser-Brunner obtained these two diagnostic characters solely from the latter specimen (Fig. 4e). The diagnostic character (clavus ossicles being broader than the spaces between them) is

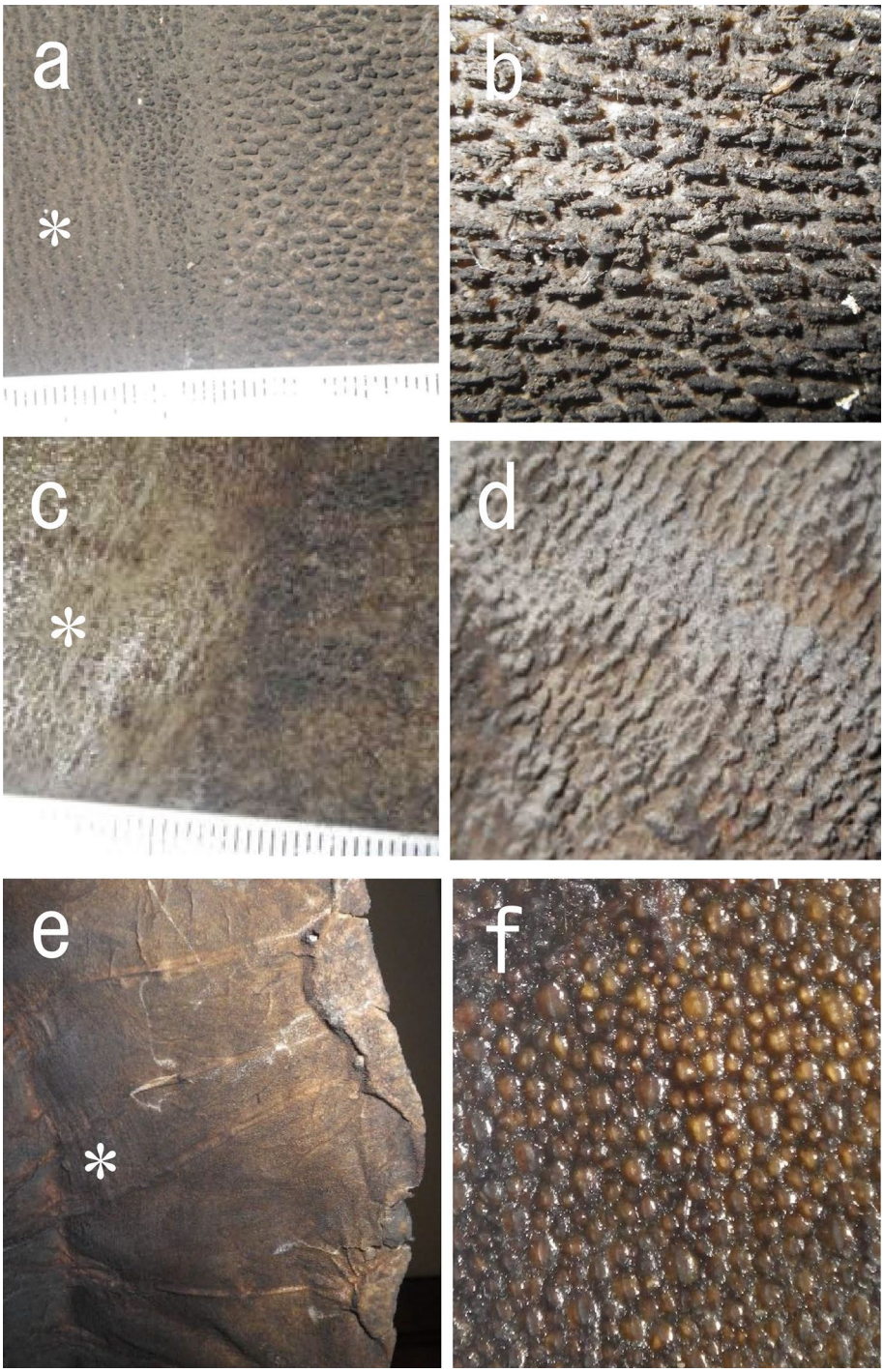

Fig. 6 Smooth band and body scales of *Mola*. **a**, **b** the holotype of *Orthragoriscus ramsayi* (junior synonym of *Mola alexandrini*), BMNH 1883.11.29.22, 229.1 cm TL, mounted skin), smooth band (**a**), body scales (**b**); **c**, **d** holotype of *M. alexandrini* [MZUB (unnumbered), 190.0 cm TL, mounted skin], smooth band (**c**), body scales (**d**); **e**, **f** neotype of *Mola mola* [holotype of *Ozodura orsini*, MZUB (unnumbered), 59.7 cm TL, mounted skin], smooth band (**e**), body scales (**f**). *Asterisks* indicate the smooth band at the base of the clavus between the dorsal and anal fins

