

# Five new subspecies of *Mastigias* (Scyphozoa: Rhizostomeae: Mastigiidae) from marine lakes, Palau, Micronesia

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Published behavioural, DNA sequence, and morphologic data on six populations of *Mastigias*, five from marine lakes and one from the lagoon, in Palau are summarized. Each marine lake population is distinguished from the lagoon population and from other lake populations by a unique suite of characteristics. Morphological differences among *Mastigias* populations in Palau are greater than those recorded between any previously described species of *Mastigias*, whereas molecular differences are far less ( $\leq 2.2\%$  in COI and ITS1) than those found between medusae identified in the field as *Mastigias papua* ( $>6\%$  in COI and ITS1). Thus, each marine lake population in Palau is described as a new subspecies of *Mastigias* cf. *papua*: *remengesau* (in Uet era Ongael), *nakamurai* (in Goby Lake), *etpisoni* (in Ongeim'l Tketau), *saliu* (in Clear Lake), and *remeliiki* (in Uet era Ngermeuangel).

## INTRODUCTION

To some naturalists, *Mastigias* medusae in marine lakes, Palau, symbolize the evolutionary process (Faulkner, 1974). In the first scientific publication on marine lake *Mastigias*, Hamner & Hauri (1981) suggested that different long-distance horizontal migrations and different morphologies among populations isolated in three different lakes 'might be considered of specific or subspecific importance' yet, because one species of *Mastigias* from the lagoon probably colonized all three lakes, they cautioned that 'differences may be only of local significance.' Recent publications (summarized in the next paragraph and in Table 1) on the behaviour, morphology, and molecular genetics of the three populations studied by Hamner & Hauri (1981) plus two other marine lake populations and populations in the surrounding lagoon have increased our understanding of the nature and magnitude of these differences.

Diel horizontal migrations show greater variety in direction and strength among marine lake populations than they do among populations in the lagoon (Dawson & Hamner, 2003; Table 1). Morphological variation is also greater among marine lake populations than it is among populations in the lagoon (Dawson, 2005a; Table 1). Indeed, morphological differences among lake populations exceed those

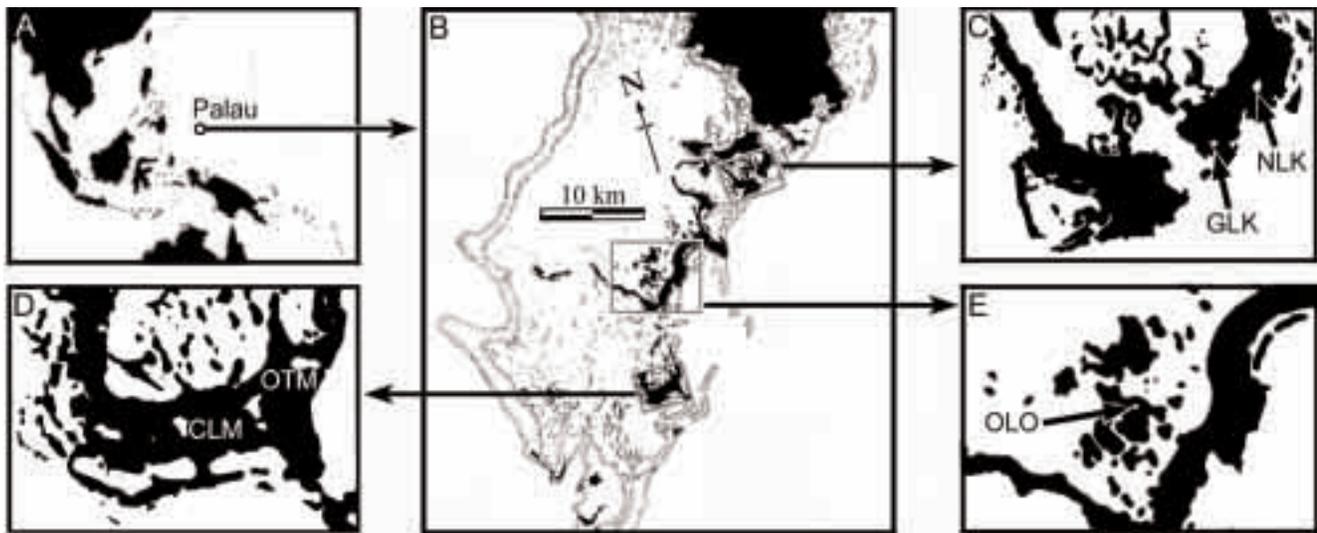
recorded between many previously described nominal species of *Mastigias* (*M. albipunctata* Stiasny, 1920; *M. andersoni* Stiasny, 1926; *M. gracilis* (Vanhöffen, 1888); *M. ocellatus* (Modeer, 1791); *M. pantherinus* Haeckel, 1880; *M. papua* (Lesson, 1830); *M. roseus* (Reynaud, 1830); *M. sidereus* Chun, 1896) throughout the Indo-West Pacific in terms of, for example, the number of velar lappets, length of mouth arms, length of terminal clubs, number of adradial canal origins at the gastrovascular cavity, number of anastomoses among perradial canals, and the width of the subgenital ostia (Dawson, 2005a). However, DNA sequencing of mitochondrial cytochrome *c* oxidase subunit I (COI) shows mean pairwise sequence differences among lake populations (0.77%, SD 0.52%) and differences between lake and lagoon populations (0.52%, SD 0.42%) of *Mastigias* are similar in magnitude to intra-specific differences among *Mastigias* within the lagoon (0.26%, SD 0.19%; Dawson, 2005a; see also Dawson & Hamner, 2005). This result is corroborated by preliminary DNA sequencing of nuclear Internal Transcribed Spacer One (ITS1) which found differences of 3.39% (SD 0.72 %) between lagoon locations, 0.58% (SD 0.18%) between lake locations, and 1.74% (SD 1.22%) between lagoon and lake locations (Dawson, 2005a). These sequence differences are considerably less than those seen between medusae identified as *Mastigias papua* in coastal marine environ-

ments of Indonesia (Berau, eastern Kalimantan), Palau, and Papua New Guinea (Tufi, Northern Province [PNG]; >6% in COI and ITS1; Dawson, 2004, 2005a) or between traditionally recognized species of *Aurelia* (>13% in COI, >10% in ITS1; Dawson & Jacobs, 2001) or of *Cassiopea* (10.9–23.4% in COI; Holland et al., 2004). Integrating these behavioural, morphological, and molecular data leads logically to the conclusion that, in order to recognize the unique evolutionary histories and close evolutionary relationships of *Mastigias* in Palau, each marine lake population should be recognized as a distinct subspecies.

