



## Redescription of *Prosaetes rhinodontis* (Wright, 1876) (Crustacea: Copepoda: Siphonostomatoida), an enigmatic parasite of the whale shark, *Rhincodon typus* Smith (Elasmobranchii: Orectolobiformes: Rhincodontidae)

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### Abstract

The siphonostomatoid copepod *Prosaetes rhinodontis* (Wright, 1876) is redescribed in detail based on adult female specimens recently collected from the sieve-like gill rakers of a whale shark, *Rhincodon typus* Smith, held in captivity off the coast of Motobu-cho, Okinawa-jima Island, Japan. Comparisons with other caligiform copepod species previously identified as *Dysgamus atlanticus* Steenstrup & Lütken, 1861 and described as *Echthrogaleus pectinatus* Kirtisinghe, 1964 from a whale shark revealed that these two taxa are conspecific with *P. rhinodontis*. The latter is transferred herein from the Pandaridae to the Cecropidae based on the relatively slim shape of its maxilliped corpus, and an amended diagnosis of *Prosaetes* C. B. Wilson, 1907 is provided. Neotype material of *P. rhinodontis* was selected from a previous collection of 173 specimens removed from a whale shark caught alive off the coast of Yonabaru-cho, Okinawa-jima Island, Japan, and subsequently held in captivity, albeit briefly, in the Okinawa Churaumi Aquarium, Motobu-cho, Okinawa-jima Island, Japan. Asymmetrical clusters of *P. rhinodontis* females on the host's gill rakers were observed in this study, which suggest that this aggregative behavior most likely does not facilitate their attachment to the host but rather is a strategy used to augment their reproductive fitness. We also postulate that *P. rhinodontis* grazes on the epithelium of the host's gill rakers and is, in contrast to other cecropids, a relatively vagile species.

**Key words:** taxonomy, Japan, aquarium, captivity

### Introduction

The siphonostomatoid copepod *Stasiotes rhinodontis* was established by Wright (1876) as a new genus and species in the Pandarina (now the Pandaridae Milne Edwards, 1840) based on 40–50 adult female specimens collected from presumably two whale sharks, *Rhincodon typus* Smith, harpooned in waters off the Seychelles. It is relevant to clarify at this point in time the authorship date for *S. rhinodontis*, which has been historically cited as either 1874 (see Wilson 1907; Yamaguti 1963; Heegaard 1972) or 1876 (see Wilson 1944). Although the former is indeed the year in which Wright's paper was recited before the Royal Irish Academy, the latter is recognized as valid herein, as indicated above, since Wright's paper was formally printed on July 1876 of Series 2, Volume 2, Part 6 of the *Proceedings of the Royal Irish Academy*.

As the name *Stasiotes* had already been used by Jan (1862) for a genus of snakes, Wilson (1907) subsequently proposed *Prosaetes* as a replacement name for the preoccupied *Stasiotes* Wright, 1876. Wilson (1944) later transferred *Prosaetes rhinodontis* (Wright, 1876) to the now defunct caligid genus *Dysgamus* Steenstrup & Lütken, 1861, since he believed that the former taxon and his adult female copepod specimens identified as *Dysgamus atlanticus* Steenstrup & Lütken, 1861, from a whale shark captured off Cuba, represented congeneric species. Although Heegaard (1972) subsequently synonymized four nominal species

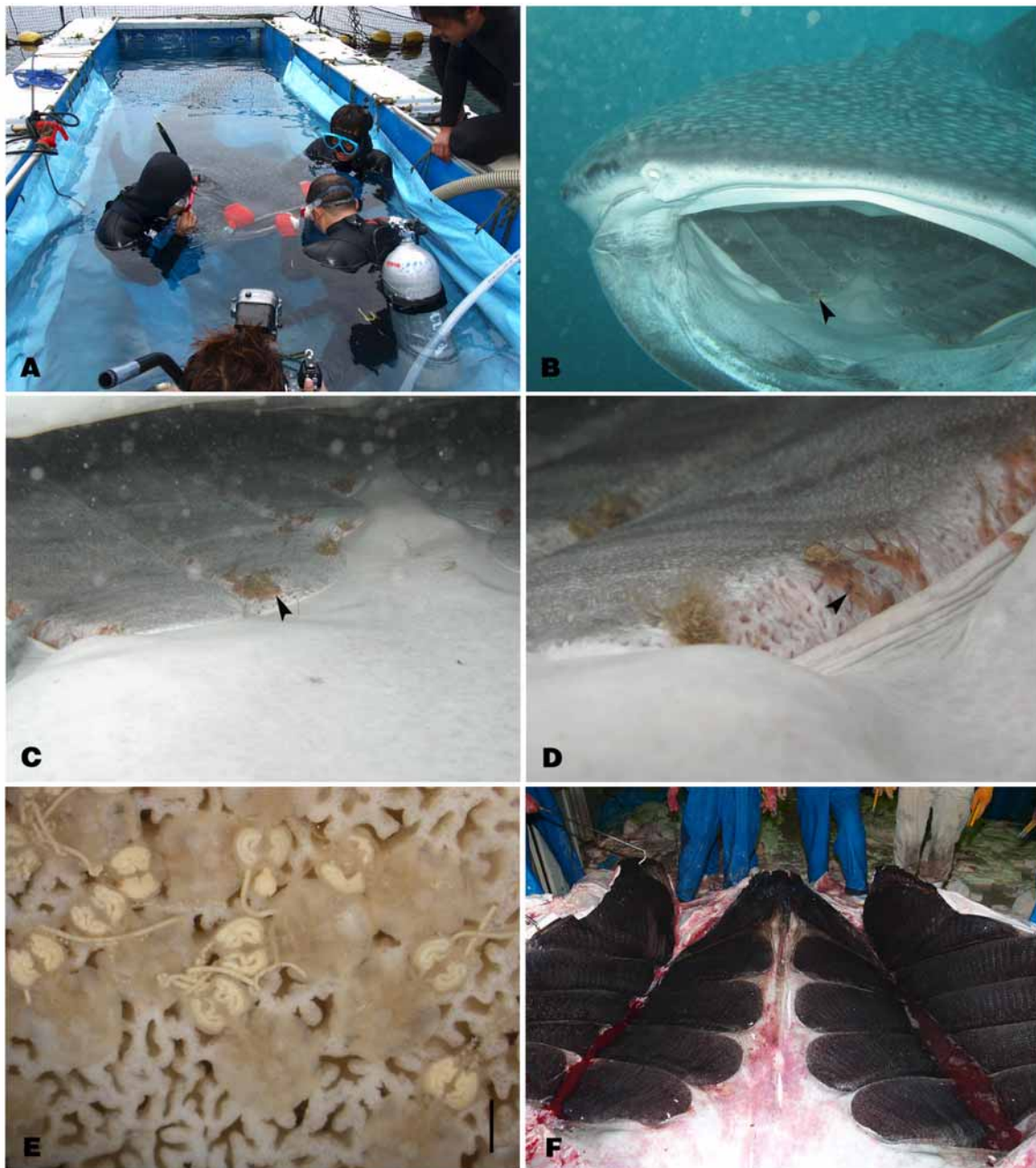
of *Dysgamus*, including *D. atlanticus*, with the caligid *Euryphorus nordmanni* Milne Edwards, 1840, he failed to comment on the identity of Wilson's material of *D. atlanticus*. Despite Heegaard's (1972) action, adult female copepod specimens attributed as *D. atlanticus* were later reported, but not described, from a whale shark that had died 40 hours after being placed in an aquarium at the Okinawa Expo Memorial Park Aquarium (presently named Okinawa Churaumi Aquarium), Okinawa-jima Island, Japan (Williams & Williams 1986). Heegaard (1972) also recognized, as did Yamaguti (1963), that Wilson's (1944) generic placement of *rhinodontis* was unsound and as such relegated *Dysgamus rhinodontis* (Wright, 1876) back to *Prosaetes*. Although the genus *Stasiotes* Jan, 1862 is now considered a junior synonym of the colubrid snake genus *Cemophora* Cope, 1860 (see Williams & Wilson 1967; Williams & Wallach 1989), *Prosaetes* must continue to be used in place of the junior homonym *Stasiotes* Wright, 1876 since there is no Article of the International Code of Zoological Nomenclature (1999) that allows reinstatement of the junior homonym. Despite this resolution of the nomenclature of *P. rhinodontis*, the identification of this parasite and generic definition of *Prosaetes* remain elusive (Kabata 1979; Kazachenko 2001; Boxshall & Halsey 2004). The present report provides the first complete description of *P. rhinodontis* and an improved definition of *Prosaetes* based on: a) material recently collected from a whale shark held in captivity off the northwestern coast of Okinawa-jima Island, Japan; b) re-examination of Wilson's (1944) and Williams & Williams' (1986) material of *D. atlanticus*; and c) comparisons with the original description of *Echthrogaleus pectinatus* Kirtisinghe, 1964, a species considered to be a doubtful member of *Echthrogaleus* Steenstrup & Lütken, 1861 (Kabata 1979) and currently regarded as a species inquirendum (Boxshall & Halsey 2004). Also, neotype material is designated, the familial membership of *P. rhinodontis* is re-evaluated, and the biology of this parasite is discussed.