also largely congruent with our observations. However, the character 'absence of smooth band' contradicts our finding of a smooth band present on the holotype of *O. ramsayi* (Fig. 6a; cf. Strom 2016). The smooth band was probably simply overlooked by Fraser-Brunner (1951), since this feature is not as clear in *M. alexandrini* as in *M. mola*, owing to different morphology of the body scales (Sawai et al. 2017a). Furthermore, the smooth band tends to become indistinct on a mounted skin (Sawai et al. 2015b), possibly owing to the application of chemical coatings used for preservation. Thus, although the absence of a smooth band has generally been regarded as a diagnostic character for distinguishing between *M. ramsayi* and *M. mola* (cf. Jawad et al. 2012; Thys et al. 2013), it is not a valid diagnostic character.

The holotype of *O. ramsayi* is a mounted skin (poor condition) in BMNH (Fig. 2). The catalogue number of the former was given as BMNH 1888.11.29.22 in some literature (e.g. Bray and Hoese 2006; Matsuura 2017), but the correct

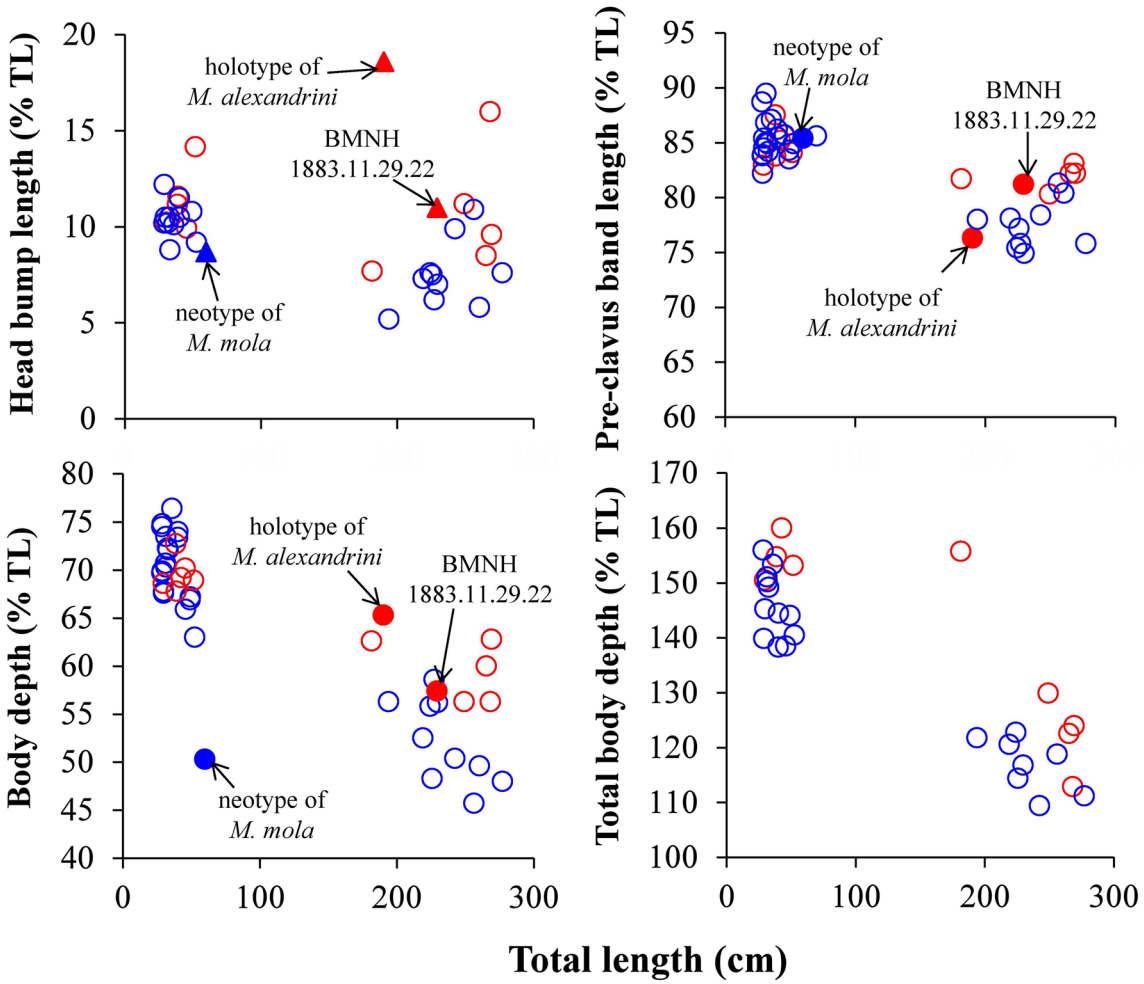

Fig. 7 Relationship between total length and body proportions. *Red Mola alexandrini*, *blue Mola mola*, *open symbols*, non-type material, *solid symbols*, type specimens, *circles* measurements from specimens, *triangles*, measurements obtained from photographs