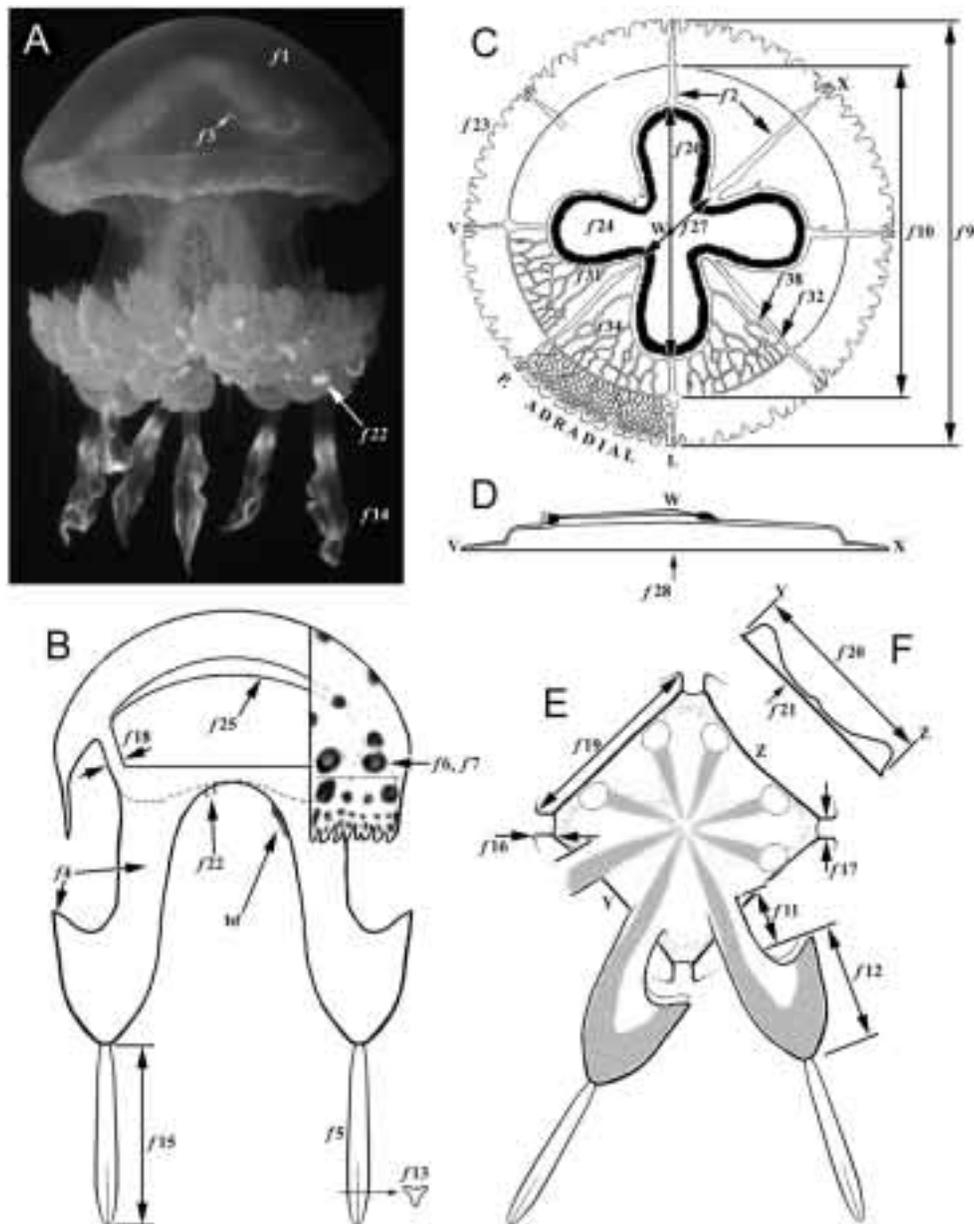
The species of *Mastigias* to which the new subspecies should be referred, however, is unclear. The COI and ITS1 sequence differences of >6% sequence divergence among medusae identified as *Mastigias papua* in Berau, Palau, and PNG indicate three cryptic species (Dawson, 2004, 2005a). The type locality of *M. papua* (Lesson) is 'des côtes de Waigiou', i.e. Waigeo Island, west of New Guinea (L. van Ofwegen, personal communication, source Lamarck, 1835, pt. III, p. 184), a thousand kilometres or more from any of the medusae sampled in Berau, Palau, and PNG. It seems plausible, therefore, that putative *M. papua* in Palau have been misidentified (e.g. Uchida, 1947), although verifying or refuting this hypothesis beyond reasonable doubt likely demands revision of the genus, which is far beyond the scope of this study. As such, I have referred the five new subspecies to *Mastigias* cf. *papua* and note here that the species identification may be amended in the future.

## MATERIALS AND METHODS

*Mastigias* were studied in Palau (Figure 1) primarily between April 1996 and October 1998 with occasional observations thereafter until August 2004. Univariate and multivariate statistical morphological analyses of macromorphological features (see Figure 2), which require destructive sampling (i.e. dissection and dismemberment), are described in detail in Dawson (2005a). These quantitative data were recalculated as ratios of bell diameter (bd) for this study, to standardize across size-classes and facilitate comparisons between populations. Swimming behaviours—including swimming speed, frequency and degree of turns, and shadow avoidance—and the spatial distribution of medusae during diel horizontal and vertical migrations were compared statistically among lakes as described in Dawson & Hamner (2003). Cytochrome *c* oxidase subunit I (COI) was purified, amplified, and sequenced from 126 *Mastigias* medusae—122 from Palau, 2 from Kakaban Island (Berau, Indonesia, collected November 2002), and 2 from Tufi (Northern Province, Papua New Guinea, collected January 2002)—using PCR primers LCO1490 or LCOjf or AaCOIi-L with AaCOIi-H or HCO2198 or mpHCO as described in Dawson & Hamner (2005) and Dawson (2005a). Internal Transcribed Spacer One (ITS1) was purified, amplified, and sequenced from 13 medusae—12 from Palau, 1 from Tufi—using PCR primers jfITS1-5f with jfITS1-3r or 28S2r following Dawson (2004, 2005a).



**Figure 1.** Maps showing the position of (A) Palau in the Western Pacific; (B) the major islands within Palau that contain the majority of marine lakes, including those with endemic subspecies of *Mastigias*; (C) Goby Lake, GLK, and Uet era Ngermeuangel, NLK; (D) Clearwater Lake, CLM, and Ongeim'l Tketau, OTM; and (E) Uet era Ongael, OLO.



**Figure 2.** The morphology of *Mastigias*. (A) Photograph of an approximately 15 cm bell diameter [bd] medusa from Goby Lake; (B) sketch of a longitudinal section along the interradial axis of the medusa [i.e. through the plane of the paper after rotation of the medusa in A through approximately 30° to the left]; (C) sketch of the subumbrellar surface of the bell, and (D) cross-section through the bell along line VWX; (E) schematic of the oral disc, in oral aspect, showing two of the eight oral arms, and (F) cross-section through the oral disc along line YZ or its orthogonal. Features listed in Table 1 or discussed in the text include the following. Bell colour (*f*1). Perradial and interradial canal colour (*f*2). The presence of pigmented flecks at the roots or along the length of radial canals (*f*3). Oral arm colour (*f*4). Terminal club colour (*f*5). Abundance (*f*6) and colour (*f*7) of spots on the exumbrellar surface. Bell diameter (*f*9). Ring canal diameter (*f*10). Length of the simple, unwinged, portion of the oral arm (*f*11). Length of the winged portion of the oral arm (*f*12). Shape (*f*13; particularly in cross-section), number (*f*14), and length (*f*15) of the terminal clubs. Length (*f*16), width (*f*17), and depth (*f*18) of the oral pillars. Width of the subgenital ostia (*f*19). Diameter (*f*20) and depth (*f*21) of the oral disc. Presence of intermediate filaments on the oral arm and oral disc (*f*22). Number of velar lappets [i.e. all lappets except the two at each rhopalium] (*f*23). Shape of the gastrovascular cavity (*f*24). Colour of the subgenital porticus (*f*25). The interradial (I. *f*26) and perradial (P. *f*27) diameters of the gastrovascular cavity. Bell thickness (*f*28). The number of adradial canal origins at the gastrovascular cavity (*f*31). The number of perradial (*f*32) and adradial (*f*34) anastomoses in the radial canals that are circumscribed by the ring canal. The number of sinuses originating at adradial (*f*38) canals. Radial canals are named consistent with the phylogenetic hypothesis of Uchida (1926: 87). Nine features are not indicated in the figure: the mass of the whole medusa (*f*8), the number of perradial (*f*29) and interradial (*f*30) canal origins at the gastrovascular cavity [the number of origins was invariant; Dawson 2005a], the number of interradial anastomoses (*f*33), the number of sinuses originating at the gastrovascular cavity (*f*35), and perradial (*f*36), interradial (*f*37), and ring canals (*f*39), and the number of anastomoses leading to two sinuses (*f*40). bf, brood filaments. Modified from Dawson (2005a).

Specimens were deposited at the California Academy of Sciences (CAS) in USA, the Netherlands National Museum of Natural History 'Naturalis' (NNM), and the Palau International Coral Reef Centre (PICRC) in Palau.

## SYSTEMATICS

Order RHIZOSTOMEAE Cuvier, 1799  
 Suborder KOLPOPHORAE Stiasny, 1921  
 Superfamily KRIKOMYARIAE Stiasny, 1921  
 Family MASTIGIIDAE Stiasny, 1921  
 Genus *Mastigias* L. Agassiz, 1862  
 Species cf. *papua* (Lesson, 1830)  
*Mastigias* cf. *papua remengesau* ssp. nov.  
 (Figures 2, 3B & 4; Table 1)

*Mastigias* sp.: Dawson et al., 2001; Dawson & Hamner, 2003, 2005; Dawson, 2004, 2005a.

### *Type material*

Holotype: medusa preserved in 4% formalin. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m) [RMNH Coel. 33304]. Collected by M.N Dawson and E. Basilius, 04 October 2004.

Paratypes: five medusae preserved in 4% formalin. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m) [RMNH Coel. 33305]. Collected by M.N Dawson and E. Basilius, 04 October 2004.

Three medusae preserved in 4% formalin. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m) [RMNH Coel. 33306]. Collected by L.E. Martin, 18 August 2004.

Eight medusae preserved in 4% formalin. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m) [CASIZ 171882]. Collected by M.N Dawson and E. Basilius, 04 October 2004.