## Material and methods

The whale shark was caught opportunistically on 7 November, 2007 in a set net placed in the western North Pacific Ocean, offshore from Umino Fishing Port, Chinen-son, southeastern Okinawa-jima Island, Okinawa Prefecture, Japan, and then transported alive the next day by Okinawa Churaumi Aquarium staff firstly in a net cage towed behind a vessel to Umino Fishing Port, secondly in the net cage lifted onto a dump truck bed lined with a plastic sheet and flooded with seawater to Yamagawa Port (about 2 km south of the Okinawa Churaumi Aquarium, Motobu-cho, northwestern Okinawa-jima Island), and lastly in the net cage first lifted out of the dump truck bed and then towed behind a vessel to a multi-sea pen system moored about 0.6 km offshore from Yamagawa Port, where it was cared for in captivity with other whale sharks until its death on 9 May, 2008. Copepods were collected from this whale shark (designated No. 31 by the Okinawa Churaumi Aquarium staff; 4.60 m total length and 595 kg at time of death) on the following three occasions: a) by using a combination of fine-tipped forceps to pluck them off the sieve-like gill rakers (sensu Gudger 1941) and gently scraping a cotton gloved-hand over the surface of the gill rakers on 12 and 30 April, 2008 when the host was temporarily held in a small FRP vessel inside the sea pen for routine health inspections (Fig. 1A); and b) on 9 May, 2008 by post-mortem dissection of a portion of the 5th gill raker containing attached copepods. All specimens, including the *in situ* sample, were preserved in 70% ethanol. Five specimens from the 12 April collection were measured with an ocular micrometer after being soaked overnight in lactic acid. Measurements given are in millimeters unless stated otherwise and represent the range followed by the mean in parentheses. Another three specimens from the 12 April collection (designated specimen No. 1–3 in the text) were each dissected on a wooden slide (see Humes & Gooding 1964) and then carefully examined using an Olympus BX51 compound microscope equipped with Phase Contrast. All drawings were made with the aid of a drawing tube. Anatomical terminology follows Kabata (1979) and Huys & Boxshall (1991), and fish names conform to FishBase (Froese & Pauly 2010).

Wilson's (1944) and Williams & Williams' (1986) material of *D. atlanticus* deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., were also re-examined for comparative purposes: 15 adult female "paratypes" (USNM 78928), skin of *Rhinodon typicus* [sic], Havana, Cuba, collection date not provided on vial label, identified by C. B. Wilson (although the date was not written on the label, it is most likely identical to that of the subsequent lot); nine adult females (USNM 78975), skin

of *Rhinodon typicus* [sic], Havana, Cuba, 2 February, 1937, identified by C. B. Wilson; 173 adult females (USNM 228527), host name not provided on vial label, North Pacific Ocean, Japan, 1986, identified by R. F. Cressey (although the host name was not printed on the label and Dr. Roger Cressey had identified this material, we are confident that these specimens represent those collected by Williams & Williams (1986) as these authors: 1) duly acknowledged Dr. Cressey for confirming their identification of copepods from “*Rhincodon typhus* [sic]” as *D. atlanticus*; and 2) explicitly stated that 130 of an estimated 500–600 female *D. atlanticus* specimens were deposited at USNM)). Two specimens each from USNM 78928 and 228527 (designated in the text as specimen No. 4 & 5 and 6 & 7, respectively) were completely dissected for detailed examination.



**FIGURE 1.** Digital photographs showing: (A) whale shark No. 31 temporarily held in a FRP vessel offshore from Yamagawa Port, Motobu-cho, Japan, on 12 April, 2008 during a health inspection by M. Yanagisawa and his staff at the Okinawa Churaumi Aquarium; (B) *Prosaetes rhinodontis* (Wright, 1876) females attached to the gill rakers of whale shark No. 31 on 31 March, 2008; (C & D) same as (B) but on 12 April, 2008; (E) *P. rhinodontis* females attached *in situ* to a portion of the 5<sup>th</sup> gill raker that was removed posthumously from whale shark No. 31; and (F) the gill rakers of a whale shark not infected by *P. rhinodontis*. Scale bar in E = 2.00 mm.

## Results

### *Prosaetes rhinodontis* (Wright, 1876)

(Figs 2–4)

*Stasiotes rhinodontis* Wright, 1876: 584; Wilson 1907: 439; Wilson 1944: 533; Yamaguti 1963: 102; Heegaard 1972: 316; Boxshall & Halsey 2004: 848.

*Prosaetes rhinodontis* (Wright, 1876): Wilson 1907: 439; Yamaguti 1963: 128; Heegaard 1972: 316; Kabata 1979: 212; Kazachenko 2001: 16; Boxshall & Halsey 2004: 847.

nec *Dysgamus atlanticus* Steenstrup & Lütken, 1861: Wilson 1944: 531; Williams & Williams 1986: 209.