catalogue number is BMNH 1883.11.29.22 (The Natural History Museum 2017). The original description of *O. ramsayi* by Giglioli (1883: 315) was brief and lacked detail, but four salient characters were mentioned. These were the overall shape and size of the fish, the form of the clavus, and a fourth character that is somewhat unclear: "small carinate horny scales, which appear to cover the osseous granulation of the dermis", which may pertain to the morphology of the body scales or alternatively refer to the presence of clavus ossicles. Our examination of the holotype revealed that the state of several of its features (clavus ossicles, rounded clavus, smooth band, rectangular body scales, head bump, chin bump) are consistent with those of *Mola* sp. A sensu Yoshita et al. (2009) (Figs. 6a–b; Table 2). Four of these characters (rounded clavus, smooth band, head bump, chin bump) are also evident on a photograph of the recently restored holotype of *O. ramsayi* (Strom 2016).

Therefore, we propose that the holotypes of *M. alexandrini* and *M. ramsayi* represent the same species and furthermore match genetically with *Mola* sp. A sensu Yoshita et al. (2009). This conclusion is strongly supported by the reported distributions of these species, evidenced by their type localities (Mediterranean Sea and Australia, respectively), which have since been confirmed by additional specimens identified as these purported species in molecular and morphological studies (i.e. Yoshita et al. 2009; Ahuir-Baraja et al. 2017; Nyegaard, unpublished data).

Although the scientific name of this species has been accepted as *M. ramsayi* based on Fraser-Brunner (1951), *M. alexandrini* was used as a valid name by others (e.g. Barnard 1935, 1947, 1948; Smith 1950, 1965). Therefore, we conclude that *M. alexandrini* is a valid species according to Article 23.9.1.1 of ICZN (1999). Moreover, to date, the maximum recorded (not estimated) weight of *M. alexandrini* is 2,300 kg for a 272 cm TL female caught by set net off the coast of Kamogawa, Japan, on 16 August 1996 (Roach 2003; Nakatsubo et al. 2007b; Pope et al. 2010; Sawai 2017). This specimen, which is currently regarded as the world's

heaviest bony fish specimen, was previously identified as *M. mola* (Roach 2003; Pope et al. 2010). Here, we re-identify it as *M. alexandrini*—from the head bump, chin bump, and rounded clavus (see also Nakatsubo et al. 2007b: table 2; Soichi 2009: fig. 2B; Pope et al. 2010: fig. 1). Therefore, the world's heaviest bony fish that has been actually weighed and recorded to date is a specimen of *M. alexandrini*, and not *M. mola*. However, this species may grow even larger; we could confirm a maximal length of 332.0 cm TL for a female specimen (not weighed) caught off Aji Island, Miyagi, Japan, on 11 August 2004 (Fig. 4a; see also Yoshita et al. 2009).

Neotype designation for *Tetraodon mola* Linnaeus 1758

Tetraodon mola Linnaeus 1758 is considered valid as one of two species of *Mola*, that is, *Mola mola* by Fraser-Brunner (1951), which has since been widely accepted (e.g. Martin and Drewry 1978; Parenti 2003; Bray 2008; Eschmeyer et al. 2017). Yoshita et al. (2009) and Matsuura (2015) suggested that genetically identified *Mola* sp. B has the morphological characteristics of this species that were proposed by Fraser-Brunner (1951). Although the presence of a smooth band at the base of the clavus is not a valid diagnostic character, the other morphological characters are consistent with those found in *Mola* sp. B, and distinguish *M. mola* from *Mola alexandrini* and *Mola tecta* (Fig. 1b; Table 2). Therefore, we conclude that Fraser-Brunner's (1951) *M. mola* and *Mola* sp. B (of later investigators) represent the same species.

