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Morphologic and molecular redescription of *Catostylus mosaicus conservativus* (Scyphozoa: Rhizostomeae: Catostylidae) from south-east Australia

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Two reciprocally monophyletic mitochondrial clades of the commercially valuable jellyfish *Catostylus mosaicus* are endemic to south-eastern Australia. Here, medusae in the two clades are shown to differ also in colour and in the dimensions of their papillae, oral disk, and bell depth. They are referred to two varieties recognized in 1884 by von Lendenfeld. The clade occupying localities adjacent to Bass Strait is redescribed as subspecies *C. mosaicus conservativus*; the clade from New South Wales and southern Queensland spans the type locality (Port Jackson) of *C. mosaicus* and is designated *C. mosaicus mosaicus*. Their ecology and colour, in the context of von Lendenfeld's original descriptions, and the implications for fisheries are discussed.

INTRODUCTION

Catostylus mosaicus (Quoy & Gaimard, 1824) is a rhizostome jellyfish endemic to eastern Australia. Originally described from Port Jackson (Sydney) in New South Wales (Quoy & Gaimard, 1824), the species is thought to range from Port Phillip (Melbourne) in Victoria to the Torres Strait (Kramp, 1965; Southcott, 1982), i.e. across three biogeographic boundaries. Given recent reports of multiple cryptic species in widely distributed scyphozoans (Dawson & Jacobs, 2001; Dawson, 2004; Holland et al., 2004) the taxonomic singularity of *C. mosaicus* might best be viewed with caution.

von Lendenfeld (1884) reported *C. mosaicus* of two distinct colour types: a blue morph in Port Phillip and a brown morph in Port Jackson. He considered the geographic, environmental, and morphological differences sufficient to recognize two varieties, possibly species: a blue 'conservativa' and brown 'symbiotica'. The names were attributed on the basis that the blue form '[conserved] the habits of its ancestors' while the brown colour was due to 'yellow cells … known as Zooxanthella[e].'

The validity of these varieties is questionable on several grounds. First, colour is geographically inconsistent. Although brown morphs were never found in Port Phillip, von Lendenfeld (1884) reported blue morphs in the vicinity of Sydney, albeit occasionally and in low frequency. Blue medusae are also common, along with a 'milky-white' morph, in Queensland's waters (Southcott, 1982). Second, colour may have been temporally inconsistent. Quoy & Gaimard (1824) originally described *C. mosaicus* in Port Jackson as 'toute blanche ou plutôt glauque' i.e. all white or rather dull blue-green. von Lendenfeld (1884) himself noted, when proposing the two varieties, that all prior descriptions from Sydney were of blue to grey medusae, not the bright brown medusae despite their colour being 'so very striking'. Third, *C. mosaicus* in Port Jackson may be variegated, from bread-white through blue to coffee coloured (von Lendenfeld, 1884; Mayer, 1910). Finally, the difference in colour may not be attributable to the establishment of symbioses with zooxanthellae (Kingsford et al., 2000; Pitt, 2000). Neither Mayer (1910) nor Kramp (1961, 1965) recognized the varieties proposed by von Lendenfeld (1884) in their monographs on the medusae.

However, recent ecological data have indicated distinct stocks of *C. mosaicus* in New South Wales (Pitt & Kingsford, 2000a), a result supported by phylogeographic analyses using mitochondrial cytochrome *c* oxidase subunit I (COI; Dawson, 2005). The COI sequence data also reveal reciprocally monophyletic 'Southern' (Victoria and Tasmania) and 'Central' (New South Wales and Brisbane) clades of medusae that apparently diverged during the early Pleistocene

(Dawson, 2005). Resolving the taxonomic status of the disputed varieties of *C. mosaicus* is given practical significance due to the interest in developing a commercial fishery of *C. mosaicus* (e.g. Pitt, 2000; Pitt & Kingsford, 2003a,b). Here, I present new morphological data and affirm von Lendenfeld's (1884) conclusion that there are two distinct evolutionary lineages within *C. mosaicus*.

MATERIALS AND METHODS

Catostylus medusae were sampled from locations in south-east Australia for DNA sequence and/or morphological analyses (Figure 1). Oral arm tissues were preserved in 90% ethanol for DNA analyses. Mitochondrial cytochrome *c* oxidase subunit I (COI) and nuclear Internal Transcribed Spacer One (ITS1) were sequenced from 65 and 49 medusae, respectively, as described by Dawson (2005). Eighteen morphological features (Figure 2) were measured on 23 medusae (7 *Catostylus mosaicus mosaicus*, 16 *C. mosaicus conservativus*, all sampled destructively), preserved in good condition in 4% formalin in seawater, during August 2003. Correlations among features were examined using Spearman's Rank correlation and all features related to bell diameter using ordinary least-squares regression. Differences between Central and Southern groups were tested using analysis of covariance (ANCOVA; Steele & Torrie, 1980). Oral disc thickness and bell thickness were measured several times in different positions on each individual (see Figure 2), so the geometric means (Steele & Torrie, 1980) of these values were used as indices of oral disc thickness and bell thickness in regression and ANCOVA. The features that could be measured non-destructively were also recorded for additional formalin-fixed specimens in the Australian Museum's collection.