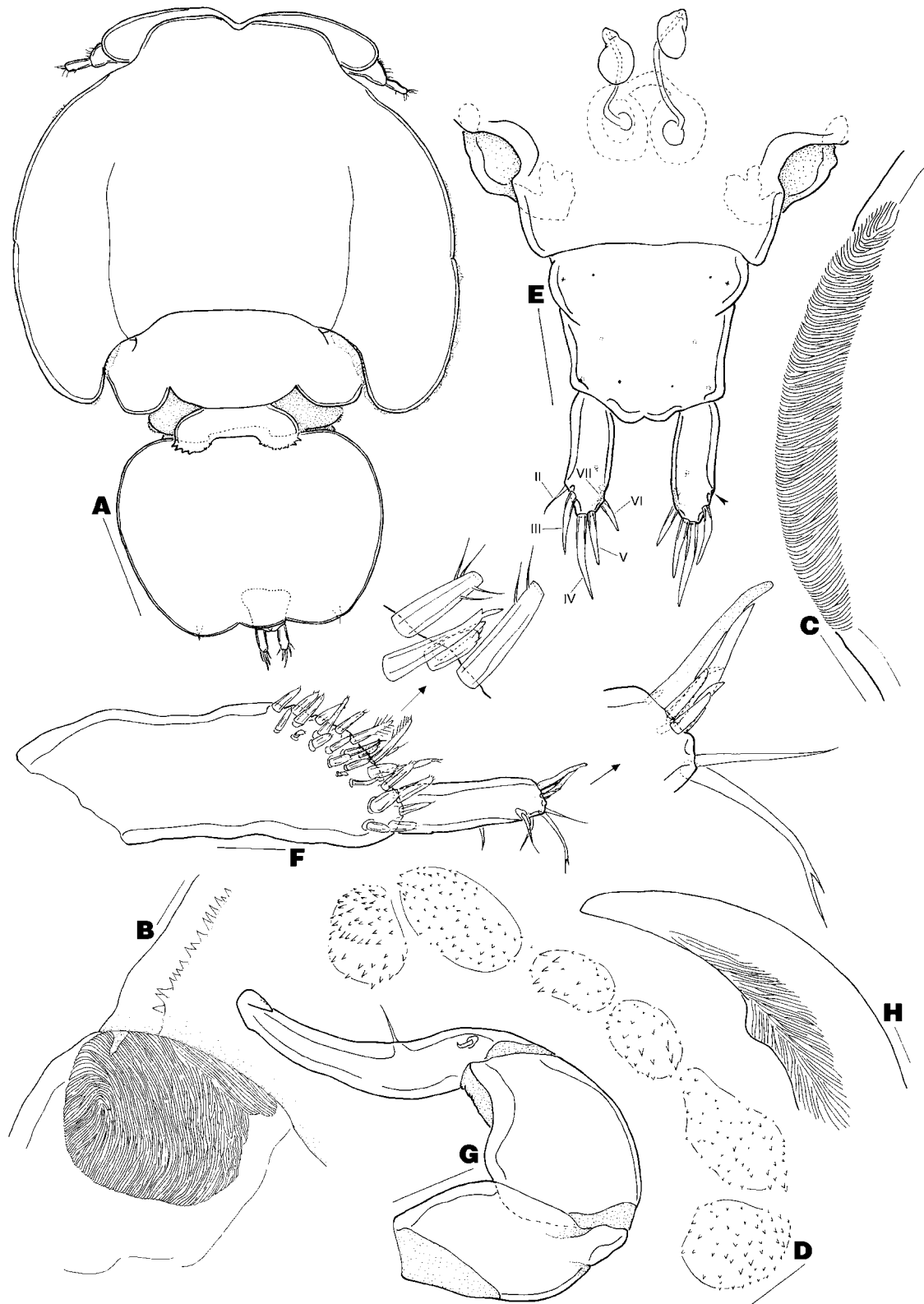
*Dysgamus rhinodontis* (Wright, 1876): Wilson 1944: 533; Yamaguti 1963: 102; Heegaard 1972: 316.

*Echthrogaleus pectinatus* Kirtisinghe, 1964: 89; Kabata 1979: 220; Pillai 1985: 196; Boxshall & Halsey 2004: 798.  
[New synonymy]

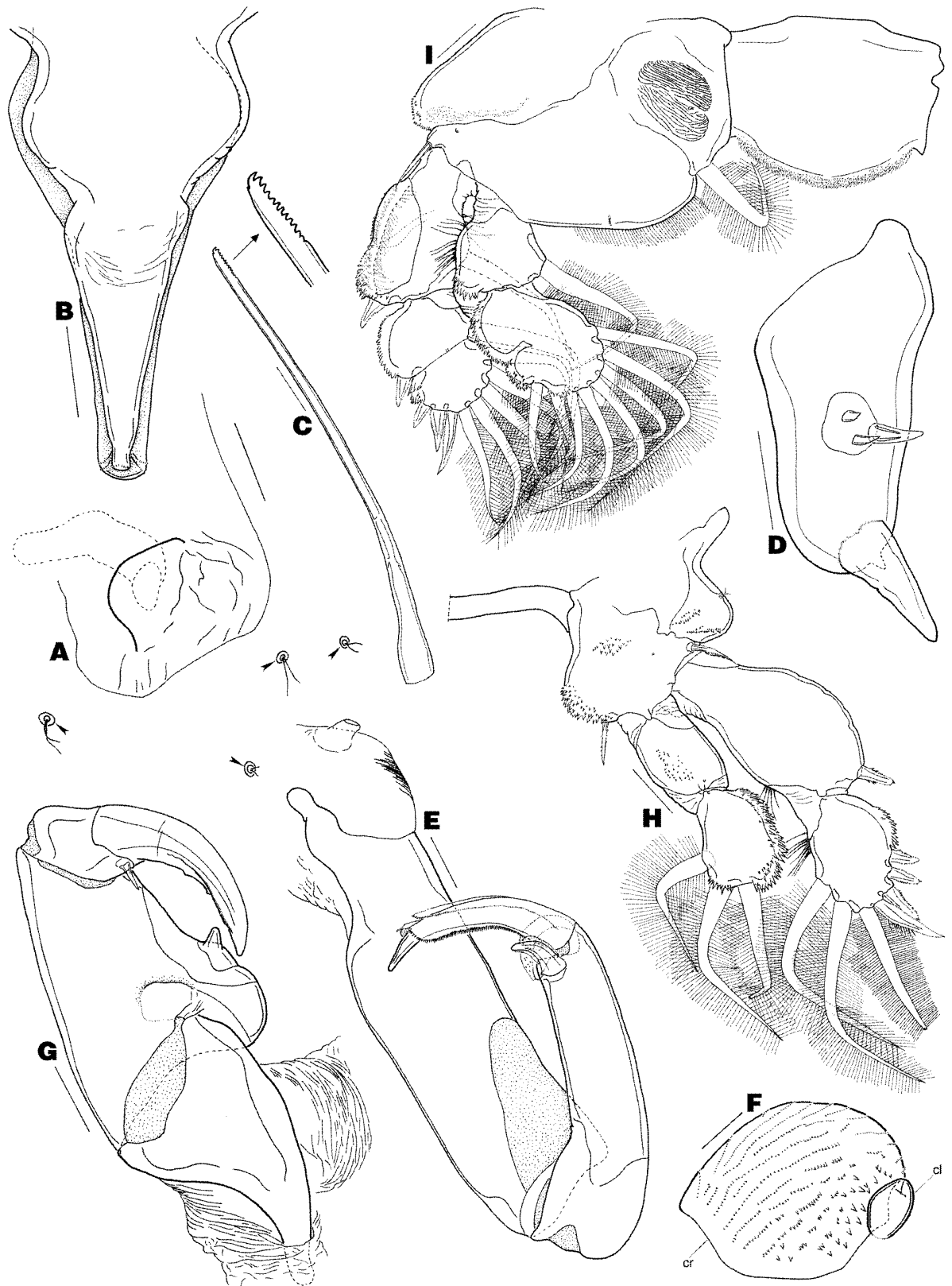
**Material examined.** A total of 121 adult females from 1 whale shark, *Rhincodon typus* Smith, captured alive on 7 November, 2007 in the western North Pacific Ocean, offshore from Umino Fishing Port, Chinen-son (26°11'N, 127°48'E), Okinawa-jima Island, Okinawa Prefecture, Japan, and then held in captivity from 8 November, 2007 to 9 May, 2008 by the Okinawa Churaumi Aquarium in the East China Sea, offshore from Yamagawa Port (26°40'N, 127°52'E), Motobu-cho, Okinawa-jima Island, Okinawa Prefecture, Japan: 53 adult females from live host on 12 April, 2008; 32 adult females from live host on 30 April, 2008; 36 adult females from dead host on 9 May, 2008. Twenty adult females (NSMT–Cr 21025) from the 12 April, 2008 sample are deposited in the Crustacea collection at the National Museum of Nature and Science (NSMT), Tokyo, Japan. The remaining specimens are kept in the personal collection of the authors.