One medusae preserved in 4% formalin. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m) [PICRC-CNI 009]. Collected by L.E. Martin, 18 August 2004.

### *Comparative material examined*

Ten 50 mm immature medusae, three 100 mm female medusae, seven 100 mm male medusae, four 150 mm female medusae, three 150 mm male medusae. (Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, May 1997 to October 1998. Morphometrics measured destructively.

### *Type locality*

Uet era Ongael, Ongael, Koror State, Palau; 07° 15.45'N 134° 22.98'E. Also known as Ongael Lake (e.g. Dawson et al., 2001; Dawson & Hamner, 2003).

### *Diagnosis*

Large white spots abundant across exumbrella, blue colour often present in bell, along interradial and per-radial canals, in oral arms, and terminal clubs. Eight terminal clubs, one per oral arm, may be unequal lengths, medium to long, mottled, triangular in cross-section, tapering quickly at distal end. Filaments on oral arms usually disc-shaped, slightly raised from oral arms. Highly anastomosing adradial canals, often containing white flecks, form fine mesh, some interradial and perradial anastomoses. Cytosine at position 280 of COI (appendix 1).

### *Description*

The most ornate of the lake medusae, solid white spots of various sizes on exumbrella, the light fringe of the oral arms, pale filaments, and mottling of terminal clubs all offset by blue background pigmentation. Smaller individuals are deeper blue. Blue can obscure the base brown colour attributable to zooxanthellae particularly in the bell and terminal clubs, but usually does not in medium to large animals. Medusae are often elongate, due to trailing terminal clubs shaped like a prism tapering at the distal end. However, length of terminal clubs can vary considerably, even within an individual. One terminal club arises from the tip of each oral arm, contributing to an overall quite symmetrical appearance of subspecies *remengesau*. Filaments are relatively evenly distributed discs lying close to the mouths of the oral arms. Medusae grow to a little over 15 cm bd. Detailed measurements of features are in Table 1 and Dawson (2005a). Complete sequences are available in GenBank (accession nos. AY902978–AY902992).

### *Habitat*

Medusae are planktonic and occasionally abundant in, but also sometimes absent from, this holomictic marine lake. They can be found throughout the water column (0 m to ~4 m depth) depending on the time of day (Dawson & Hamner, 2003). When medusae have been present, the water column (measurements at metre intervals averaged over the depth of the lake; N=2 dates) has ranged from 30.0–30.2°C (mean 30.1 ± 0.3°C) and 33.1–34.0 psu (mean 33.6 ± 0.9 psu); dissolved oxygen 5.4 mg l<sup>-1</sup> (one sample date only). Benthic scyphistoma have not been observed but almost certainly must be present in the lake.

*Distribution*

*Mastigias* cf. *papua remengesau* occurs only in Uet era Ongael, Koror State, Palau.

*Etymology*

The subspecies name is a patronym in honour of the fifth and most recently elected President of Palau, President Tommy E. Remengesau Jr (2000–present). Of the five marine lakes discussed herein, Uet era Ongael was the most recent to form (Dawson & Hamner, 2005).

*Mastigias* cf. *papua nakamurai* ssp. nov.  
(Figures 2, 3C & 5; Table 1)

*Mastigias* sp.: Hamner & Hauri, 1981; Hamner & Hamner, 1998; Heeger, 1998, pp. 202–212; Dawson et al., 2001; Dawson & Hamner, 2003, 2005; Dawson, 2005a.

*Type material*

Holotype: medusa preserved in 4% formalin. (Goby Lake, Ngermeuangel, Koror State, Palau; 07° 18.88'N 134° 30.10'E; water depth: <1 m) [RMNH Coel. 33307]. Collected by M.N Dawson, October–December 1998.

Paratypes: three medusae preserved in 4% formalin. (Goby Lake, Ngermeuangel, Koror State, Palau; 07° 18.88'N 134° 30.10'E; water depth: <1 m) [CASIZ 171883]. Collected by M.N Dawson, October–December 1998.

One medusa preserved in 4% formalin. (Goby Lake, Ngermeuangel, Koror State, Palau; 07° 18.88'N 134° 30.10'E; water depth: <1 m) [PICRC-CNI 011]. Collected by M.N Dawson, October–December 1998.

*Comparative material examined*

Ten 50 mm immature medusae, five 100 mm female medusae, five 100 mm male medusae, two 150 mm female medusae, seven 150 mm male medusae, one 150 mm medusa sex not recorded. (Goby Lake, Ngermeuangel, Koror State, Palau; 07° 18.88'N 134° 30.10'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, May 1996 to December 1997. Morphometrics measured destructively.

*Type locality*

Goby Lake, Ngermeuangel, Koror State, Palau; 07° 18.88'N 134° 30.10'E.

*Diagnosis*

Small yellow spots on exumbrella confined to bell margin distal of ring canal, blue colour very rare;

ground colour brown from zooxanthellae. Usually one terminal club on each of eight oral arms; clubs medium length, shaped like a flame, cross-section like a tricorn. Moderately complex canal structure, often containing white flecks at anastomoses with gastrovascular cavity, many adradial but few interradiial or per-radial anastomoses.

*Description*

The base brown colour in subspecies *nakamurai* medusae is supplemented by blue pigmentation in some small (~<5 cm bd) medusae and by small yellowish spots around the bell margin and white or yellow patches medially on the terminal clubs in many medusae of most sizes. Terminal clubs may be relatively long and are often shaped like a flame in larger medusae, although they come in various shapes and sizes, even on single medusae. Filaments are small clubs distributed unevenly across, and protruding slightly above the mouths of, the oral arms. The overall appearance of subspecies *nakamurai* medusae, therefore, is somewhat irregular and asymmetrical, a condition that can sometimes be quite exaggerated in the oral arms. Medusae grow to a little over 15 cm bd. Detailed measurements of features are in Table 1 and Dawson (2005a). Thymine at position 519 of COI distinguishes *nakamurai* from all other marine lake subspecies bar *remengesau*. Complete sequences are available in GenBank (accession nos. AY902993–AY903007).

*Habitat*

Medusae are planktonic and abundant year-round in the mixolimnion (0 m to 7 m depth) of this meromictic marine lake. When medusae have been present, the water column (measurements at metre intervals averaged from 0–7 m) has ranged from 28.9–32.1°C (mean 30.6 ±0.2°C; N=72) and 22.5–28.6 psu (mean 25.6 ±0.3psu; N=72); dissolved oxygen 0.5–5.4 mg l<sup>-1</sup> (mean 3.4 ±0.2 mg l<sup>-1</sup>; N=70). Benthic scyphistoma are attached to decaying leaves, wood, and other hard substrate predominantly between ~4 m and ~6 m depth.

*Distribution*

*Mastigias* cf. *papua nakamurai* occurs only in Goby Lake, Koror State, Palau.