However, there is no known type material of *Tetraodon mola* (see Tortonese 1990; Eschmeyer et al. 2017). For comparison with *M. alexandrini*, we investigated the description of *Tetraodon mola* by Linnaeus (1758). The original Latin description was brief: "*T. laevis compressus, cauda truncata: pinna brevissima dorsali analique annexa*" (= Tetraodon smooth compressed, tail truncated: connected to short-based dorsal and anal fins). It is likely that Linnaeus (1758) described *Ranzania laevis* owing to the terms 'smooth' and 'short dorsal and anal fins,' which are in contrast to the coarse body scales of *M. mola*. Retzius (1785) indicated that the skin of *M. mola* is rough and that of *R. laevis* is smooth, and also pointed out that figures of *R. laevis* in Bianchi (1746), cited by Linnaeus, represent *R. laevis*, and not *M. mola*. Accordingly, Retzius (1785) believed that Linnaeus described the species without examining any specimens, but only based on the literature. Indeed, three references, Artedi (1738), Bianchi (1746) and Gronovius (1754), were used for the description of this species by Linnaeus (1758). Artedi (1738) did not include any illustrations but the following descriptions, which indicate species of *Mola*: "*cutis dura and aspera*" (= skin hardened and rough); "*pondus 100 librarum*" (= 100 pounds weight); "*cauda semicircularis*" (= semicircular tail); "*ossicula in pinnis*" (= ossicle in fin). Most of the eleven references cited by Artedi (1738) also indicated species of *Mola* (i.e. Rondelet 1554: 424, unnumbered fig.; Salviani 1554: 154, fig. P55; Gesner 1563: 85 left, unnumbered lower fig.; Gesner 1604: 640, unnumbered fig.; Plinius Secundus et al. 1608: 1365, 1391; Aldrovandi 1613: 412, unnumbered fig.; Jonston 1632: 419; Jonston 1650: 30, pl. 9, fig. 2; Charleton 1668: 129; Willughby 1686: 151; Ray 1713: 51), but exceptionally Gesner (1604: 635, unnumbered upper fig.) described a fish with a caudal fin, which cannot be interpreted as a species of *Mola*. Presumably, Artedi (1738) cited that reference by mistake. The description and illustration of Bianchi (1746) also represent *R. laevis* (Wheeler 1979). The description in Gronovius (1754) is brief and without illustrations, and does not have information enough to specify the species, but rather two references are cited: Jonston (1660) and unpublished data of Peter Artedi (Arted. mss. ad Sebam). However, the description of 'Mola peregrina' in Jonston (1660: pl. 9, fig. 1) clearly represents *R. laevis*, as pointed out by Gudger (1936). Steenstrup and Lütken (1898: 59) mentioned that Linnaeus (1758) described *T. mola* based on descriptions of species of *Mola* and *R. laevis*. The type locality of *T. mola* is the Mediterranean Sea, and *M. alexandrini*, *M. mola,* and *R. laevis* do occur in this area, but not *M. tecta*. Therefore, we consider that Linnaeus (1758) described *T. mola* only based on the previous descriptions of *R. laevis* and *M. alexandrini* and/or *M. mola*. This is consistent with the fact that the type material of *T. mola* cannot be found to date, despite searches for the holotype by previous and present investigators at the Linnaean fish collections of the Swedish Museum of Natural History (Fernholm and Wheeler 1983; Sven Oscar Kullander, personal communication), at the Linnean Society of London (Wheeler 1985; The Linnean Society of London 2017), and at the Museum of Evolution (formerly, the Zoological Museum of the University of Uppsala, Sweden) (Wheeler 1991; Erica Mejlon, personal communication).

Tetraodon mola was described based on multiple species, and a name-bearing type is necessary to define the nominal taxon objectively (ICZN 1999, Art. 75.1). *Tetraodon mola*, however, should not be regarded as a synonym of *R. laevis*, because the descriptions that Linnaeus (1758) based his designation on included species of *Mola*; thus confusion should be avoided by changing the current status, which has long been accepted (ICZN 1999, Art. 23.2). The type locality of *T. mola* is the Mediterranean Sea, and *M. mola* is more dominant in the Mediterranean than *M. alexandrini*, based on our genetic and morphological examinations of specimens from this area (Sawai and Yamanoue, unpublished data). Accordingly then, the current status of *M. mola* is appropriate and should not be changed.

Ozodura orsini was regarded as a synonym of *T. mola* because the holotype has the following characters, diagnostic for this species: 13 clavus fin rays; 7 clavus ossicles; conical body scales (branching tips lost owing to chemical coating) [see below "Comparisons"; Figs. 3b, c (right), 6f; Table 2]. This holotype was obtained from the Adriatic Sea in the Mediterranean (Ranzani 1839); MZUB maintains a research collection with proper facilities for preserving name-bearing types, and this specimen is herein designated as the neotype of *T. mola*, in accordance with Article 75.3 of ICZN (1999).

Additionally, previous genetic studies suggested the possibility that two clades of *M. mola* (Atlantic vs. Pacific) can be divided into the distinct species/subspecies (Bass et al. 2005; Yoshita et al. 2009; Ahuir-Baraja et al. 2017; Sawai et al. 2017a; Nyegaard et al. 2017). However, our data are not sufficient and further study is needed.