Figure 1. Map of south-eastern Australia showing sample locations (circles), other known locations of *Catostylus* (crosses) and regions mentioned in the text, state capitols (squares), and -70 m and -100 m bathymetric contours. QMH, Mooloolaba Harbour; NSL, Smiths Lake; NBL, Budgewoi Lake; NBB, Botany Bay; NLI, Lake Illawarra; NCL, Coila Lake; VGL, Gippsland Lakes; VPA, Port Albert; VPP, Port Philip; TTE, Tamar Estuary. Inset: biogeographic regions of south-east Australia consistent with phylogeographic data (modified from Dawson, 2005, figure 1b).

Two-dimensional plots representing morphological similarity were calculated by multi-dimensional scaling (MDS) of re-scaled, weighted, measurements. Values for all features were first expressed as a ratio of bell diameter (except papilla length and width which were not correlated with bell diameter), then rescaled between 0 and 1 by dividing each observed value by the maximum value observed for that feature. Features constituting repeat measurements of the same structure (e.g. bell depth was measured in five different positions) were then down-weighted by a factor equivalent to the number of repeat measurements in the dataset (e.g. each measure of bell depth received one-fifth weight). The MDS in SPSS v. 10 for Macintosh used Euclidean distances (Sneath & Sokal, 1973, pp. 249–250) and was considered complete when S-stress decreased by ≤0.001 during successive iterations.

SYSTEMATICS

Order RHIZOSTOMEAE Cuvier, 1799
Suborder DACTYLIOPHORAE Stiasny, 1921
Superfamily INSCAPULATAE Stiasny, 1921
Family CATOSTYLIDAE Gegenbaur, 1857
Genus *Catostylus* L. Agassiz, 1862
Catostylus mosaicus mosaicus von Lendenfeld, 1884
(Figures 2–4)

Cephea mosaica: Quoy & Gaimard, 1824.
Crambessa mosaica symbiotica: von Lendenfeld, 1884, 1887.
Catostylus mosaicus: Mayer, 1910; Kramp, 1961, 1965; Pitt & Kingsford, 1999, 2000a,b, 2003a,b; Kingsford et al., 2000; Pitt, 2000; Rouse & Pitt 2000.

Type material

Holotype: neither the holotype *Catostylus* (*Crambessa*) *mosaicus* (Quoy & Gaimard, 1824) nor any other type material could be located at the Australian Museum (Sydney), Museum Victoria (Melbourne), Naturalis - National Museum of Natural History Leiden, or Muséum National d'Histoire Naturelle (Paris), the most likely repositories for an Australian rhizostome collected during a French cruise. Searching online databases or personal enquiries at the American Museum of Natural History, California Academy of Sciences, Natural History Museum (London), South Australian Museum, and the National Museum of Ireland (Natural History) were also unsuccessful.

Neotype: medusa preserved in 4% formalin. (Sylvania Marina at mouth of St Georges River opposite Kogarah Bay, Botany Bay, New South Wales, Australia; approximately 33°58'S 151°11'E; water depth: <1 m) [Australian Museum G16878]. Collected by L.E. Martin and M.N Dawson, 29 December 2002.

Type locality

'dans la rade de Sydney, au Port-Jackson' (Quoy & Gaimard, 1824), New South Wales, Australia; estimated as approximately 33°49'S 151°16'E.

Comparative material examined

One medusa preserved in 4% formalin. (Sylvania Marina at mouth of St Georges River opposite Kogarah Bay, Botany Bay, New South Wales, Australia; approximately 33°58'S 151°11'E; water depth: <1 m) [Australian Museum, G16879]. Collected by L.E. Martin and M.N Dawson, 29 December 2002. (Plus one medusa, same collection data, sampled destructively.)

Six medusae preserved in 4% formalin. (Southern shore of Coila Lake, New South Wales, Australia; approximately 36°01'S 150°07'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, 22 December 2002 (all sampled destructively).

Three medusae preserved in 4% formalin. (Vales Point Power House, Budgewoi Lake, New South Wales, Australia; 33°14'S 151°34'E; sea-level) [Australian Museum, G15790]. Collected by chief chemist Vales Point power house, May 1969.

Diagnosis

Catostylus mosaicus with papillae often small or absent, even in large medusae. Generally brown; bell margin occasionally pale. Eleven diagnostic nucleotides in cytochrome *c* oxidase subunit I (position state): 5' – 13 A, 139 C, 140 C, 184 A, 217 G, 316 G, 364 T, 397 C, 436 T, 469 A, 478 A – 3'.