*Etymology*

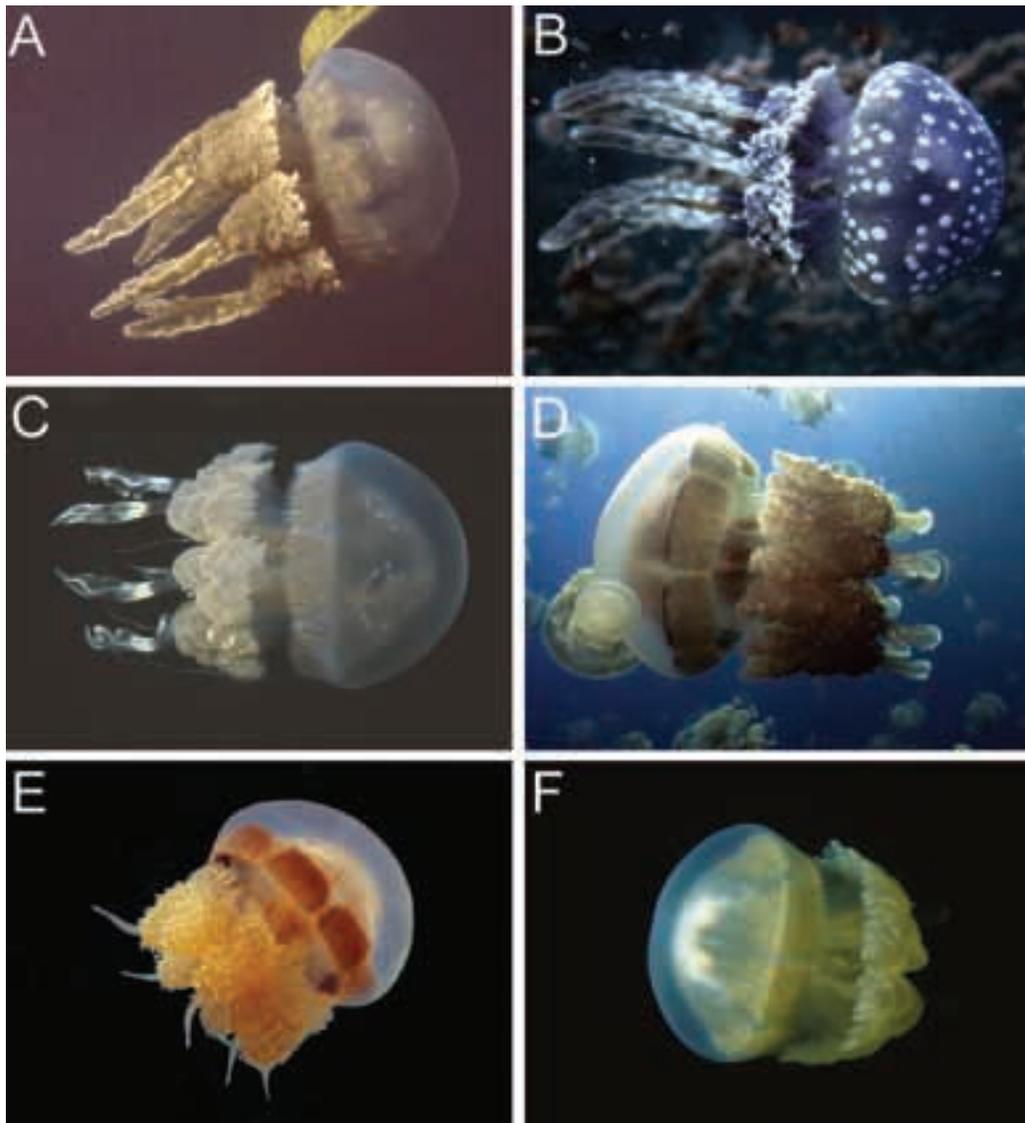
The subspecies name is a patronym in honour of the fourth elected President of Palau, President Kuniwo Nakamura (1992–2000). Of the five marine lakes discussed herein, Goby Lake was penultimate to form.

**Table 1.** Summary of behavioural, molecular, and morphological features of *Mastigias medusae* populations in the lagoon and in marine lakes, Palau. **Behavioural** data taken from Hamner & Hauri (1981) and Dawson & Hamner (2003). Instantaneous swimming direction not included because it is implicit in the pattern of diel horizontal migration. Subspecies that have the same numerical- or letter-codes for any particular character have statistically similar behaviour. **Molecular** data summarized from Dawson (2005a) and Dawson & Hamner (2005). COI: letters indicate the geographic location of haplotypes (using first letters of place names) and numbers indicate different haplotypes from the same location; if an haplotype is found in more than one location, it is arbitrarily given a letter code from one of the locations in which it occurs. ITS1: different letter codes indicate genetic distances greater than zero. **Morphologic** data summarized from Dawson (2005a) and presented for continuous features (i.e. features 8–12, 15–21, 23, 26–38) as proportions of bell diameter (minimum–median–maximum) except for mass [= (mass/d<sup>3</sup>)\*10000]; the number of terminal clubs and the states of qualitative features (i.e. features 1–7, 13, 14, 22, 24, 25) are presented in order of frequency of occurrence summed across size-classes. Key to character states: b, blue; g, greenish; w, white; y, yellow. 0, absent; 1, present; 2, common; 3, abundant (except for terminal club shape). Terminal club shape: 0, circle; 1, teardrop cross-section; 2, flat; 3, tricorn; 4, four-cornered. a, on oral arms; d, on oral disc c, cruciform; k, crooked. n.a., not applicable. OA, oral arms. <sup>sml</sup>, superscript letter indicates each size-class (small, medium, large) in which at least one population differed statistically in continuous features.

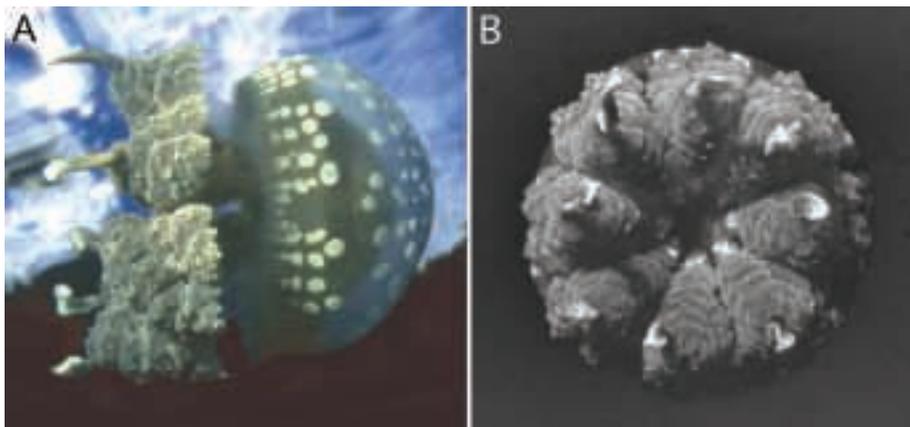
|                                      | Subspecies and location                     |  |                              |                                    |                                      |  |
|--------------------------------------|---|--|------------------------------|------------------------------------|--------------------------------------|--|
|                                      | <i>Mastigias</i> cf. <i>papua</i><br>lagoon | <i>remengesau</i><br>Uet era Onael     | <i>nakamura</i><br>Goby Lake | <i>etpisoni</i><br>Ongeim'l Tketau | <i>sali</i><br>Clear Lake            | <i>remeliiki</i><br>Uet era Ngermeuangel |
| <b>Behaviour</b>                     |   |  |                              |                                    |                                      |  |
| Diel vertical migration?             | yes   | yes                                    | yes                          | yes                                | ?                                    | yes                                      |
| Diel horizontal migration?           | eastward                                    | eastward then westward<br>(occasional) | eastward                     | eastward then westward<br>(strong) | eastward then westward<br>(moderate) | eastward and westward                    |
| Turning frequency                    | i   | ?                                      | j                            | i                                  | ?                                    | j  |
| Shadow avoidance                     | no  | yes                                    | yes                          | yes                                | no                                   | no                                       |
| Swim speed (small, large)            | a, e  | bc, f                                  | b, fg                        | d, h                               | cd, fg                               | bc, g                                    |
| <b>Molecules</b>                     |   |  |                              |                                    |                                      |  |
| COI                                  | L1-7  | O1                                     | L1                           | L2                                 | C1-2                                 | B1-3                                     |
| ITS1 (preliminary)                   | L   | OL                                     | G                            | OT                                 | C                                    | B  |
| <b>Morphology</b>                    |   |  |                              |                                    |                                      |  |
| 1 bell colour                        | 0 b   | b 0                                    | 0 b                          | 0                                  | 0                                    | 0  |
| 2 canal colour                       | b 0   | 0 b                                    | 0                            | 0                                  | 0                                    | 0  |
| 3 canals flecked                     | 2 1 0                                       | 1 2 0                                  | 2 1 0                        | 0 1 2                              | 0 1 2                                | 0  |
| 4 oral arm colour                    | w y b 0                                     | w 0 b y                                | 0 w y                        | 0 w                                | 0                                    | 0  |
| 5 club colour                        | b y   | b 0                                    | y 0 b                        | 0                                  | 0                                    | 0  |
| 6 spot abundance                     | 3 2   | 3 2                                    | 1 2                          | 0 1 2                              | 0 1 2 3                              | 0  |
| 7 spot colour                        | w y g                                       | w                                      | y                            | w                                  | w y                                  | n.a.                                     |
| 8 mass <sup>sml</sup>                | 0.66-0.91-1.49                              | 0.62-0.74-1.08                         | 0.52-0.70-1.11               | 0.61-0.77-0.95                     | 0.59-0.83-1.03                       | 0.53-0.69-0.83                           |
| 10 ring canal diameter <sup>ml</sup> | 0.73-0.81-0.90                              | 0.76-0.78-0.83                         | 0.74-0.78-0.89               | 0.72-0.79-0.85                     | 0.76-0.79-0.82                       | 0.77-0.81-0.87                           |