**Redescription of adult female.** Total body length (excluding setae on caudal rami) 5.90–6.70 (6.14). Prosome (Fig. 2A) composed of dorsoventrally flattened cephalothorax (incorporating first pedigerous somite) and 1 free thoracic somite comprised of second and third pedigerous somites fused together. Paired frontal plates (Fig. 2A) well-developed, lacking lunules, and ventrally fused to anterior margin of cephalothorax but demarcated dorsally by posterior suture line. Cephalothorax, large, representing about 60% of total body length, wider than long [ $3.5\text{--}3.9$  (3.7)  $\times$   $3.9\text{--}4.3$  (4.11)], flattened dorsoventrally, slightly indented on mid-lateral margin, and dorsally divided into 3 zones (2 lateral and 1 cephalic-thoracic) by pair of longitudinal suture lines; each lateral zone with prominent posterior lobe typically extending to posterior margin of free thoracic somite; ornamented with weak marginal membrane, sensilla (not figured) on dorsal surface, adhesion pad (Fig. 2B) on anterolateral corners of ventral surface, and row of serrations (Fig. 2B) along ventrolateral surface. Free thoracic somite wider than long [ $0.95\text{--}1.05$  (1.01)  $\times$   $2.22\text{--}2.55$  (2.41)], with well-developed lateral plate, sensilla (not figured) on dorsal surface, and adhesion pad (Fig. 2C) on ventrolateral margin of each lateral plate. Urosome (Fig. 2A) comprised of fourth pedigerous somite, genital complex, and 1 free abdominal somite. Fourth pedigerous somite relatively small, wider than long [ $500\text{--}600$   $\mu\text{m}$  (545  $\mu\text{m}$ )  $\times$   $1.15\text{--}1.25$  (1.21)], with sensilla (not figured) on dorsal surface and strongly serrated posterodorsal plate (4 large and 3 small teeth on left side; 6 large, 2 small, and 2 minute teeth on right side); latter also grooved along posterior midline and typically extending over proximal margin of genital complex. Genital complex suborbicular, wider than long [ $1.85\text{--}2.15$  (1.95)  $\times$   $2.25\text{--}2.57$  (2.41)], dorsoventrally compressed, with small rounded posterolateral lobes, sensilla (not figured) on dorsal surface, transverse row of 6 denticulate patches (Fig. 2D) arranged in crescentic pattern at midline of anteroventral surface, and genital apertures (Fig. 2E) situated ventrally near junction of abdomen. Abdomen (Figs 2A, E) short, wider than long [ $375\text{--}400$   $\mu\text{m}$  (382.5  $\mu\text{m}$ )  $\times$   $387.5\text{--}425$   $\mu\text{m}$  (410  $\mu\text{m}$ )], concealed partially or entirely by genital complex, with several groups of pores and sensilla on dorsal and ventral surfaces. Caudal ramus (Fig. 2E) longer than wide [ $225\text{--}262.5$   $\mu\text{m}$  (240  $\mu\text{m}$ )  $\times$   $87.5\text{--}112.5$   $\mu\text{m}$  (102.5  $\mu\text{m}$ )], with 6 setae (seta I absent) and mid-dorsal sensillum; setae III–VI highly sclerotized; seta IV longest; all setae naked. Egg sacs (Fig. 1E) uniseriate, straight, not concealed by genital complex.

Antennule (Fig. 2F) 2-segmented; proximal segment longer than distal segment, armed with 28 spinulate and highly sclerotized setae (26 on ventrodorsal surface; 2 on dorsodorsal surface); distal segment slim, bears aesthetasc and 12 setae (seta on posterodorsal corner with bifurcate tip). Antenna (Fig. 2G) 3-segmented,



**FIGURE 2.** *Prosaetes rhinodontis* (Wright, 1876), adult female. (A) habitus, dorsal; (B) adhesion pad and serrations along left anterolateral margin of cephalothorax, ventral; (C) adhesion pad on right anterolateral margin of first free thoracic somite, ventral; (D) spinules on anteromedian surface of genital complex, ventral; (E) genital apertures, abdomen, and caudal rami (socket of missing seta indicated by arrowhead), ventral; (F) left antennule, with detail of elements near anterodistal margin of proximal segment and apical margin of distal segment, ventral; (G) right antenna, posterior; (H) tip of right antenna, ventral. Scale bars: A = 1.00 mm; B, C = 50  $\mu$ m, D, F = 100  $\mu$ m; E, G = 200  $\mu$ m; H = 25  $\mu$ m.



**FIGURE 3.** *Prosaetes rhinodontis* (Wright, 1876), adult female. (A) left postantennal process (setulate papillae indicated by arrowheads), ventral; (B) oral cone, anterior; (C) left mandible, with detail of distal end, anterior; (D) left maxillule, ventral; (E) left maxilla, posteroventral; (F) detail of clavus (cl) and crista (cr) from left maxilla, dorsal; (G) right maxilliped, posterior; (H) left leg 1, anterior; (I) right leg 2, anterior. Scale bars: A, C, D = 50  $\mu$ m; B, E, H, I = 100  $\mu$ m; F = 25  $\mu$ m; G = 200  $\mu$ m.

comprising coxa, basis, and 1-segmented endopod incorporating distal claw. Coxa unarmed but with inner distal sclerotized ridge; basis stout, unarmed; terminal segment uncinat, long, bears 1 shorter seta proximally and 1 longer seta about halfway and fine surface ridges (Fig. 2H) along inner distal margin. Postantennal process (Fig. 3A) rudimentary, represented by small obtuse sclerite on ventral surface of cephalothorax, with 4 setulate papillae located on adjacent surface. Oral cone (Fig. 3B) elongate, extending slightly beyond maxillary bases, bears several serrated membranes at tip. Mandible (Fig. 3C) modified into elongate stylet bearing outer distal tooth and 12 inner distal teeth. Maxillule (Fig. 3D) small, unilobate, with palp completely fused to praecoxal endite; former represented by 3 outer naked surface setae and latter with 2 unequal apical elements. Maxilla (Figs 3E–F), brachiform, 2-segmented, composed of elongate, unarmed syncoxa and slender basis; latter with inner subapical rounded, spinulate crista plus short, thumb-shaped clavus adjacent to its base and long apical calamus and short apical canna; calamus and canna each furnished with finely serrated membranes. Maxilliped (Fig. 3G) large, subchelate, 3-segmented (comprising protopod (corpus) and subchela consisting of free endopodal segment (shaft) and claw), and located on prominent pedestal. Corpus robust, with slightly raised protrusion on proximal region of posterior surface and well-developed spiniform process on myxal region; shaft short, with naked distal seta; claw elongate, recurved, with striated flange along inner margin and fine surface ridges (not figured) on anterodistal surface.