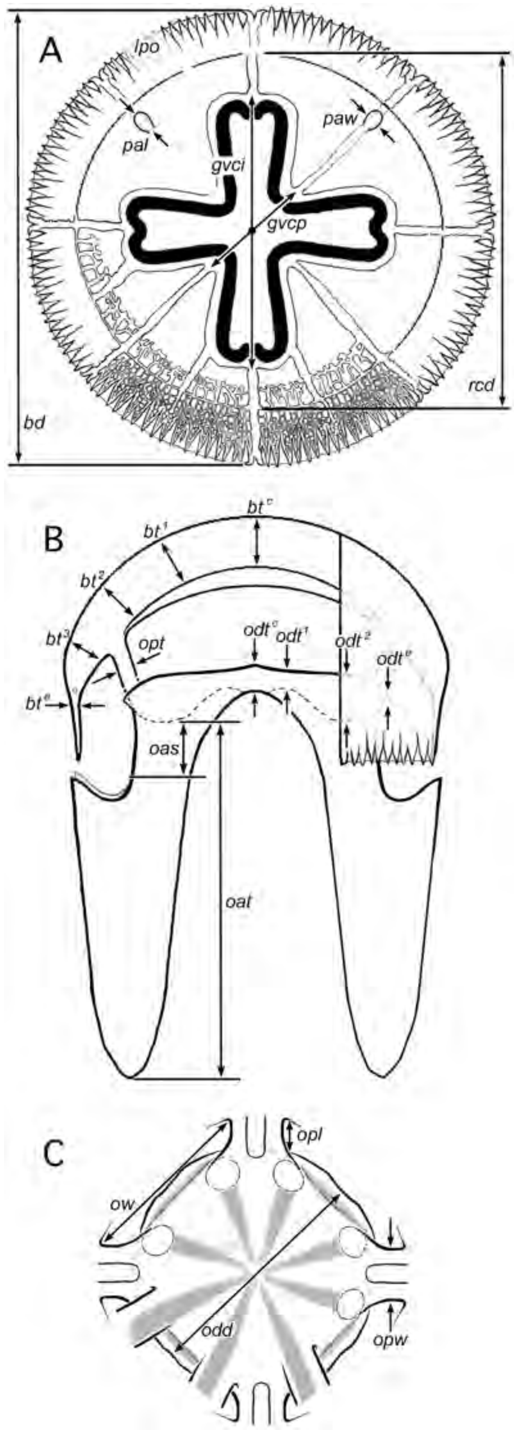

Figure 2. Sketches of (A) the subumbrella of *Catostylus mosaicus*; (B) a longitudinal section along the interradial axis of the medusa; and (C) the oral disc, in oral aspect. Colour was noted at the time of collection and 17 other measurements were made on preserved specimens: *bd*, bell diameter; *rcd*, ring canal diameter; mass (not shown); *lpo*, number of velar lappets per octant; *oat*, total length of oral arm; *oas*, length of smooth portion of oral arm; *pal*, papilla length; *paw*, papilla width; *opl*, oral pillar length; *opw*, oral pillar width; *opt*, oral pillar thickness; *ow*, ostium width; *odd*, oral disc diameter; *odt*, oral disc thickness (4 positions); *gvcp*, gastrovascular cavity width along the perradial axis; *gvci*, gastrovascular cavity width along the interradial axis; *bt*, bell thickness (5 positions). All dimensions in millimetres, mass in grams.