Comparisons

The total counts of the rays of three fins (pectoral fin rays, dorsal fin rays, and anal fin rays) among three species of *Mola* are similar to each other (Table 2), and thus cannot be a useful diagnostic character. Concerning average clavus fin rays and average D + C + A fin rays, those of *M. alexandrini* and *M. tecta* are similar to each other, but higher than those counts for *M. mola* (Table 2). Concerning specimens in which the final number (the constant number) of clavus ossicles has been formed (specimens >65 cm TL), the average number of clavus ossicles among the three species of *Mola* clearly differs: 11.8 in *M. alexandrini* vs. 8.6 in *M. mola* vs. 5.8 in *M. tecta* (Table 2). The shape of the clavus rear margin in large specimens is clearly distinguishable among the three species of *Mola*: rounded in *M. alexandrini* vs. wavy (or lobed) in *M. mola* vs. rounded with an indent in *M. tecta* (Fig. 1). Although the presence or absence of a smooth band at the base of the clavus is not a useful character for distinguishing the three species of *Mola* (Table 2), the presence of a smooth band back-fold is likely to be a useful key character for *M. tecta* (Fig. 1; Table 2). However, meticulous examination is needed because the back-fold in small preserved specimens of *M. tecta* may be difficult to detect (see Table 2; Nyegaard et al. 2017). In addition, a back-fold is occasionally found in some specimens of both *M. alexandrini* and *M. mola*, although they appear faint (Table 2; Sawai and Nyegaard, personal observation). The presence of a head bump and a chin bump is a valid diagnostic character for *M. alexandrini* only in large specimens (Figs. 1, 4; Table 2), but a small head bump and a small chin bump are occasionally found in some specimens of *M. mola* (Sawai, personal observation). The shape of the body scales is clearly different among the three species of *Mola*: rectangular or line shaped in *M. alexandrini* vs. conical with branching tips or dot shaped in *M. mola* vs. conical without branching tips or simple and dot shaped in *M. tecta* (Fig. 1).

Two diagnostic characters of *Mola*, as proposed by Fraser-Brunner (1951), were found only on a small number of specimens of *M. alexandrini*, as they require dissection or X-ray examinations for accurate assessment. The clavus ossicles in *M. alexandrini* tend to be broader than the spaces between them, while the clavus ossicles in *M. mola* tend to be narrower than the spaces between them (see Fraser-Brunner 1951: figs. 14, 16; Sawai et al. 2017a; Sawai, personal observation). The clavus ossicles on the paraxial rays in *M. alexandrini* are separate and smaller than the remaining ossicles, whereas the clavus ossicles on the paraxial rays in *M. mola* are united to form a single ossicle which is larger than the other ossicles (see Fraser-Brunner 1951: figs. 14, 16; Sawai et al. 2017a: fig. 3A; Sawai, personal observation). In *M. tecta*, the clavus ossicles on the paraxial rays are clearly separate and similar in size to the adjacent clavus ossicles, and a smooth band back-fold exists between the paraxial clavus ossicles (Nyegaard et al. 2017).

Furthermore, four diagnostic characters (number of clavus ossicles, shape of the clavus margin, head bump, chin bump) change as individuals grow larger, becoming well evident in large specimens but not useful as diagnostic characters in small specimens (Table 2). Macroscopic observations of body scale morphology on larger specimens revealed differences among the three species of *Mola* (Fig. 1); yet, based on examinations of small specimens, scale morphology may appear superficially similar among the species when the scales are less developed (Sawai, personal observation). However, scale morphology in *M. tecta* appears to be established at >50 cm TL (Nyegaard et al. 2017). Similarly, Yoshita et al. (2009) proposed four morphometric features that differ between *M. alexandrini* and *M. mola*, with large specimens of both species displaying extreme differences (especially, the BD/TL and TBD/TL of *M. alexandrini* were higher by 7.5 % than those of *M. mola*), while small specimens of the two species were similarly proportioned (Fig. 7; Table 1). This also appears to be the case for *M. tecta* (Nyegaard et al. 2017), although future investigators should take care to examine the body proportions of numerous individuals.

The smallest specimens of *M. alexandrini* (i.e. NMNZ P.056071, 29.3 cm TL, Fig. 4f) and *M. mola* (i.e. NSMT-P75065, 28.2 cm TL, Fig. 8f) examined in this study were distinguished molecularly (Yoshita et al. 2009; Nyegaard et al. 2017), but were similar in appearance. Presumably, small specimens of *M. tecta* are morphologically similar to the other two species of *Mola*. This points to the difficulty of identifying small specimens of *Mola* and highlights the need to include small specimens of *Mola* in future investigations combining morphology and molecular analyses.