Legs 1–4 biramous (Figs 3H–I, 4A–B); leg 1 with bimerous rami; legs 2 and 3 with trimerous exopod and bimerous endopod; leg 4 rami incompletely 2-segmented. Armature on rami of legs 1–4 as follows (Roman numerals = spines; Arabic numerals = setae):

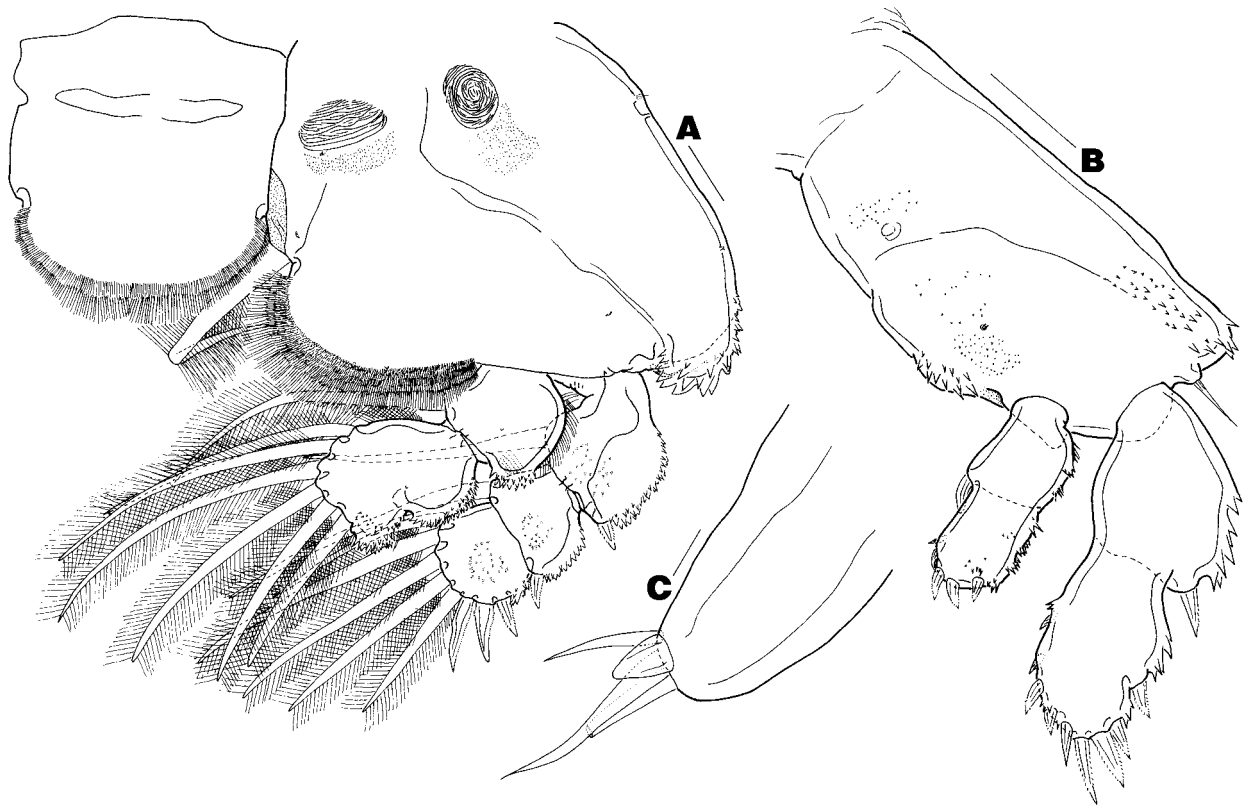
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-1	I-0; III,I,3	0-0; 3
Leg 2	0-1	1-0	I-1; I-1; II,I,5	0-1; 8
Leg 3	0-1	1-0	I-1; I-1; II,I,5	0-1; 6
Leg 4	0-0	1-0	I-0; III,I,V	0-I; I,I,III

Leg 1 (Fig. 3H) intercoxal sclerite naked and elongate. Protopodal segments with several denticulate patches; outer and inner setae on basis spiniform. Exopod longer than endopod, with setules along inner margin of both segments and relatively strong denticles along proximolateral margin of distal segment; all spines with serrulate margins. First endopodal segment with denticulate patch on anterior surface; terminal segment with relatively strong denticles along outer margin and at insertion point of middle seta. Leg 2 (Fig. 3I) intercoxal sclerite subquadrate, with numerous fine short spinules along distal margin. Coxa with denticles along outer margin, fine spinules on anterior surface, and large adhesion pad near inner margin. Basis with fine setules along inner distal margin; outer seta naked. Exopod with setules along inner margin of first two segments; proximal segment with minute triangular hyaline process on mid-lateral margin, denticles along outer margin of both anterior and posterior surfaces, and lateral row of setules along posterior surface; last two segments with strong denticles along outer margin; all spines with serrulate margins. Proximal endopodal segment with lateral setules and distolateral group of strong denticles; distal segment with mid-lateral indentation, setules along inner margin, and strong denticles along outer margin and at insertion point of second outermost seta.

Leg 3 (Fig. 4A) intercoxal sclerite large, with several rows of long stiff spinules along distal margin. Coxa with large denticles along distolateral margin and 2 sets of adhesion pads and fine spinules on anterior surface. Basis with numerous rows of progressively longer stiff setules along inner distal margin. Exopod with minute hyaline knob on anterior surface of proximal segment and setules along inner margin of first two segments; all segments with strong denticles along outer margin and on posterior surface; all spines with serrulate margins. Endopod ornamented as in leg 2, except without denticles at insertion point of second outermost seta. Leg 4 (Fig. 4B) lacking intercoxal sclerite and proximally fused to ventrolateral surface of somite. Coxa with strong denticles near distolateral margin and patch of fine spinules and nipple-like protuberance near inner margin. Basis with fine spinules near inner margin and strong denticles on inner distal corner. Exopod 1.5 times longer

than endopod, with larger denticles along outer margin of both segments and smaller denticles near insertion point of most spines on terminal segment. Endopod with small denticles along outer margin of both segments and scattered on anterior surface of terminal segment. Most spines on rami serrulate.

Leg 5 (Figs 2A, 4C) vestigial, unsegmented, situated on posteroventral surface of genital complex, bears stout spine and 3 naked setae apically. Leg 6 (not figured) rudimentary, represented by unarmed genital operculum at gonopore opening.



**FIGURE 4.** *Prosaetes rhinodontis* (Wright, 1876), adult female. (A) left leg 3, anterior; (B) left leg 4, anterior; (C) right leg 5, ventral. Scale bars: A, B = 100  $\mu$ m; C = 50  $\mu$ m.

**Adult male.** Unknown.

**Variability.** Specimen No. 1 with additional denticles between insertion point of each ramus on right leg 1, highly deformed exopod on left leg 2, and additional small patch of spinules on posterior surface of terminal endopodal segment of left leg 3. Specimen No. 2 lacking inner adhesion pad and 2 spinular patches on coxa of right and left leg 3 and having additional patch of denticles along proximal inner margin of basis and row of strong denticles along outer distal corner of first exopodal segment of right and left leg 1, additional short inner spine on proximal exopodal segment of right and left leg 4, and only 4 spines on terminal endopodal segment of left leg 4. Specimen No. 3 with 7 patches of denticles on anteromedian surface of genital complex, 8 teeth (6 large, 1 small, and 1 apically bifurcate) on left side and 8 teeth (5 large, 3 small) on right side of posterodorsal plate of fourth pedigerous somite, additional patch of denticles along proximal inner margin of basis of right and left leg 1, additional row of strong denticles along outer distal margin of first exopodal segment of right leg 1, only 3 spines and 4 setae on terminal exopodal segment of right leg 2, vestigial innermost seta on terminal endopodal segment of right leg 3, and additional short inner spine on proximal exopodal segment of right leg 4.

**Attachment site.** The copepod uses its antennae and maxillipeds to attach to the surface of the host's sieve-like gill rakers.