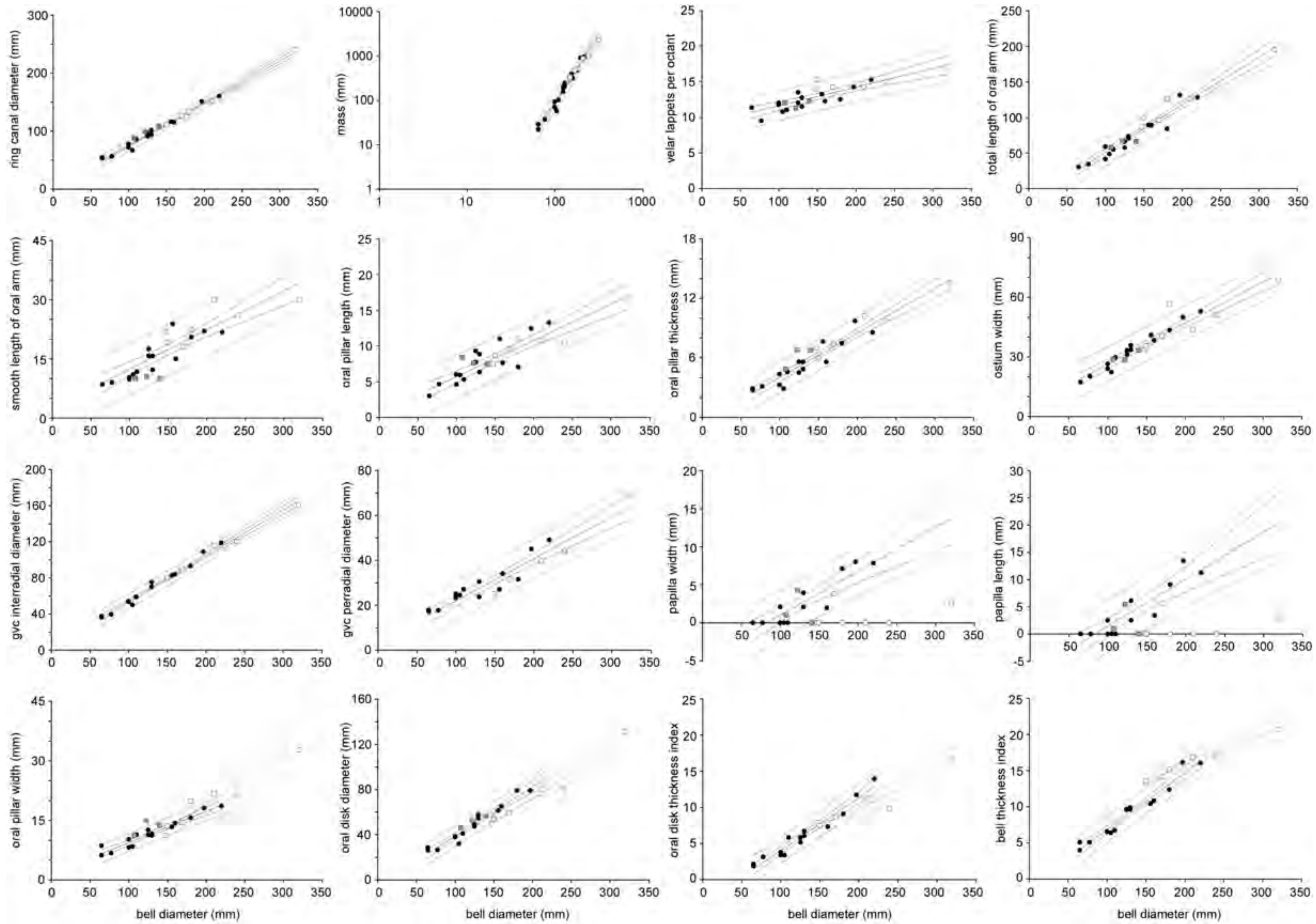

Figure 3. Ordinary least-squares regression of morphological features of *Catostylus mosaicus mosaicus* (white squares) and *Catostylus mosaicus conservativus* (black circles) against bell diameter. The line of best-fit (solid), with 95% confidence limits for mean (inner, dashed) and individual (outer, dotted) prediction intervals, is plotted for all regressions that were significantly non-zero (Table 1); separate lines are plotted for regressions that differed significantly between the two subspecies (Table 1). All values plotted are the arithmetic mean of two measurements per medusa bar those for *rcd*, *mass* (single measurement), *lpo*, *oat*, *oas* (mean of four measurements), *odt*, *bt* (geometric means). States for three medusae from Budgewoi Lake, New South Wales (G15790, Australian Museum; grey squares) are also plotted, but were not used to calculate regressions because sequence data were not available to confirm subspecies assignment.