|  |                |                |                |                |                |                |
|--|----------------|----------------|----------------|----------------|----------------|----------------|
| 11 OA unwinged length <sup>sml</sup>       | 0.05-0.09-0.12 | 0.05-0.09-0.12 | 0.05-0.10-0.17 | 0.09-0.11-0.18 | 0.04-0.09-0.15 | 0.07-0.10-0.17 |
| 12 OA winged length <sup>sml</sup>         | 0.20-0.25-0.32 | 0.17-0.24-0.32 | 0.13-0.17-0.23 | 0.13-0.21-0.30 | 0.16-0.24-0.32 | 0.13-0.16-0.27 |
| 13 club shape                              | 3 2            | 3 0 2          | 3 2 1 0        | 3 2 0 1        | 3 2 0 4 1      | 2 0 3          |
| 14 club number <sup>sml</sup>              | 8-8-8          | 8-8-8          | 3-8-8          | 5-8-12         | 6-8-8          | 0-5-8          |
| 15 club length <sup>sml</sup>              | 0.27-0.66-0.98 | 0.15-0.35-0.59 | 0.11-0.19-0.37 | 0.05-0.11-0.18 | 0.03-0.15-0.21 | 0.04-0.10-0.28 |
| 16 pillar length <sup>sml</sup>            | 0.02-0.04-0.11 | 0.02-0.03-0.05 | 0.02-0.03-0.09 | 0.02-0.02-0.04 | 0.02-0.02-0.05 | 0.02-0.03-0.07 |
| 17 pillar width <sup>sml</sup>             | 0.04-0.10-0.12 | 0.08-0.10-0.14 | 0.06-0.10-0.15 | 0.04-0.08-0.10 | 0.08-0.10-0.11 | 0.05-0.07-0.10 |
| 18 pillar depth <sup>sml</sup>             | 0.02-0.02-0.04 | 0.01-0.02-0.03 | 0.01-0.02-0.04 | 0.01-0.02-0.02 | 0.02-0.02-0.03 | 0.01-0.02-0.03 |
| 19 ostia width <sup>ml</sup>               | 0.23-0.27-0.32 | 0.26-0.29-0.33 | 0.22-0.27-0.33 | 0.25-0.29-0.32 | 0.26-0.30-0.38 | 0.26-0.31-0.37 |
| 20 disc diameter <sup>ml</sup>             | 0.38-0.42-0.52 | 0.37-0.47-0.53 | 0.33-0.43-0.49 | 0.34-0.41-0.49 | 0.37-0.43-0.51 | 0.30-0.40-0.49 |
| 21 disc depth † <sup>sml</sup>             | 0.01-0.02-0.04 | 0.02-0.02-0.08 | 0.01-0.02-0.04 | 0.01-0.02-0.06 | 0.01-0.02-0.04 | 0.02-0.02-0.04 |
| 22 arm filaments                           | a d            | a d            | a 0 d          | a d 0          | a d 0          | 0 a            |
| 23 lappet number <sup>sml</sup>            | 0.05-0.10-0.18 | 0.05-0.09-0.17 | 0.05-0.09-0.19 | 0.07-0.11-0.23 | 0.06-0.09-0.19 | 0.12-0.16-0.23 |
| 24 GVC shape                               | c              | c              | c k            | c k            | c              | k c            |
| 25 porticus colour                         | 0 b            | 0 b            | 0 b            | 0              | 0              | 0              |
| 26 GVC interradi al diameter <sup>sl</sup> | 0.45-0.56-0.66 | 0.51-0.55-0.64 | 0.51-0.56-0.62 | 0.45-0.53-0.59 | 0.52-0.56-0.63 | 0.48-0.54-0.62 |
| 27 GVC perradi al diameter <sup>sml</sup>  | 0.11-0.26-0.33 | 0.18-0.22-0.28 | 0.23-0.30-0.37 | 0.24-0.33-0.40 | 0.16-0.24-0.31 | 0.21-0.30-0.39 |
| 28 bell depth ‡ <sup>sml</sup>             | 0.07-0.09-0.13 | 0.07-0.08-0.12 | 0.04-0.08-0.11 | 0.06-0.08-0.10 | 0.06-0.08-0.10 | 0.04-0.06-0.09 |
| 31 adradial origins <sup>sml</sup>         | 0.08-0.25-0.29 | 0.07-0.12-0.25 | 0.05-0.11-0.23 | 0.05-0.09-0.25 | 0.05-0.09-0.26 | 0.06-0.09-0.21 |
| 32 perradi al anastomoses <sup>sml</sup>   | 0.00-0.05-0.15 | 0.00-0.02-0.05 | 0.00-0.01-0.01 | 0.00-0.00-0.01 | 0.00-0.00-0.02 | 0.00-0.00-0.02 |
| 33 interradi al anastomoses <sup>sml</sup> | 0.00-0.04-0.09 | 0.00-0.01-0.04 | 0.00-0.00-0.01 | 0.00-0.00-0.01 | 0.00-0.00-0.01 | 0.00-0.00-0.01 |
| 34 adradial anastomoses <sup>sml</sup>     | 0.56-1.21-2.87 | 0.47-0.98-1.48 | 0.22-0.46-1.03 | 0.07-0.22-0.52 | 0.03-0.28-1.13 | 0.06-0.15-0.28 |
| 38 adradial sinuses § <sup>ml</sup>        | 0.00-0.00-0.02 | 0.00-0.03-0.06 | 0.00-0.03-0.10 | 0.00-0.02-0.11 | 0.00-0.03-0.08 | 0.00-0.04-0.12 |

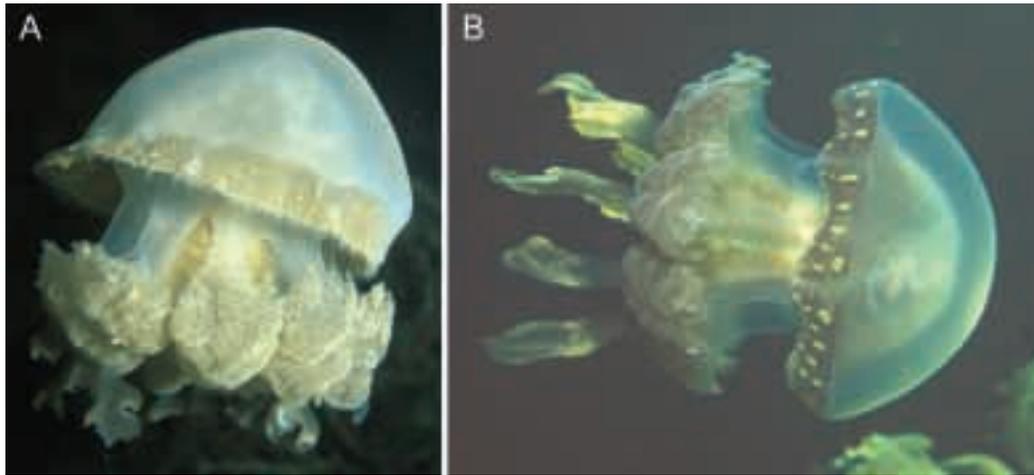
†, only data for one of four repeat measurements (i.e. bd/3 from centre; one of the more informative positions) reported here; ‡, only data for one of five repeat measurements (i.e. centre of bell; one of the more informative positions) reported here. §, four other sinus counts, which showed much less variation not reported here. Shadow avoidance: ‘no’ may be equivalent to weak; ‘yes’ equivalent to strong.



**Figure 3.** Typical morphologies of *Mastigias* subspecies in Palau. (A) The ancestral *Mastigias* cf. *papua* lagoonal form, Big Jellyfish Cove, Palau, ~20 cm bd; (B) subspecies *remengesau*, Uet era Ongael, ~10 cm (photograph by L. Sharron, courtesy of Coral Reef Research Foundation); (C) subspecies *nakamura*, Goby Lake, ~15 cm; (D) subspecies *etpisoni*, Ongeim'l Tketau, ~15 cm; (E) subspecies *salii*, Clear Lake, ~15 cm; (F) subspecies *remeliiki*, Uet era Ngermeuangel, ~10 cm.



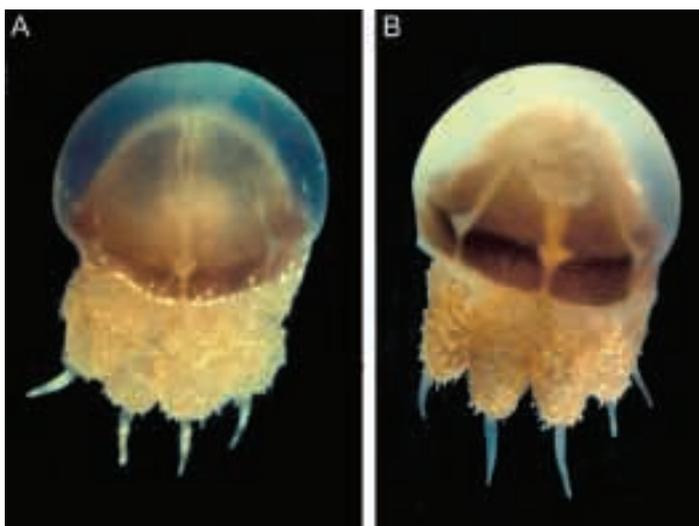
**Figure 4.** Subspecies *remengesau*, Uet era Ongael. Medusae ~15 cm bd. (A) Lateral view of medusa; (B) view of oral surfaces, showing the symmetry of the medusa; notice the brood filaments carrying planulae at the base of the oral arms.