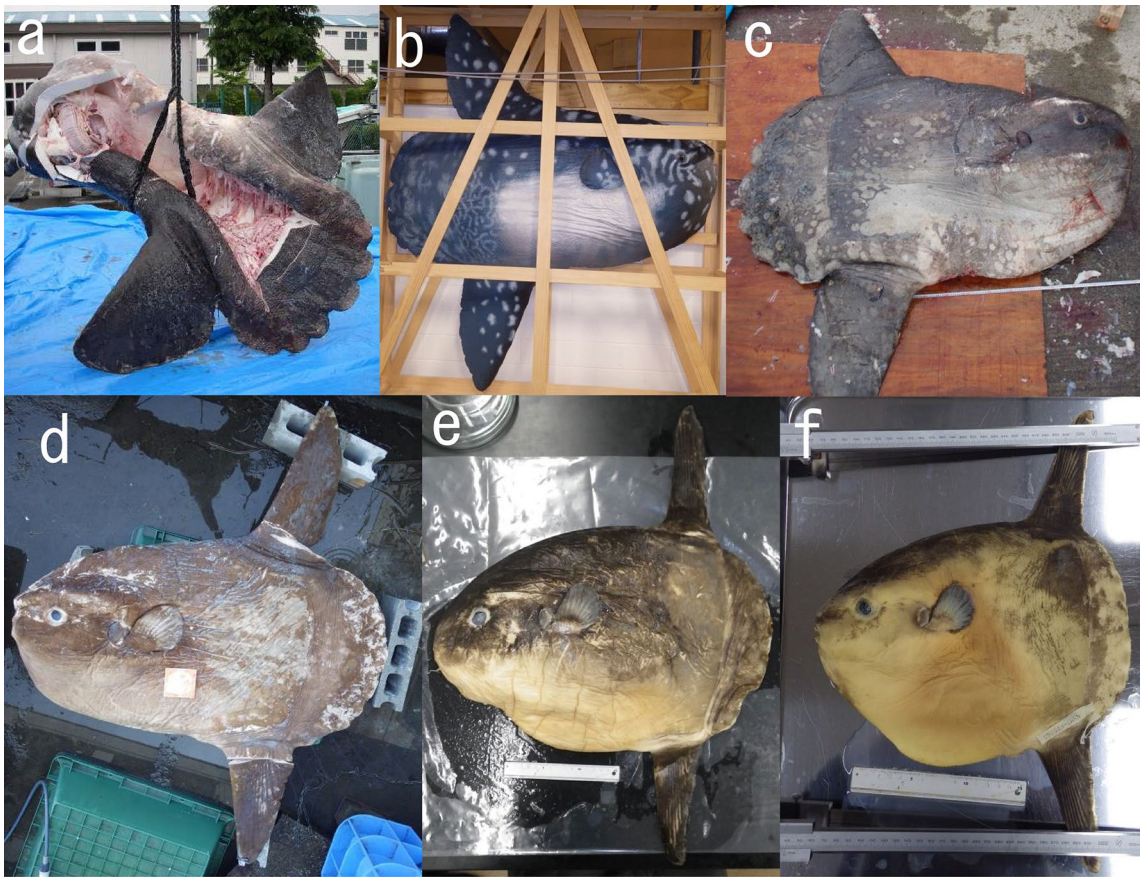

Fig. 8 Specimens of *Mola mola*. **a** YI-16, 277.0 cm TL; **b** NMNZ P.002629, 253.6 cm TL (cast); **c** YI-18, 193.7 cm TL (photographed by Y. Yoshita); **d** KAUM–I. 19082, 126.4 cm TL; **e** NSMT-P 76575, 45.5 cm TL; **f** NSMT-P 75065, 28.2 cm TL. *Red square*, 10 cm × 10 cm

Several diagnostic characters of the three species of *Mola* develop with age. The head and chin profiles in *M. alexandrini* acquire bumps with age (Figs. 1a, 4). The shape of the clavus margin in *M. mola* becomes wavy or lobed with age, as the clavus edge grows beyond the ossicles (Figs. 1b, 8). In contrast, the external morphology of *M. tecta* >50 cm TL does not change significantly with age (Fig. 1c; Nyegaard et al. 2017). The clavus ossicles of *M. mola* develop and increase in number in specimens up to approximately <60 cm TL, when they reach a stable number (Sawai, unpublished data). In *M. tecta*, the final number of clavus ossicles is reached at >65 cm TL (Nyegaard et al. 2017); in *M. alexandrini*, the final number of clavus ossicles is established in specimens by at least 60 cm TL. Lateral ridges above and below the eyes develop with age in *M. alexandrini* and *M. mola* (Figs. 1, 4, 8); however, the dorso-lateral ridge in *M. tecta* remains slight and short with age (Nyegaard et al. 2017). The tips of the dorsal and anal fins change from an acute angle to an obtuse angle with age in all three species of *Mola* (Figs. 4, 8; Nyegaard et al. 2017). Clavus fin rays were not readily visible in large specimens owing to the thickness of the subcutaneous gelatinous layer (Table 2); thus, dissection was needed to count the rays in large specimens. A study of these morphological characters with ontogenetic development is still needed, since this study did not obtain data for medium-sized specimens.