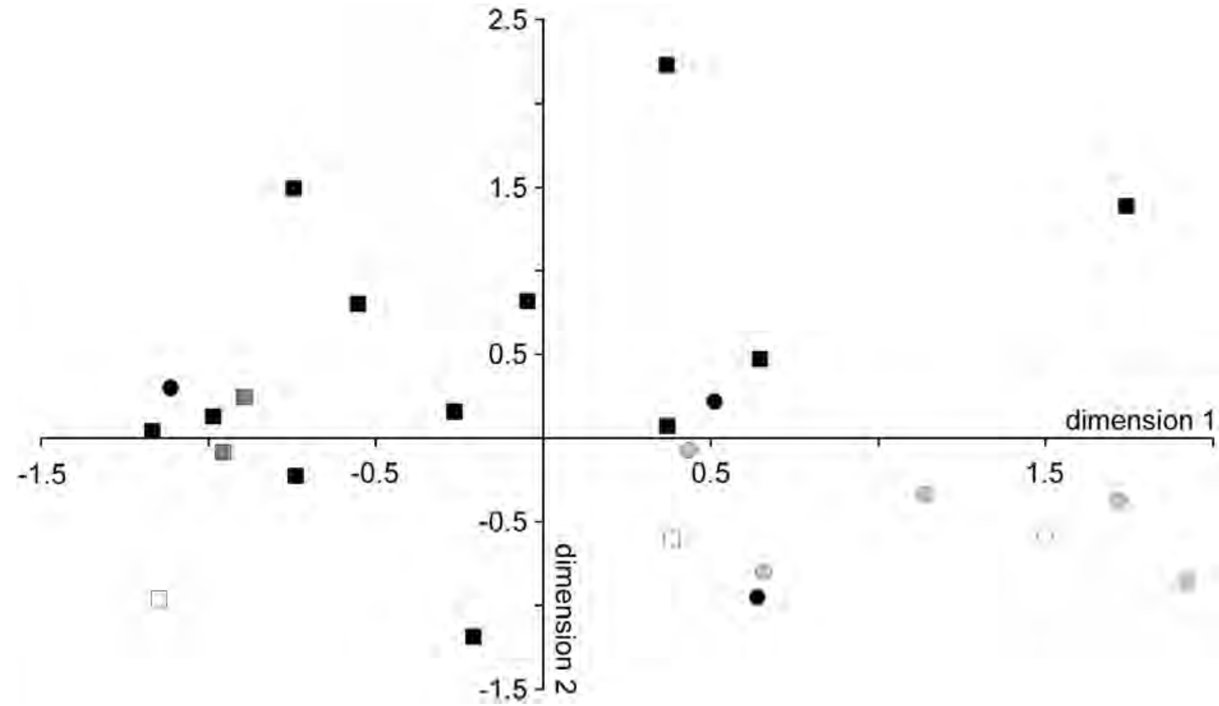

Figure 4. Two-dimensional MDS plot indicating morphological similarity in continuous features between *Catostylus mosaicus mosaicus* (circles: NBB, white: NCL, grey: Budgewoi Lake, black) and *Catostylus mosaicus conservativus* (squares: VGL, white; VPA, grey; TTE, black) medusae. Stress = 0.180, RSQ = 0.861. Colour of medusae is not included in the analysis because it is a categorical feature. An outlier, a three-rayed medusa from NCL is not shown (coordinates [-3.2, -1.3]).

Description

Bell diameter of medusae 147–320 mm. Exumbrella coarsely granulated, becoming smoother toward bell margin. Clubs, filaments, and appendages absent from oral disk and eight three-winged, pyramidal, cauliflower-textured oral arms. Total oral arm length (*oat*) = 1.23*r* ±0.04*r*, where *r* is bell radius (mean ±SE); *oat* = 5.2*oas* ±0.3*oas*. Sixteen radial canals connected directly with the central stomach: four perradial, four interradial, eight adradial. Perradial and interradial canals each terminated at a rhopalium; adradial canals terminated at ring canal. Reticulated branches anastomosing with radial canals inside the ring canal do not connect directly with the central stomach. Canals marginal to the ring canal highly reticulated. *odd* = 0.72*r* ±0.02*r*; 12 to 18 velar lappets per octant. See Table 1, Figure 3. *Catostylus mosaicus mosaicus* COI (GenBank accession nos. AY319476, AY737184–AY737211; Appendix 1) is monophyletic with respect to *C. mosaicus conservativus*. *Catostylus mosaicus mosaicus* ITS1 is highly variable (GenBank accession nos. AY737137–AY737158).

Etymology

Medusae were not found in the type locality, Port Jackson, but were collected from locations close to (e.g. Botany Bay, Sydney) and surrounding (e.g. Botany Bay and Budgewoi Lake) Port Jackson, so the clade takes the nominotypical subspecies epithet '*mosaicus*', which has priority over, and is also preferable in a literal sense to '*symbiotica*' suggested by von Lendenfeld (1884) because the eponymous symbiotic relationship with zooxanthellae may not occur (Kingsford et al., 2000; Pitt, 2000).

Catostylus mosaicus conservativus von Lendenfeld, 1884
(Figures 2–4)

Crambessa mosaica conservativa: von Lendenfeld, 1884, 1887.
Catostylus mosaicus: Mayer, 1910; Kramp, 1961.

Type material

Holotype: there is no record of any type material of *Catostylus mosaicus conservativus* (= *Crambessa mosaica conservativa*), per the search described above.

Neotype: medusa preserved in formalin. (Williamstown Pier, Port Phillip Bay, Victoria, Australia; 37°52'S 144°53'E; water depth: ≤1 m) [Melbourne Museum, F81511]. Collected by R. Condon, 23 February 1996.

Paratype: medusa preserved in 4% formalin. (Deviot Point, Tamar Estuary, Tasmania, Australia; approximately 41°13'S 146°56'E; water depth: <2 m) [Australian Museum, G16826]. Collected by M.N Dawson, 04 February 2003.