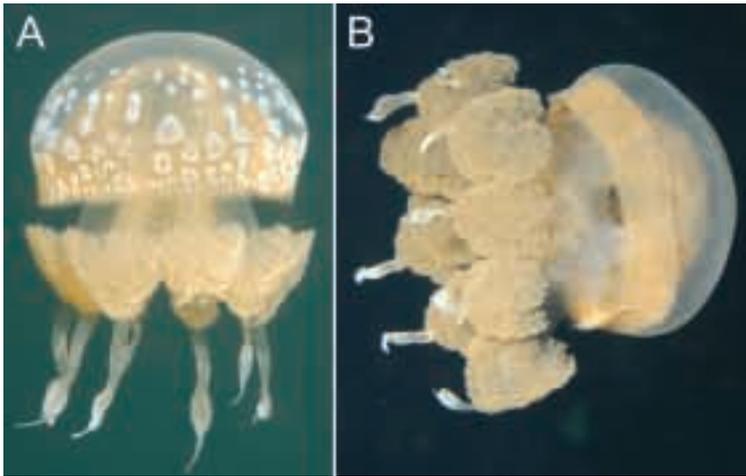
**Figure 5.** Subspecies *nakamurai*, Goby Lake. Medusae ~10–15 cm bd showing some variation in spots around the bell margin and in shapes of terminal clubs. (A) Lateral view showing less spotted, shorter irregular terminal clubs; (B) lateral view showing more spotted, medium-length often flame-like terminal clubs. Photographs by L. Sharron, courtesy of Coral Reef Research Foundation.



**Figure 6.** Subspecies *etpisoni*, Ongeim'l Tketau. (A, B) Large medusae, ~15–20 cm bd (photographs by P.L. Colin, L.E. Martin, respectively); (C) small medusae, few centimetres bell diameter (photograph by L.E. Martin). Spots on exumbrella are just visible around bell margin in (B) and (C).



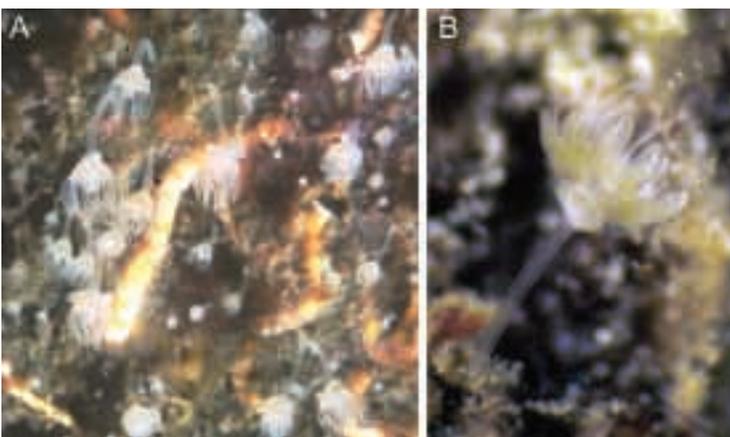
**Figure 7.** Subspecies *saliii*, Clear Lake. Examples of (A) a modestly pigmented and (B) an unpigmented form. Medusae ~15 cm bd.



**Figure 8.** Subspecies *remeliiki*, Uet era Ngermeuangel. (A) Spotted form occurs at frequency ~2% of the population; (B) unspotted form occurs at frequency ~98% of the population. Both medusae ~8–10 cm bd (photographs by L.E. Martin).



**Figure 9.** The ancestral *Mastigias* cf. *papua* lagoonal form in Ngerchaol Cove, Palau; medusa ~15 cm bd.



**Figure 10.** (A) Scyphistomae of *Mastigias* cf. *papua etpisoni* at ~10 m depth in Ongeim'l Tketau. The largest polyps in the image are ~6 mm from base to tentacle tip; (B) a strobila of *Mastigias* cf. *papua etpisoni*, diameter of developing ephyra is ~1–2 mm (photograph by L.J. Bell).

*Mastigias* cf. *papua etpisoni* ssp. nov.  
(Figures 2, 3D & 6; Table 1)

*Mastigias* sp.: Hamner & Hauri, 1981; Hamner, 1982; Hamner et al., 1982; Muscatine & Marian, 1982; Muscatine et al., 1986; McCloskey et al., 1994; Colin & Arneson, 1995, p. 76, figure 288; Hamner & Hamner, 1998; Heeger, 1998, pp. 202–212, plates 3–3, 3–4, 3–6 to 3–10; Dawson et al., 2001; Dawson & Hamner, 2003, 2005; Dawson, 2005a.

*Type material*

Holotype: medusa preserved in 4% formalin. (Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E; water depth: <1 m) [RMNH Coel. 33308]. Collected by M.N Dawson, 25 September 1998.

Paratypes: two medusae preserved in 4% formalin. (Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E; water depth: <1 m) [RMNH Coel. 33309]. Collected by M.N Dawson, 25 September 1998.

One medusae preserved in 4% formalin. (Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E; water depth: <1 m) [CASIZ 171884]. Collected by L.J. Bell, 20 January 2000.

Three medusa preserved in 4% formalin. (Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E; water depth: <1 m) [PICRC-CNI 004]. Collected by L.J. Bell and L.E. Martin, 29 March 2004.

*Comparative material examined*

Ten 50 mm immature medusae, five 100 mm female medusae, five 100 mm male medusae, seven 150 mm female medusae, three 150 mm male medusae. (Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, April 1996 to March 1997. Morphometrics measured destructively.

*Type locality*

Ongeim'l Tketau, Mecherchar, Koror State, Palau; 07°09.72'N 134°22.51'E. Also referred to as Jellyfish Lake, Ongerul Tketau Uet (e.g. Hamner et al., 1982), Uet ra Edead Eil Malk (Hamner & Hauri, 1981), and Tourist Lake.

*Diagnosis*

Rarely spots on exumbrella, ground colour brown from zooxanthellae, no blue pigment. Very short, stubby, terminal clubs, sometimes missing from, or occurring in multiples on, each of eight oral arms; distal end like the blade of a paddle or a tricorn in cross-

section. Moderately simple canal structure, usually without flecks.

*Description*

The base brown colour in subspecies *etpisoni* medusae is supplemented only rarely by faint white spots occasionally visible in few medusae of most size-classes. Subspecies *etpisoni* medusae are generally robust medusae, the largest observed being ~23 cm bd although the largest present usually are ~18–20 cm. The most obvious feature is broad but very short terminal clubs which are sometimes absent and other-times bifurcated. Filaments occur as small protruding clubs distributed often sparsely and unevenly across the oral arms. Detailed measurements of features are in Table 1 and Dawson (2005a). Adenine at position 82 of COI distinguishes subspecies *etpisoni* from all other marine lake subspecies. Complete sequences are available in GenBank (accession nos. AY903008–AY903021).

*Habitat*

Medusae are planktonic and, with one known exception (late-1998 to mid-2000), abundant year-round in the mixolimnion (0 m to 13 m depth) of this meromictic marine lake. When medusae have been present, the water column (measurements at metre intervals averaged from 0–13 m) has ranged from 29.1–32.4 °C (mean 31.2 ±0.1 °C; N=93) and 26.9–30.3 psu (mean 28.9 ±0.1 psu; N=93); dissolved oxygen 2.1–5.0 mg l<sup>-1</sup> (mean 3.3 ±0.2 mg l<sup>-1</sup>; N=86). Benthic scyphistomae are attached to decaying leaves, wood, and other hard substrate predominantly between 6 m and 14 m depth; they have also been observed on decaying wood at <1 m depth (L.J. Bell & L.E. Martin, personal communication).

*Distribution*

*Mastigias* cf. *papua etpisoni* occurs only in Ongeim'l Tketau, Koror State, Palau.

*Etymology*

The subspecies name is a patronym in honour of the third elected President of Palau, President Ngiratkel Etpison (1989–1992). Ongeim'l Tketau is deeper than, and formed before, Goby Lake.