## Discussion

**Taxonomy.** Careful examination of our specimens and those of Wilson (1944) and Williams & Williams (1986) gathered from *Rhincodon typus* Smith revealed that all three samples contain individuals of the same species. Wilson described the carapace (= cephalothoracic shield) of his specimens as having two lateral lobes partially divided at the center, a short and narrow lobe at each posterior corner tipped with a small spine, and a median posterior lobe carrying a pair of dorsolateral plates. Based on our examination of his material, the lateral lobes (= lateral zones) are indeed superficially divided by a small mid-lateral constriction but are, nonetheless, confluent with the posterior lobes as described above, the posterior lobes are unarmed as described above (Wilson may have misinterpreted a fragment or fold of the marginal membrane as a spine), and the median posterior lobe actually represents the fused second and third pedigerous somites, which are, as a unit, free from the cephalothorax as described above. Wilson also misinterpreted the arthrodistal membrane connecting the antennal claw and basis as a distinct segment and overlooked many features described above such as the denticle patches on the anteroventral surface of the genital complex, 9 additional setal elements on the distal antennular segment, the proximal seta on the antennal claw, the well-developed spiniform process on the myxal area of the maxilliped corpus, ornamentation on the protopodal segments of legs 1–4, the outer and inner setae on leg 1 basis, the armature element on each protopodal segment of leg 2, the articulation between the second and third exopodal segments of legs 2 and 3, the outer element on the basis and middle exopodal segment of leg 3, and two setae on the caudal ramus. Wilson observed a rod-like seta on the lateral margin of the basal segment of the antenna, an apical element on the distal endopodal segment of leg 1, an outer element on both endopodal segments of leg 2 and the proximal endopodal segment of leg 3, and 5 additional outer elements on the proximal exopodal segment of leg 4, but no such structures were observed by us. Several variable features were noted in the two specimens dissected from Wilson's collection as follows: specimen No. 4 with 8 teeth (7 large, 1 small) on left side and 8 teeth (6 large, 1 small, and 1 minute) on right side of posterodorsal plate of fourth pedigerous somite and an additional short inner spine on the proximal exopodal segment of right and left leg 4 (also observed in specimens No. 2 and No. 3 described above); and specimen No. 5 with 8 teeth (6 large, 2 small) on left side and 8 teeth (7 large, 1 small) on right side of posterodorsal plate of fourth pedigerous somite and an additional spinulate patch on the posterior surface of the proximal exopodal segment of right leg 4. Williams & Williams' (1986) material agrees with our specimens in nearly all respects. However, some variability in the two specimens dissected from their collection was observed as follows: specimen No. 6 with 7 teeth (6 large, 1 minute) on left side and 8 teeth (7 large, 1 small) on right side of posterodorsal plate of fourth pedigerous somite, only 2 outer surface setae on the left maxillule, an additional seta on the distal endopodal segment of right leg 2, armature of II, I, 4 on the distal exopodal segment of right and left leg 3, and an additional spinulate patch on the posterior surface of the proximal exopodal segment of right leg 4; and specimen No. 7 with 10 teeth (1 large, 5 small, and 4 minute) on left side and 7 teeth (5 large, 2 small) on right side of posterodorsal plate of fourth pedigerous somite, additional setules along the proximal outer margin of the distal endopodal segment of right and left leg 1 and an additional spinulate patch on the posterior surface of the proximal exopodal segment of right and left leg 4. Collectively the specimens examined above conform well to Wright's (1876) original description and remarkably good illustrations of *Prosaetes rhinodontis*. The main differences between the material examined in this study and Wright's description, which we attribute to Wright's misinterpretations of morphological details in his material rather than to intra- or interspecific variation, involve the number of free thoracic somites (second and third pedigerous somites fused vs. free), the maxillary clavus (present vs. absent), and segmentation of legs 2 to 4 (exopod of legs 2 and 3 trimerous vs. bimerous; rami of leg 4 bimerous vs. unimerous). A close comparison of our material with the original cursory description and figures of *Echthrogaleus pectinatus* Kirtisinghe, 1964, a pandarid copepod species collected from a whale shark purchased at a fish market in Colombo, Sri Lanka (Kirtisinghe 1964), also indicated that this species is morphologically similar to *P. rhinodontis*. Both taxa share a similar body shape and tagmosis, strongly serrated posterodorsal plate on the free fourth pedigerous somite, rounded crista on the maxilla, and armature and segmentation of legs 1, 2 and 4 (leg 3 was not described nor illustrated by Kirtisinghe). Hence, there is

little doubt that *E. pectinatus* is conspecific with *P. rhinodontis*—as such the former taxon is treated herein as a junior synonym of the latter. It is now evident that *P. rhinodontis* is not only host specific to *R. typus* but is widely distributed, occurring in the Caribbean Sea, Indian Ocean, and western North Pacific Ocean. The latter is not unexpected considering the whale shark is a circumtropical and epipelagic species (Compagno 2001). In addition to *P. rhinodontis*, three other parasitic copepods have been reported from the whale shark: the lernaeopodid *Acespadia pomposa* Leigh-Sharpe, 1933 and the pandarids *Pandarus smithii* Rathbun, 1886 and *Pandarus rhincodonicus* Norman, Newbound & Knott, 2000 (Leigh-Sharpe 1933; Kensley & Grindley 1973; Norman *et al.* 2000).

Wright (1876) did not provide reasons for including *P. rhinodontis* in the Pandarina (= Pandaridae) but briefly commented that it resembled *Demoleus* Heller, 1865 based on Heller's (1865) work. According to Kabata (1979), the Pandaridae and Cecropidae Dana, 1849 are closely related groups since many features, such as the presence of three free thoracic somites, dorsal plates on one or more body somites, adhesion pads on the appendages and ventral body surface, and marginal serrations on the cephalothoracic shield, overlap between these two groups. Kabata further stated that the two families can be separated by the structure of the corpus (protopod) on the female maxilliped: it is slender in the Cecropidae but squat, with the subchela typically oriented at right angles to the long axis of the corpus when closed, in the Pandaridae. The latter feature is, however, not entirely consistent in the Pandaridae as females of *Dinemoura discrepans* Cressey, 1967 have a relatively slim maxilliped corpus (see Cressey 1967, fig. 205). We agree with Benz & Deets (1988) that a phylogenetic analysis combining representatives from both the Pandaridae and Cecropidae is needed to test the validity of separating these two families. Notwithstanding, *P. rhinodontis* is tentatively transferred at this juncture from the Pandaridae to Cecropidae based on its relatively slim maxilliped corpus. The host preference of *P. rhinodontis* also conforms well to the ecological life history trait of the Cecropidae—all members of this group are parasitic on epipelagic fishes (Kabata 1979; Benz & Deets 1988). Since Wilson's (1907) diagnosis of *Prosaetes* is imprecise, an amended diagnosis is provided below.

### ***Prosaetes* C. B. Wilson, 1907**

**Amended diagnosis.** Female body composed of caligiform cephalothorax incorporating first pedigerous somite only, first free thoracic somite comprising fused second and third pedigerous somites bearing well-developed lateral plate, second free thoracic somite consisting of fourth pedigerous somite bearing strongly serrated posterodorsal plate, suborbicular genital complex, and 1 free abdominal somite. Caudal ramus with 6 setae (seta I absent). Egg sacs uniseriate, straight. Paired frontal plates well-developed, without lunules. Antennule 2-segmented. Antenna 3-segmented, comprising coxa, basis, and 1-segmented endopod incorporating distal claw. Postantennal process vestigial. Oral cone elongate. Mandible modified into elongate stylet. Maxillule small, unilobate. Maxilla brachiform, 2-segmented, composed of syncoxa and basis; basis with crista and clavus in addition to calamus and canna. Maxilliped subchelate, comprising protopod and subchela consisting of free endopodal segment and claw. Leg 1 with 2-segmented rami. Legs 2 and 3 with 3-segmented exopod and 2-segmented endopod. Leg 4 rami incompletely 2-segmented. Leg 5 vestigial, unsegmented, situated on posteroventral surface of genital complex. Leg 6 rudimentary, represented by unarmed genital operculum. Male unknown. Parasite of the whale shark.