Table 1. *Morphological features of* Catostylus mosaicus mosaicus *and* Catostylus mosaicus conservativus *(collected 2002–2003, preserved in 4% formalin in seawater), generally described by linear regression of continuous features on bell diameter (d) and reported in the form y = md + c, except for colour and mass (which was log-log transformed: log y = m* $log_{10}[d] + c$*), where estimates of m and c are given ±1SE.* F*-statistics and associated* P*-values are given for ANCOVA testing the hypothesis of no difference between groups. When the hypothesis was rejected, separate regressions are provided for the two subspecies. Significant differences are annotated with superscript m or c, indicating the parameter tested (testing for a difference in c is contingent on no difference in m). *,* P*<0.05 after sequential Bonferroni correction (Rice, 1989) for 16 ANCOVA tests and for 21 regressions. All dimensions in millimetres, mass in grams.*

	ANCOVA		*C. mosaicus mosaicus* and *C. mosaicus conservativus*		
Feature	*F*	*P*	m ±SE	c ±SE	r^2
Ring canal diameter	${}^{c}F_{1,19}$ 0.034	0.856	0.732 ±0.014	1.487 ±2.337	0.992*
Mass (log_{10})	${}^{m}F_{1,19}$ 4.423	0.049†	3.031 ±0.100	-4.129 ±0.215	0.978*
Lappets per octant	${}^{c}F_{1,18}$ 5.070	0.037	0.026 ±0.004	9.002 ±0.585	0.739*
Oral arm length (tot)	${}^{c}F_{1,20}$ 4.064	0.057	0.669 ±0.032	-15.828 ±5.193	0.954*
Oral arm length (smth)	${}^{c}F_{1,19}$ 3.368	0.082	0.099 ±0.011	2.531 ±1.860	0.794*
Oral pillar length	${}^{c}F_{1,16}$ 0.719	0.407	0.051 ±0.005	0.596 ±0.807	0.833*
Oral pillar thickness	${}^{c}F_{1,16}$ 0.873	0.361	0.045 ±0.003	-0.446 ±0.421	0.934*
Ostium width	${}^{c}F_{1,20}$ 0.228	0.638‡	0.207 ±0.014	5.561 ±2.308	0.910*
GVC diameter (inter)	${}^{m}F_{1,15}$ 4.567	0.049†‡	0.504 ±0.013	3.681 ±2.188	0.988*
GVC diameter (per)	${}^{m}F_{1,15}$ 4.584	0.049‡‡	0.187 ±0.014	3.267 ±2.365	0.909*

			C. mosaicus mosaicus			*C. mosaicus conservativus*		
			m ±SE	c ±SE	r^2	m ±SE	c ±SE	r^2
Colour			Brown (NCL, NBB)			Blue (VGL, VPA), White (TTE)		
Papilla width	${}^{m}F_{1,16}$ 14.652	0.001*	0.008 ±0.011	-0.069 ±2.357	0.092	0.058 ±0.008	-4.740 ±1.070	0.828*
Papilla length	${}^{m}F_{1,16}$ 17.249	0.001*	0.006 ±0.016	-0.028 ±3.369	0.028	0.087 ±0.012	-7.208 ±1.638	0.822*
Oral pillar width	${}^{m}F_{1,19}$ 8.664	0.008††	0.114 ±0.014	-3.806 ±2.876	0.933*	0.079 ±0.006	1.543 ±0.773	0.931*
Oral disc diameter	${}^{c}F_{1,18}$ 13.575	0.002*	0.443 ±0.039	-15.91 ±8.317	0.970*	0.437 ±0.027	-4.899 ±3.464	0.952*
Oral disc thickness index§§	${}^{m}F_{1,18}$ 9.498	0.006	0.049 ±0.007	0.174 ±1.548	0.899*	0.073 ±0.005	-3.255 ±0.609	0.952*
Bell thickness index§	${}^{m}F_{1,18}$ 28.640	0.000*	0.042 ±0.003	7.418 ±0.701	0.977*	0.079 ±0.005	-0.994 ±0.630	0.953*

†, variances significantly different at P=0.043; if proceed to test c, $F_{1,20}$=0.000, P=0.992; ‡, variances significantly different at P=0.028, but slopes still statistically similar (P=0.094) therefore continue to test c; ††, if proceed to test c, $F_{1,20}$=0.530, P=0.475; ‡‡, if proceed to test c, $F_{1,16}$=4.096, P=0.060; †‡, if proceed to test c, $F_{1,16}$=0.590, P=0.454; §, each of the three most central (of five total) measurements differed significantly between *C. mosaicus mosaicus* and *C. mosaicus conservativus* at $P \leq 0.003$; §§, thickness at the middle of the disc differed significantly between the subspecies at P<0.001.

Type locality

Port Phillip Bay, Melbourne, Victoria, Australia; approximately 38°06'S 144°53'E.

Comparative material examined

Six medusae, collected with holotype, preserved in 4% formalin. (Deviot Point, Tamar Estuary, Tasmania, Australia; approximately 41°13'S 146°56'E; water depth: <2 m) [Australian Museum, G16827]. Collected by M.N Dawson, 04 February 2003.

Thirteen medusae preserved in 4% formalin. (Dock at end of Laura Street, Lakes Entrance, Gippsland Lakes, Victoria, Australia; approximately 37°52'S 147°59'E; water depth <2 m) [Australian Museum, G16828]. Collected by L.E. Martin and M.N Dawson, 23 December 2002.