*Mastigias* cf. *papua saliii* ssp. nov.  
(Figures 2, 3E & 7; Table 1)

*Mastigias* sp.: Dawson et al., 2001; Dawson & Hamner, 2003, 2005; Dawson, 2004, 2005a.

*Type material*

Holotype: medusa preserved in 4% formalin. (Clear Lake, Mecherchar, Koror State, Palau; 07°09.19'N

134°21.62'E; water depth: <1 m) [RMNH Coel. 33310]. Collected by M.N Dawson, 27 October 1998.

Paratypes: four medusae preserved in 4% formalin. (Clear Lake, Mecherchar, Koror State, Palau; 07°09.19'N 134°21.62'E; water depth: <1 m) [CASIZ 171885]. Collected by M.N Dawson, 27 October 1998.

One medusa preserved in 4% formalin. (Clear Lake, Mecherchar, Koror State, Palau; 07°09.19'N 134°21.62'E; water depth: <1 m) [PICRC-CNI 024]. Collected by M.N Dawson, 27 October 1998.

#### *Comparative material examined*

Ten 50 mm immature medusae, five 100 mm female medusae, five 100 mm male medusae, five 150 mm female medusae, five 150 mm male medusae. (Clear Lake, Mecherchar, Koror State, Palau; 07°09.19'N 134°21.62'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, September to October 1998. Morphometrics measured destructively.

#### *Type locality*

Clear Lake, Mecherchar, Koror State, Palau; 07°09.19'N 134°21.62'E.

#### *Diagnosis*

Ground colour tan from zooxanthellae. Medium-short terminal clubs, usually one occasionally none per oral arm, circular in cross-section, lanceolate. Simple to moderately complex canal structure, usually without flecks. Thymine at position 91 and Cytosine at position 563 of COI.

#### *Description*

The base tan colour in subspecies *salii* medusae is variously supplemented by blue pigmentation in inter-radial and perradial canals and sometimes abundant white or yellow spots across the exumbrella or around the bell margin. Terminal clubs are generally short and notably lanceolate, almost always occurring one per oral arm. Filaments on oral arms can be common; they are small, club-shaped, and protrude from among the mouths. Medusae appear generally quite symmetrical. They can be large, growing to ~20 cm bd. Detailed measurements of features are in Table 1 and Dawson (2005a). Complete sequences are available in GenBank (accession nos. AY903022–AY903033).

#### *Habitat*

Medusae are planktonic and occasionally abundant in, but also can be absent from, the mixolimnion (0 m to 9 m depth) of this meromictic marine lake. When medusae have been present, the water column (measurements at metre intervals averaged from 0–9 m) has ranged from 30.5–31.5°C (mean 30.8 ±0.7°C; N=4)

and 22.6–28.1 psu (mean 24.0 ±4.3 psu; N=4); dissolved oxygen 3.9–4.2 mg l<sup>-1</sup> (mean 4.1 ±1.7 mg l<sup>-1</sup>; N=2). Benthic scyphistoma have been found attached to decaying leaves at approximately 6–7 m depth.

#### *Distribution*

*Mastigias* cf. *papua salii* occurs only in Clear Lake, Koror State, Palau.

#### *Etymology*

The subspecies name is a patronym in honour of the second elected President of Palau, President Lazarus E. Salii (1985–1988). Clear Lake is approximately the same depth, and presumably similar age, as Ongeim'l Tketau.

*Mastigias* cf. *papua remeliiki* ssp. nov.

(Figures 2, 3F & 8; Table 1)

*Mastigias papua*: Faulkner, 1974, p. 179, plate 107.

*Mastigias* sp.: Hamner & Hauri, 1981; Hamner & Hamner, 1998; Heeger, 1998, pp. 202–212; Martin, 1999; Dawson et al., 2001; Dawson & Hamner, 2003, 2005; Dawson, 2005a.

#### *Type material*

Holotype: medusa preserved in 4% formalin. (Uet era Ngermeuangel, Ngermeuangel, Koror State, Palau; 07°19.36'N 134°30.50'E; water depth: <1 m) [RMNH Coel. 33311]. Collected by M.N Dawson, October–December 1998.

Paratypes: three medusae preserved in 4% formalin. (Uet era Ngermeuangel, Ngermeuangel, Koror State, Palau; 07°19.36'N 134°30.50'E; water depth: <1 m) [CASIZ 171886]. Collected by M.N Dawson, October–December 1998.

Three medusae preserved in 4% formalin. (Uet era Ngermeuangel, Ngermeuangel, Koror State, Palau; 07°19.36'N 134°30.50'E; water depth: <1 m) [PICRC-CNI 002]. Collected by L.J. Bell and L.E. Martin, 23 March 2004.

#### *Comparative material examined*

Ten 50 mm immature medusae, five 100 mm female medusae, five 100 mm male medusae. (Uet era Ngermeuangel, Ngermeuangel, Koror State, Palau; 07°19.36'N 134°30.50'E; water depth: <1 m). Collected by L.E. Martin and M.N Dawson, May–December 1996. Morphometrics measured destructively.

#### *Type locality*

Uet era Ngermeuangel, Ngermeuangel, Koror State, Palau; 07°19.36'N 134°30.50'E; water depth: <1 m).

Also referred to as Jellyfish Lake, Koror (e.g. Hamner & Hauri, 1981; Hamner & Hamner, 1998) and Big Jellyfish Lake (e.g. Martin, 1999; Dawson et al., 2001).

#### Diagnosis

Exumbrellar spots almost always absent, but if present then abundant and irregularly shaped; ground colour golden-brown from zooxanthellae, no blue pigment. Paddle-shaped, lanceolate, or rarely tricornate terminal clubs of variable length but always short, usually <1 per oral arm, sometimes absent. Simple canal structure, mostly without flecks, few adradial anastomoses. Guanine at position 187 and Thymine at position 448 of COI.

#### Description

The base golden-brown colour in subspecies *remeliiki* medusae is supplemented in approximately 2% of the population by many irregular white patches distributed on the exumbrella. Terminal clubs are short but, relative to the overall size of the medusae—the largest observed is 14 cm bd although the largest present usually are ~8–12 cm—can appear moderately long. The terminal clubs are predominantly paddle-shaped and slightly concave like a spoon, but they may be three-rayed and flame-like or absent even on the same medusa, resulting in a count of typically fewer than eight terminal clubs per medusa. Club-shaped filaments, if present, are sparsely and unevenly distributed on the oral arms, protruding above the mouths. The small size and diminutive features of subspecies *remeliiki* is emphasized by a particular softness of the mesoglea, giving a fragile appearance. This can be offset by very irregularly shaped oral arms giving an ungainly squat look. Detailed measurements of features are in Table 1 and Dawson (2005a). Complete sequences are available in GenBank (accession nos. AY903034–AY903047).

#### Habitat

Medusae are planktonic and, from all known records, abundant year-round in the mixolimnion (0 m to 16 m depth) of this meromictic marine lake. When medusae have been present, the water column (measurements at metre intervals averaged from 0–16 m) has ranged from 30.2–32.8°C (mean 31.8 ±0.1°C; N=67) and 24.5–31.5 psu (mean 28.0 ±0.3 psu; N=67); dissolved oxygen 2.6–5.4 mg l<sup>-1</sup> (mean 3.6 ±0.1 mg l<sup>-1</sup>; N=63). Benthic scyphistomae are attached to decaying leaves, wood, and other hard substrate predominantly between 6 m and 16 m depth.

#### Distribution

*Mastigias* cf. *papua remeliiki* occurs only in Uet era Ngermeuangel, Koror State, Palau.

#### Etymology

The subspecies name is a patronym in honour of the first elected President of Palau, President Haruo I. Remeliik (1981–1985). Of the five marine lakes discussed herein, Uet era Ngermeuangel was the first to form.

#### Remarks

The only known sexual dimorphism in the studied populations of *Mastigias* in Palau, is the occurrence in mature females (and absence from mature males) of brood filaments at the base of the oral arms at the oral disc (Figures 2 & 4B). All immature medusae lack the brood filaments, which should not be confused with the oral arm filaments that also occasionally occur among the mouths near the centre of the oral disc, particularly in lagoon *Mastigias* cf. *papua*.

Small medusae of each lake subspecies are morphologically most similar to each other, with larger medusae developing the characteristics of the subspecies and becoming more distinct from other lake subspecies and from the ancestral lagoonal form *Mastigias* cf. *papua* (Figures 3A & 9). However, even large medusae in subspecies *remengesau* closely resemble the lagoon morphotype *Mastigias* cf. *papua*. All other lake subspecies are clearly distinct in having, to different degrees, greatly reduced (or absent) endogenous pigmentation (i.e. not photopigmentation attributable to zooxanthellae), exumbrellar spots, and terminal clubs.