**Type and only known species.** *Stasiotes rhinodontis* Wright, 1876 by original designation.

Among the Cecropidae, *Prosaetes* shares 2 (vs. 3) free thoracic somites and relatively unmodified (vs. lamelliform) rami on legs 2–4 with *Cecrops* Leach, 1816, *Philorthagoriscus* Horst, 1897, and *Luetkenia* Claus, 1864. *Prosaetes* can be easily distinguished from these three genera, as well as *Entepherus* Bere, 1936 and *Orthagoriscicola* Poche, 1902, by the absence of a posteromedian sinus on the genital complex (slight indentation in *Cecrops*; highly indented in other genera), presence of a crista and clavus plus the usual calamus and canna on the maxillary basis (*Cecrops* and *Orthagoriscicola* possess a crista plus calamus and canna; other genera with digitiform clavus plus calamus and canna), and retention of many plesiomorphic features such as cylindrical caudal rami (rounded in other genera except *Philorthagoriscus*), 3 armature

elements on the reduced maxillulary palp (1–2 in other genera except *Philorthagoriscus*), well-developed plumose setae on legs 1–3 (leg setae greatly reduced in other genera), 3-segmented exopod on leg 2 (2-segmented in other genera), 8 setae on the distal endopodal segment of leg 2 (1 in *Orthagoriscicola*; 7 in other genera), 3-segmented exopod on leg 3 (1-segmented in *Orthagoriscicola*; 2-segmented in other genera), 6 setae on the distal endopodal segment of leg 3 (0 in *Orthagoriscicola*; 5 in *Entepherus*; 4 in other genera), incompletely 2-segmented rami in leg 4 (1-segmented in other genera), 9 elements on the distal exopodal segment of leg 4 (4 in *Orthagoriscicola*; 8 in *Philorthagoriscus*; 7 in other genera), and 5 elements on the distal endopodal segment of leg 4 (0 in *Orthagoriscicola*; 3 in *Cecrops* and *Philorthagoriscus*; 4 in other genera). A highly unusual feature exhibited by *Prosaetes* is the presence of 28 setae on the proximal antennulary segment, which diverges from the typical limit of 27 setae reported in the Cecropidae (see Benz & Deets 1988) and the majority of taxa in other caligiform groups (see Boxshall & Halsey 2004). This supernumerary state appears to be stable in *Prosaetes* as it was found in all dissected specimens examined in this study and has been reported, although infrequently, in other caligiform taxa [e.g., *Caligus longipedis* Bassett-Smith, 1898 and *Synestius caliginus* Steenstrup and Lütken, 1861 (see Ho & Lin 2004)].

**Neotype material.** A neotype (USNM 1138870) was selected from Williams & Williams' (1986) collection of 173 well-preserved, adult female specimens of *Prosaetes rhinodontis* deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Although Williams & Williams (1986) collected this material on 12 July, 1985 at the Okinawa Expo Memorial Park Aquarium (now named Okinawa Churaumi Aquarium), Japan, during a post-mortem examination of one *R. typus* specimen, historical records kept at this aquarium indicate that the host specimen was caught fortuitously on 10 July, 1985 in a net placed off the coast of Yonabaru-cho, southeastern Okinawa-jima Island (this whale shark was found dangling in the water with the caudal end entangled in the net near the surface and the opposite end bumping into the sea bottom), and then immediately transported alive, probably on a dump truck bed, to the aquarium. Based on this information we are certain that this whale shark specimen was infected with *P. rhinodontis* at the time of capture since it is highly unlikely that the large number of parasites (ca. 500–600 individuals), all at the adult stage, observed by Williams & Williams (1986) had accumulated on this host individual within a 3-day period. Further, the presence of a single pedunculate barnacle, *Conchoderma virgatum* (Spengler, 1790), with a capitular length of 6.0 mm, attached to the dorsal surface of a *P. rhinodontis* individual collected by Williams & Williams (1986) indicates that this whale shark was infected by *P. rhinodontis* approximately 3–60 days prior to its death considering that the growth rate for *C. virgatum* has been estimated to range from 0.1–1.9 mm capitular length per day (see Eckert & Eckert 1987). The type locality of the neotype is accordingly designated the western North Pacific Ocean, off Yonabaru-cho (26°11'N, 127°46'E), Okinawa-jima Island, Okinawa Prefecture, Japan, rather than the Okinawa Churaumi Aquarium.

Neotype specimen is a non-ovigerous adult female preserved in 70% ethanol, light tan in color, and 6.02 mm long. Posterodorsal plate on fourth pedigerous somite with 6 large teeth on left side and 7 large teeth on right side. Genital complex with spermatophore cemented to each copulatory pore. Terminal endopodal segment of left leg 2 with abnormal innermost seta. All other features, such as the body shape and tagmosis, ornamentation of the cephalothorax and genital complex, and construction and armature of appendages, as described above.

**Justification for neotype material.** Edward P. Wright was a competent Irish naturalist, qualified in medicine, a lecturer in Zoology (1858–1868) at Trinity College, Dublin, Ireland, and Curator of the herbarium (1870–1910) at Trinity College (Webb 1991). Prior to his latter appointment, Wright made a zoological expedition to the Seychelles in 1867, where he collected copepod samples from presumably two whale sharks which served as the basis for his description of *Prosaetes rhinodontis*. There is no indication that type specimens were deposited nor intended to be deposited in Wright's original description of *P. rhinodontis*. Our recent correspondence with Mr. Mark Holmes, Keeper of Crustacea at the National Museum of Ireland, confirmed that specimens of *P. rhinodontis* are indeed absent from Wright's crustacean collection housed at this museum.

A neotype is required for *P. rhinodontis* as confusion over the identity of this species has led to repeated

misidentifications of this parasite species and the spurious establishment of a new species for this taxon. We have verified that all extant material, including the neotype, of *P. rhinodontis* presently available for study (more than 300 specimens) conform to Wright's original description of this species. We anticipate that *P. rhinodontis* will be encountered more frequently in the immediate future due to the increasing number of whale sharks captured alive worldwide for display in public aquaria, high demand for whale shark products in Asia, and expansion of the whale shark ecotourism industry (see Colman 1997; Compagno 2001; Stevens 2007). The neotype and redescription provided herein of *P. rhinodontis* will, therefore, facilitate comparisons with future collections of this parasitic copepod from the whale shark.

Wright's original material of *P. rhinodontis* was collected from presumably two whale sharks harpooned in waters off the Seychelles. The neotype was collected, on the other hand, from the same fish species captured in the western North Pacific Ocean, off the southeastern coast of Okinawa-jima Island, Japan. Kirtisinghe's (1964) material of *P. rhinodontis* was collected considerably closer to the type locality, i.e. from a whale shark captured in the Indian Ocean off the coast of Colombo, Sri Lanka, but the whereabouts of his material remain unknown. Admittedly, selecting a neotype collected more than 8,000 km from the type locality is not ideal from a purist point of view. However, we believe it is warranted in this case since it is unlikely that new specimens of *P. rhinodontis* will be collected any time soon from the Seychelles, a country which recently afforded the whale shark the status of a protected species in Seychelles territorial waters under the auspices of "The Wild Animals (Whale Shark) Protection Regulations 2003" (see Rowat & Engelhardt 2007). In addition, we have established in this study that *P. rhinodontis* is a cosmopolitan and host specific parasite of the whale shark.