Eight medusae preserved in 4% formalin. (Port Albert, Victoria, Australia; approximately 38°40'S 146°41'E; water depth: <2 m) [Australian Museum, G16829]. Collected by L.E. Martin and M.N Dawson, 24 December 2002.

Sixteen medusae sampled destructively (12 medusae Tamar Estuary, 2 medusae Gippsland Lakes, 2 medusae Port Albert; collection data as above).

Diagnosis

Catostylus mosaicus with papillae conspicuous in large medusae. Generally blue or white. Eleven diagnostic nucleotide positions in cytochrome c oxidase subunit I (position state): 5' – 13 G, 139 T, 140 T, 184 G, 217 A, 316 A, 364 C, 397 T, 436 C, 469 G, 478 G – 3'.

Description

Bell diameter of medusae 65–220 mm. Exumbrella coarsely granulated, becoming smoother toward bell margin. Clubs, filaments, and appendages absent from oral disc and eight three-winged, pyramidal, cauliflower-textured oral arms. Total oral arm length (*oat*) = 1.03*r* ±0.03*r* (mean ±SE); *oat* = 4.7*oas* ±0.3*oas*. Sixteen radial canals connect directly with the central stomach: four perradial, four interradial, eight adradial. Perradial and interradial canals each terminate at a rhopalium; adradial canals terminate at ring canal. Reticulated branches anastomosing with radial canals inside the ring canal do not connect directly with the central stomach. Canals marginal to the ring canal highly reticulated. *odd* = 0.79*r* ±0.02*r*. Nine to 17 velar lappets per octant. See Table 1, Figure 3. *Catostylus mosaicus conservativus* COI (GenBank accession nos. AY737212–AY737247; Appendix 1) is monophyletic with respect to *C. mosaicus mosaicus*. *Catostylus mosaicus conservativus* ITS1 is highly variable (GenBank accession nos. AY737159–AY737183).

Etymology

Subspecific name is based on von Lendenfeld's (1884) reference to a variety of *Catostylus mosaicus* (=*Crambessa mosaica*) 'conservativa' that occurred within the currently identified geographic range of, and had similar coloration to, the redescribed subspecies.

Remarks

All collection localities for both subspecies were within the known range of *Catostylus mosaicus* bar the Tamar Estuary, Tasmania, which represents a new geographic record. All medusae examined had an exumbrella covered with the 'petites plaques blanchâtres polygonales … comme des mosaiques' (Quoy & Gaimard, 1824), i.e. 'coarse granulations' (Kramp, 1961), from which the species epithet *mosaicus* was derived. The ratios *oas*:*r*, *oas*:*oat*, and *odd*:*r* and the mean number of velar lappets per octant (*lpo*) were similar to those commonly cited for *C. mosaicus* (0.5–1.5, 6, somewhat greater than 1.0, and approximately 14, respectively) as were other morphological characteristics such as the radial canal structure and the absence of appendages on the oral arms (Mayer, 1910; Stiasny, 1921; Kramp, 1961). Given the geographic locations from which the medusae were sampled, and the distinct morphologies of other sympatric scyphozoan species (e.g. *Aurelia* sp.1, *Cyanea* spp., *Phyllorhiza punctata*), the medusae examined were unequivocally *C. mosaicus* (Quoy & Gaimard).

All morphological features except papilla length and papilla width were highly correlated with each other (Spearman's $r \geq 0.700$, $P<0.001$; 79% of pairwise comparisons had $r \geq 0.833$) largely as a function of significant positive correlations with bell diameter ($0.873 \leq r \leq 0.993$, $P<0.001$; Figure 3; Table 1). Papilla length and papilla width were not significantly correlated with any other feature ($0.180 \leq r \leq 0.440$, $0.054 \leq P \leq 0.462$), including bell diameter ($r=0.434$, $P=0.056$ and $r=0.429$, $P=0.059$ respectively), but were highly correlated with each other ($r=0.989$, $P<0.001$). However, none of the 17 meristic or morphometric features considered in this study were truly diagnostic of *Catostylus mosaicus mosaicus* cf. *C. mosaicus conservativus* medusae—there were statistically significant differences in the frequency or ontogeny of only six features (Figure 3; Table 1)—and there were no clear differences in overall morphology (Figure 4). Such a pattern, accompanied by heterogeneity but not reciprocal monophyly in ITS1 (Dawson, 2005), may conceivably be attributable to any (combination) of several factors, for example, limited time (estimated at 1.4 My from a proxy COI molecular clock; Dawson, 2005), low divergent selection pressure, and slow rate of morphological and/or molecular evolution since divergence, or ongoing gene flow between populations in a zone of secondary contact in the vicinity of Cape Howe. Which factor, or combination of factors, cannot be stated with certainty at this stage, and sampling medusae in intermediate localities, such as Mallacoota Inlet, is clearly a priority in this respect.