Despite that the holotype of *M. alexandrini* and the neotype of *M. mola* are of remarkably different sizes, the diagnostic characters clearly differentiate them as different species. Specimens SLM-1 (*M. mola*; sample code YS-2 in Yoshita et al. 2009) and KMNH VR 100,123 (*M. alexandrini*; sample code OI-1 in Yoshita et al. 2009), both very large mounted skins, are valuable because the species identities, were confirmed genetically (Yoshita et al. 2009). In future studies, consideration of these large specimens may still inform our understanding of the morphology of the genus *Mola*.

Based on morphologically and genetically verified *M. alexandrini* from this and other studies, this species is widely distributed in the world's oceans (Fig. 5a; ESM Table S1). In comparison, while *M. tecta* appears to be distributed predominantly in the temperate waters of the Southern Hemisphere (Nyegaard et al. 2017: fig. 10). Based on *M. mola* specimens examined in this study as well as the

genetically identified specimens in previous studies, the distribution of *M. mola* is biased to the northern hemisphere with no records currently from the Indian Ocean (Fig. 5b; ESM Table S1). However, the distribution of each species of *Mola* needs to be reconsidered in future studies due to widespread species confusion and taxonomic problems, especially in *M. mola*.

Discussion

In the present study, *Mola alexandrini*, *Mola mola* and *Mola tecta* are found to be valid species names for *Mola* sp. A, *Mola* sp. B, and *Mola* sp. C, respectively (cf. Yoshita et al. 2009; Nyegaard et al. 2017). *Mola alexandrini*, senior synonym of *Mola ramsayi*, is herein redescribed based on 21 specimens together with the rediscovered holotype, and a neotype of *Mola mola* is designated to compare between these species, which have long been confused with each other.

The only molid genus and species newly described since Fraser-Brunner's (1951) revision was *Pseudomola lassarati*. This description was based on one specimen (109 cm TL) from the Ivory Coast (Cadenat 1959), but the whereabouts of the holotype are unknown (Parenti 2003; Eschmeyer et al. 2017). Cadenat (1959: figs. 9–11) proposed this new genus distinguishable from *Mola* and *Masturus* by the following combination of characters: body white on the abdominal region, and numerous, nonsymmetrical (not on both sides), white spots and reticulations dorsally; rectangular body scales; and clavus rounded, without median projection, ossicles, and supported by 20 fin rays. Although Blache et al. (1970) treated *P. lassarati* as valid, Tortonese (1990) treated it as a *nomen nudum*, although Tyler (1980), Parenti (2003), and Eschmeyer et al. (2017) treated it as a junior synonym of *Masturus lanceolatus*. However, the aforementioned characters of *P. lassarati* are fairly consistent with those of *M. alexandrini* (Fig. 4; Table 2), except for the reported lack of ossicles in *P. lassarati*. However, it is possible that the ossicles of *P. lassarati* were overlooked because they are relatively small compared with the large body. In addition, some specimens of *Mola alexandrini* have numerous (large or small) white spots scattered over the body (Fig. 4c), very similar to those of *Masturus lanceolatus*. Therefore, Gudger (1937) and Tyler (1980) regarded this species as a synonym of *Masturus lanceolatus*, based on the body colour. For these reasons, we conclude that *P. lassarati* is a junior synonym of *Mola alexandrini*.

Cephalus ortagoriscus Risso 1827 may possibly be another senior synonym of *Mola alexandrini* as its 18 clavus fin rays closely match the number in *Mola alexandrini* (Table 2). However, we regard this species as a *nomen dubium* because other morphological characters are unknown, as no type material can be found.

Orthagoriscus eurypterus Philippi 1892 (type locality, Chile; 222 cm TL) was regarded as a junior synonym of *Mola ramsayi* by Parenti (2003) and Eschmeyer et al. (2017). Fraser-Brunner (1951) regarded *O. eurypterus* as a questionable synonym of *Mola ramsayi*, while Oliver Schneider (1930) and Nyegaard et al. (2017) reviewed *O. eurypterus* and concluded it was possibly a junior synonym of *Mola mola*. Based on the current data, it is likely that *O. eurypterus* is a junior synonym of *Mola mola*, rather than a junior synonym of *Mola alexandrini*.

Nine nominal species (*Mola aculeata* Koelreuter 1766; *Diodon mola* Pallas 1770; *Diodon nummularis* Walbaum 1792; *Orthragoriscus hispidus* Bloch and Schneider 1801; *Cephalus pallasianus* Shaw 1804; *Mola hispida* Nardo 1827; *Diodon carinatus* Mitchill 1828; *Molacanthus pallasii* Swainson 1839; *Pallasia pallasi* Nardo 1840) were described based on the multi-pointed star forms of the prejuvenile stage of *Mola*. Thus far, prejuvenile specimens of *Mola* collected have generally been identified as *Mola mola* (Martin and Drewry 1978), while no prejuvenile specimens of the other species have ever been identified. Therefore, we could not determine whether any of the nine nominal species that were described based on prejuvenile specimens represent *Mola alexandrini*; hence, further studies are needed to clarify the status of those species.