The morphology of *Mastigias* medusae in marine lakes is a product of very rapid evolution—all populations were established shortly before or during the Holocene—and extreme isolation, as indicated by COI haplotype frequency differences (Dawson & Hamner, 2005). Assuming the time of colonization is correlated with the depth of the lake (given an approximately constant rate of sea-level rise between ~18,000 and ~5000 years BP), the overall degree of morphological divergence from the ancestral lagoon morphotype, *Mastigias* cf. *papua*, is, with one exception largely proportional to the time since isolation (Dawson & Hamner, 2005). The exception, subspecies *sali* (Clear Lake), is often not present in the medusa stage, effectively reducing the time that the medusa population has been subject to natural selection.

The physical and biological factors that result in different population dynamics of *Mastigias* medusae in different lakes, including the frequent absence of subspecies *sali*, are poorly understood. Preliminary investigations begun after the strong El Niño–La Niña events of 1997/1998 suggest variation in population dynamics likely reflect both differences in the physical environments among lakes and population specific

responses to those differences (Dawson et al., 2001) possibly due to underlying physiological differences among subspecies of medusae. For example, during 1999, the temperature in Goby Lake was generally cooler and more variable than the temperature in Uet era Ngermeuangel; subspecies *nakamurai* medusae have concomitantly lower tolerance of higher temperatures than *remeliiki* medusae (Dawson et al., 2001). Similarly, *Mastigias* scyphistomae from the cooler Goby Lake bleach at lower temperatures than scyphistomae from the warmer Ongeim'l Tketau (Figure 10; Dawson et al., 2001). Muscatine & Marian (1982) and McCloskey et al. (1994) also reported differing ammonium fluxes and carbon budgets in lagoon *Mastigias* cf. *papua* compared to subspecies *etpisoni*. However, there are currently no published long-term data describing physical, chemical, and biological variation in any of the marine lakes, so the processes that mediate the responses of medusae populations to environmental variation—particularly during 'normal', i.e. non-El Niño and non-La Niña conditions—are very poorly delineated.

The observed parallel morphological evolution (e.g. vestigialization of colour, terminal clubs) of all lake populations indicates similar directional selection pressure. It is possible that selection on morphology has also had indirect, and parallel, consequences on behavioural evolution (or vice versa, or both). For example, the absence of blue pigmentation in lake medusae coincides with the origin (independently in each lake) of short vertical movements over several metres in response to short-term diurnal changes in incident light (Dawson & Hamner, 2003; Dawson, 2005a); swimming speed is fastest in the most symmetrical lagoon-like subspecies *remengesau* while being slowest in the most squat irregular subspecies *remeliiki* (Dawson & Hamner, 2003). In these cases, morphologic and behavioural evolution appear intrinsically linked and it is somewhat artificial to separate them (or molecular genetic differences) when considering the systematics, or description of subspecies, of *Mastigias* medusae. However, similar morphological evolutionary trajectories due to parallel evolution do not preclude behavioural divergence. Unique diel horizontal migrations have evolved in, at least, Ongeim'l Tketau, Clear Lake, and Uet era Ngermeuangel, in response to different selection pressures (Hamner & Hauri, 1981; Dawson & Hamner, 2003).

Each marine lake subspecies of *Mastigias* in Palau thus has an unique suite of morphological, molecular, behavioural, and probably physiological characteristics. The morphological variation shown among subspecies in Palau is greater than that shown between many species and varieties of *Mastigias* previously

described from throughout the Indo-West Pacific (Dawson, 2005a). In contrast, molecular differences among subspecies is a small fraction of that between different medusae identified in the field as *M. papua* from Berau (GenBank accession nos. AY903048 & AY903049), PNG (GenBank accession nos. AY903050 & AY903051), and Palau (Dawson, 2004, 2005a). The medusae in Palau therefore appear to have peculiar evolutionary and taxonomic significance. Medusae in the marine lakes are also important in the economy of Palau (tens of thousands of tourists visit Ongeim'l Tketau every year; Dawson et al., 2001). Recognizing distinct subspecies in each marine lake is an appropriate reflection of their unique contributions to biodiversity in the Scyphozoa and the need to consider each as a distinct management unit.

Two elected Vice-Presidents assumed the Presidency of Palau after the premature deaths of the incumbents: Mr. Alfonso R. Oiterong (President: June 1985 to September 1985) and Mr Thomas O. Remengesau (President: August 1988 to December 1988). Due to the limited number of marine lake populations of *Mastigias* in Palau I was unfortunately unable to honour them similarly in this publication. Work in Palau was permitted by Division of Marine Resources and Koror State Government and assisted by F. Toribiong, M. Mesubed, W. Maech, E. Basilius, W. Hamner, P. Hamner, P. Colin, the Coral Reef Research Foundation, and the Palau Conservation Society. Collections in PNG were made by Coral Reef Research Foundation; collections in Berau by B. Hoeksema. I am indebted to L. Martin and L. Bell for years of fieldwork, discussion, and comments that made possible and improved the manuscript. The manuscript was also improved by P. Colin and by the detailed and helpful comments of two referees. L. van Ofwegen very kindly dusted off numerous books to find the type locality of *M. papua*. Fieldwork was funded by the University of California, the International Women's Fishing Association, the American Museum of Natural History (Lerner-Grey Award), and the British Schools and Universities Foundation.

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**Appendix 1.** *Mastigias cf. papua* cytochrome *c* oxidase subunit I (COI) 'barcode' of subspecies *remengesau* (*medusa OLO\_2c*).

5' -

ATTTGGTATTTTTCTGGTGTGTTAGGCGCAGGTTTCAGTATGATTATCAGGTTAGAGTTATCTGGTCCCG  
 GATCTATGTTGGGGGACGACCACCTCTATAATGTAGCTGTTACAGCCACGGTTTAATAAT  
 GATATTTTTCTTCGTAATGCCCGTTTTATTAGGTGGTTTTGGTAACTGGTTTGTACCATTGTATG  
 TAGGGGCTCCTGATATGGCATTCCCTCGATTAAATAATATAAGTTTTCTGGCTACTACCACCAGCTCTTATGT  
 TATTATTAGGCTCTTCCCTAGTGGAACAAGGAGTAGGTACAGGTTGGACTGTTTATCCTCCACTAAGTGCCATT  
 CAAGCACACTCAGGAGGTTCTGTTGACATGGCTATATTTAgTTTACATCTAGGGGGtGTTTCCTCCATACTAGC  
 TTCAATTAACTTTATAACTACTATACTCAACATGAGAGCTCCAGGAATGACCATGGACAAAATGCCTTTATTTG  
 TATGAGCTATATTAATAACTGCAGGTTTACTTAtACTTTCTTTACCTGtATTTGCTGGAGCTATCACCATGTTG  
 TTAACGGACAGAACTTCAATACCTCCTTCTTTGACCCTGCGGGAGGGGAGATCCTATTTTGTA-3'

*Mastigias cf. papua* COI 'barcode' variable positions; numbers indicate multiple haplotypes for a single subspecies. The three positions that show no variation among marine lakes, are variable in the ancestral lagoon populations.

|                    |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|--------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                    |   |   |   | 1 | 1 | 1 | 2 | 2 | 4 | 4 | 4 | 5 | 5 | 5 |   |
|                    | 6 | 8 | 9 | 9 | 8 | 9 | 9 | 3 | 8 | 4 | 5 | 9 | 1 | 4 | 6 |
|                    | 5 | 2 | 1 | 7 | 7 | 3 | 6 | 2 | 0 | 8 | 3 | 9 | 9 | 7 | 3 |
| <i>remengesau</i>  | G | G | C | C | A | G | T | T | C | C | G | T | T | T | T |
| <i>etpisoni</i>    | . | A | . | . | . | A | . | . | T | . | . | . | C | . | . |
| <i>saliu 1</i>     | . | . | T | . | . | A | . | . | T | . | . | . | C | . | C |
| <i>saliu 2</i>     | . | . | T | T | . | A | . | . | T | . | . | . | C | . | C |
| <i>nakamurai</i>   | . | . | . | . | . | . | . | . | T | . | . | . | . | . | . |
| <i>remeliiki 1</i> | . | . | . | . | G | . | . | . | T | T | A | . | C | C | . |
| <i>remeliiki 2</i> | . | . | . | . | G | . | . | . | T | T | . | . | C | C | . |
| <i>remeliiki 3</i> | . | . | . | . | G | . | . | . | T | T | . | C | C | C | . |