Designation of neotypes of *Catostylus mosaicus mosaicus* and *C. mosaicus conservativus* was necessitated by the absence of holotypes for both taxa, and the confusion evident in the literature since their original description by von Lendenfeld (1884). The neotype of *C. mosaicus mosaicus* was sampled from Botany Bay, i.e. the bay adjacent to the type locality, Port Jackson, because *C. mosaicus mosaicus* were not observed in Port Jackson during any of approximately one-dozen trips between July 2001 and May 2004 despite the fact that medusae with which *C. mosaicus* often co-occurs (e.g. *Aurelia* sp. or *Phyllorhiza punctata* in Botany Bay, Coila Lake, and Lake Illawarra), were observed on many occasions. The neotype of *C. mosaicus conservativus* is from Port Phillip Bay, the type locality (von Lendenfeld, 1884). A paratype of *C. mosaicus conservativus* from the Tamar Estuary is designated because medusae at this locality are genetically most similar to those from the type locality (Dawson, 2005), Port Phillip Bay, and because they were of moderate size, clearly undamaged and not malformed, and were representative of the *C. mosaicus conservativus* collected by the author; *C. mosaicus conservativus* were not found during a trip to Port Phillip Bay in December 2002. Designation of these type specimens will promote clarity in future comparisons with putative *C. mosaicus* found between Brisbane and the Torres Strait. A robust redescription of the species, *C. mosaicus*, awaits such comparisons and additional studies of congeners.

Considering only the medusae collected during this study, coloration was population specific and distinguished all southern (*C. mosaicus conservativus*) from all central (*C. mosaicus mosaicus*) medusae—a result reminiscent of the distribution of varieties proposed by von Lendenfeld (1884) and generally consistent with the biogeography of the region (e.g. Figure 1): *C. mosaicus mosaicus* is Peronian and *C. mosaicus conservativus* Maugean in distribution. However, the genetic affinities of bluish medusae from New South Wales (e.g. Quoy & Gaimard, 1824; von Lendenfeld, 1884) and of blue or white medusae from Queensland (e.g. Southcott, 1982), remain to be determined. Observations between Bateman's Bay and the Clarence River, in New South Wales (1996–1997), suggest blue medusae predominate in ocean-derived waters near the mouths of bays while white-to-brown and variegated medusae predominate upstream in more estuarine waters (K. Pitt, personal communication). The implication that coloration is ecophenotypic (K. Pitt, personal communication) means that, at this stage, colour should not be used alone to identify subspecies. The deduction that the brown coloration of *C. mosaicus mosaicus* appeared within a 40-year span in the mid-1800s and may reflect rapid evolution (von Lendenfeld, 1884) seems less likely than differential sampling.

Recognition of two subspecies of *C. mosaicus* in south-eastern Australia strengthens the evidence that the developing *C. mosaicus* fishery must account for management of multiple distinct stocks (Kingsford et al., 2000). Both ecological and molecular data indicate strongly that stock units may be small, possibly estuary-specific (Kingsford et al., 2000; Dawson, 2005). Whether populations of *C. mosaicus* in Queensland represent distinct stocks, subspecies, or even species is currently unknown, but clearly a matter of concern.

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Appendix 1. Catostylus mosaicus *cytochrome c oxidase subunit I (COI) 'barcode'. Degenerate code indicates variable nucleotides, italics indicate nucleotides that diagnose* C. mosaicus mosaicus *from* C. mosaicus conservativus *(character states given in main text).*

5'-
AACTTTATATTT*R*ATATTCGGTGCCTTYTCCRCAAKGATAGGTACRGCCTTTAGTRTGATCATA
AGACTTGAATTATCTGGACCAGGRTCTATGTTAGGYGATGATCAACTCTACAACGTGGTTGTAACT
GCTCACGC*YY*TRATTATGATATTTTTCTTTGTAATGCCTGTRTTAATAGGTGG*R*TTT
GGAAATTGATTTGTGCCTYTATATATTGG*R*GYCCCCGATATGGCTTTCCCCAGACTAAAYAA
CATTAGTTTYTGGTTGTTRCCCCCAGCACTAYTRTTACTRTTAGGTTCATCTTTAGTTGAACAAG
G*R*GTAGGAACRGGTTGAACCATMTATCCTCCACTAAGCTCCATACAARC*Y*CAYTCTGGRGGT
GCRGTAGATATGGGAATATT*Y*AGTTTACATTTAGCRGGAGCATCTTCTATTATGGGARC*Y*AT
TAATTTTATTWCTACAATTCTAAATATGAG*R*GCCCCAGG*R*ATGACGATGGACAARATTCCYT
TATTTGTATGRTCTGTTTTARTAACAGCARTATTGTTACTTTTATCCYTWCCYGTCCTARCTGGAGY
TATTACAATGTTATTAACCGATAGRAATTTTAATACATCTTTCT-3'