Ranzani (1839) counted the fin rays of the holotype of *Mola alexandrini* as 10 pectoral fin rays, 15 dorsal fin rays, and 13 anal fin rays, and the neotype of *Mola mola* as 12 pectoral fin rays, 16 dorsal fin rays, 14 anal fin rays, and 14 clavus fin rays. These counts differ from our findings (Table 2), but Ranzani (1839) possibly miscalculated the counts since it is difficult to count fin rays in mounted specimens (Fig. 3). Especially, the clavus fin rays, as well as the state of the clavus ossicles on the paraxial rays, are generally not visible in large specimens owing to the thickness of the subcutaneous gelatinous layer. Moreover, some clavus fin rays may have been included as dorsal and/or anal fin rays.

Many of the articles reviewed by Fraser-Brunner (1951) were based on cursory examinations of relatively few specimens (Matsuura 2015). Therefore, he could not fully appreciate intra- and inter-specific variations in the characters of *Mola alexandrini* and *Mola mola*. For instance, the intraspecific variation in the counts of fin rays and ossicles is higher here than would be anticipated by reading Fraser-Brunner (1951) (Table 2).

Until now, the common name 'southern ocean sunfish' has been used for *M. alexandrini*. This common name stemmed from the belief that this species occurs only in the Southern Hemisphere, as discussed by Fraser-Brunner (1951) (Thys et al. 2013). Matsubara (1955) similarly named this species 'Goshu-manbo' in Japanese ('Goshu' meaning

'Australia,' and 'manbo' meaning 'ocean sunfish'), based on the geographical distribution proposed by Fraser-Brunner (1951). It seems likely therefore that *Mola alexandrini* in the Northern Hemisphere has been widely confused with *Mola mola*. Based on the species' much wider distribution as revealed in recent studies, Thys et al. (2013) pointed out that the common name southern ocean sunfish is no longer appropriate. Therefore, we propose the common name bump-head sunfish for *Mola alexandrini*, based on its most prominent morphological character; for the same reason, we adopt the Japanese common name Ushi-manbo ('Ushi' meaning cow, referring to the head profile), as already proposed by Yamanoue et al. (2010).

Comparative materials. *Mola mola* (n = 13): BMNH2006.12.15.1, 70.1 cm TL, Whitstable, United Kingdom (51°22'N, 01°03'E); KAUM–I. 19082, 27983, 2 specimens, 109.9 and 126.4 cm TL, Ibusuki, Kagoshima, Japan (31°10'N, 130°32'E); MZUB (unnumbered) (neotype), 59.7 cm TL, Adriatic Sea (mounted skin); NMNZ P.002629, 253.6 cm TL, Palliser Bay, New Zealand (42°34'S, 175°05'E) (cast); NSMT-P 75037, 75065–75067, 4 specimens, 28.2–49.1 cm TL, North Pacific Ocean (42°46'N, 170°19'E) (sample code NP-8, 11–13 in Yoshita et al. 2009); NSMT-P 76575, 45.5 cm TL, Ryouri, Iwate, Japan (39°02'N, 141°52'E); NSMT-P 111410–111411, 2 specimens (1 male and 1 female), 28.6 and 29.6 cm TL (measured when fresh), North Pacific Ocean (38°00–04'N, 157°00–04'W); SLM-1, female, 275.0 cm TL (measured when fresh), Yunotsu, Shimane, Japan (35°05'N, 132°22'E) (sample code YS-2 in Yoshita et al. 2009 and Sawai et al. 2015b; mounted skin). *Mola tecta* (n = 26): NMNZ P.057679 (holotype), male, 101.1 cm TL (measured when fresh), North Taranaki Bight, New Zealand (38°26'S 174°09'E); 25 other specimens, listed in Nyegaard et al. (2017).

Additional data obtained in the field (not preserved whole body specimens) (Mola mola, n = 22). FI-86 (sample code in Sawai et al. 2009), female, 139.9 cm TL, Funakoshi Bay, Iwate, Japan (39°23'N, 141°58'E); KI-8 (sample code in Yoshita et al. 2009), female, 260.1 cm TL, off Kamaishi, Iwate, Japan (39°16'N, 141°53'E); NP-2–7 (sample code in Yoshita et al. 2009), 6 specimens, 28.4–33.0 cm TL, North Pacific Ocean (42°46'N, 170°19'E); OtI-8–10 (sample code in Yoshita et al. 2009), 3 specimens, 35.6–40.0 cm TL, off Otsuchi, Iwate, Japan (39°20'N, 141°55'E); YI-1, 5, 8, 16–21, 22, 24 (sample code in Yoshita et al. 2009), 11 specimens (including at least 3 males, 4 females), 49.0–277.0 cm TL, Yamada Bay, Iwate, Japan (39°29'N, 142°04'E).

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