**Biology.** Some ectoparasitic copepod taxa are known to cluster together on their fish hosts in: a) single-file [i.e. the cephalothorax of one copepod is positioned underneath the genital complex of an anterior copepod (e.g., see Kabata (1979) for clustering of *Lepeophtheirus pectoralis* (Müller, 1776) females on the inner surface of the pectoral fins of a pleuronectid flatfish)]; b) staggered formation [i.e. the lateral margins of the cephalothorax of one copepod are wedged underneath the lateral margins of the genital complexes of two anterior copepods (e.g., see Benz (1981) for aggregations of *Pandarus satyrus* Dana, 1852 individuals (primarily females) on the pectoral fins of *Prionace glauca* (Linnaeus))]; or c) both single-file and staggered arrangements (e.g., see Dojiri & Cressey (1987) for clustering of *Taeniacanthodes gracilis* Wilson, 1935 individuals (mostly females) on the fins of *Paralichthys squamilentus* Jordan & Gilbert). Wilson (1907) and Kabata (1979) noted that large numbers of the cecropid *Orthagoriscicola muricatus* (Krøyer, 1837) tend to congregate on the skin of *Mola mola* (Linnaeus), but these authors did not mention the arrangement of individuals within the clusters. In this study we observed *P. rhinodontis* females aggregating together (arrowed in Figs 1B–D), albeit in an irregular pattern, mainly along the anterior margin of the sieve-like gill rakers of whale shark No. 31. Wright (1876), Kirtisinghe (1964), and Williams & Williams (1986) also found *P. rhinodontis* in the oral area of their respective whale shark specimen, but regrettably they did not provide details about the relative position of each copepod individual. Wilson's (1944) record of this parasite from the skin of the whale shark requires verification. Benz (1981) argued that the aggregative behavior exhibited by *P. satyrus* may be biologically beneficial in terms of maximizing the limited area at the optimal attachment site, protecting copepod individuals from predation, assisting hydrodynamically in copepod attachment, and increasing the frequency of mating encounters between the small number of males and the comparatively more numerous females. Aggregation of *P. rhinodontis* females probably does not facilitate their attachment to the host since they typically clustered in an asymmetrical (Fig. 1E) rather than staggered or single-file arrangement as noted above for *P. satyrus* and *L. pectoralis*, respectively. Despite the lack of *P. rhinodontis* males among the present and historical collections, we speculate that *P. rhinodontis* females strategically aggregate to augment their reproductive fitness as evidenced by the large proportion (75% or 27/36) of ovigerous females among the *in situ* sample. Whether or not the absence of *P. rhinodontis* males among the samples obtained thus far is direct evidence that males occupy a microhabitat different from that of females, an indication that males preferentially mate with late juvenile or immature adult females and rapidly die thereafter, or a reflection of the rarity of collection of this gender remain to be determined.

Cecropids are generally considered to be relatively sedentary copepods as evidenced by the reduction and/

or loss of leg setae in both sexes, their inability to swim when placed in an aquarium, and the localized development of a shallow depression on the gill filaments, deep lesion on the skin, or proliferation of host tissue typically associated with prolonged attachment and feeding activities of these parasitic copepods (Wilson 1907; Shiino 1965; Grabda 1973; Logan & Odense 1974; Kabata 1979, 1981; Benz & Deets 1988). In whale shark No. 31, the gill raker surface flanking *P. rhinodontis* individuals (Figs 1C–D) appears noticeably discolored, and in closer view slightly pinkish which most likely indicates epidermal tissue damage, as compared to the remaining gill raker area of this host individual and the monochromatic gill rakers of a whale shark free of *P. rhinodontis* (Fig. 1F). These observations suggest that *P. rhinodontis* not only grazes on the epithelium of the host's gill rakers, probably by using its mandibles to rasp the surface of host tissue as is typical for other caligiform copepods (Kabata 1974, 1982; Boxshall 2005), but also is, unlike other cecropids, relatively vagile. The latter is further substantiated by the fact that this parasite has well-developed plumose setae on legs 1–3 (Figs 3H–I, 4A), presumably for facilitating swimming movements, and no gross host tissue responses (i.e., swelling, epithelial hyperplasia, or connective tissue encapsulation) were visible in the area immediately surrounding the parasite's body (Fig. 1E).

**Whale shark husbandry.** Okinawa Churaumi Aquarium records show that whale shark No. 31 was placed with two other whale sharks in one (designated K-2) of three sea pens at the onset of its quarantine period on 8 November, 2007. The other two adjacent sea pens, K-1 and K-3, contained two whale sharks and one whale shark plus one giant manta ray (*Manta birostris* (Walbaum)), respectively. Whale shark No. 31 was subsequently transferred to K-1 on 11 December, 2007, and on 20 March, 2008 *P. rhinodontis* was detected for the first time in the oral region of this whale shark. This parasite was observed thereafter on whale shark No. 31 on 31 March, 12 April, 15 April, 29 April, 30 April, 2 May, and 9 May, 2008. The single whale shark (designated No. 16) held in K-3 died on 7 April, 2008; whale shark No. 31 was transferred to this sea pen on 12 April, 2008. On 8 May, 2008, one day before the death of whale shark No. 31, several *P. rhinodontis* individuals were observed for the first time in the oral area of two other captive whale sharks, one (designated No. 29) held in K-1 and the other (designated No. 30) in K-2. *Prosaetes rhinodontis* was not found on the giant manta ray held in K-3 at any time during the captivity period of whale shark No. 31. Based on this information and the fact that *P. rhinodontis* most likely has a direct life cycle typical of most copepods utilizing fish hosts (see Boxshall 2005), it appears that whale shark No. 31 was most likely infected with *P. rhinodontis* at time of capture and was accordingly the source of *P. rhinodontis* individuals that subsequently colonized whale shark No. 29 and No. 30. However, whale shark No. 29 and No. 30 being independently infected by *P. rhinodontis* at time of capture or transmission of *P. rhinodontis* from either whale shark No. 29 or No. 30, or both of these sharks, to whale shark No. 31 cannot be discounted.

The whale shark is a filter-feeder, employing both ram and suction filter-feeding behaviors to capture planktonic and nektonic prey, such as crab larvae, krill, copepods, sardines and anchovies, on its gill rakers (Clark & Nelson 1997; Colman 1997; Compagno 2001; Taylor 2007). In association with this feeding habit, whale sharks in the wild have been observed to occasionally cough underwater, apparently as a mechanism to remove accumulated food particles from the gill rakers (Colman 1997; Taylor 2007). Whale sharks held in captivity by the Okinawa Churaumi Aquarium exhibit a similar erratic coughing behavior (casual observations of M. Y.). Whale shark No. 31 in particular was observed coughing noticeably frequently, however, during periods of heavy infection by *P. rhinodontis* (casual observations of M. Y.), which may represent a sign of irritation, presumably in response to the parasite's feeding and attachment activities on the gill rakers. As a caveat, we urge veterinary and husbandry staff overseeing whale sharks at public aquaria to regularly examine the oral cavity of these animals for *P. rhinodontis* during and after a lengthy quarantine period to prevent the inadvertent introduction of this parasite into display aquaria, particularly considering that this parasite can survive in an aquarium setting (see Williams & Williams 1986), can persist on captive whale sharks for a relatively lengthy period, has the ability to proliferate amongst captive whale sharks, has the potential to cause undue stress to captive whale sharks, and in view of its infection site, may reduce the feeding efficiency of a heavily infected whale shark. Further, treatment protocols to control or eradicate this parasite have not yet been developed.

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## References

- Benz, G.W. (1981) Observations on the attachment scheme of the parasitic copepod *Pandarus satyrus* (Copepoda: Pandaridae). *Journal of Parasitology*, 67, 966–967.
- Benz, G.W. & Deets, G.B. (1988) Fifty-one years later: an update on *Entepherus*, with a phylogenetic analysis of Cecropidae Dana, 1849 (Copepoda: Siphonostomatoida). *Canadian Journal of Zoology*, 66, 856–865.
- Boxshall, G.A. (2005) Crustacean parasites. Copepoda. In: Rohde, K. (Ed.), *Marine Parasitology*. CSIRO Publishing, Collingwood, pp. 123–138.
- Boxshall, G.A. & Halsey, S.H. (2004) *An Introduction to Copepod Diversity*. The Ray Society, London, 966 pp.
- Clark, E. & Nelson, D.R. (1997) Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes*, 50, 63–73.
- Colman, J.G. (1997) A review of the biology and ecology of the whale shark. *Journal of Fish Biology*, 51, 1219–1234.
- Compagno, L.J.V. (2001) *Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO Species Catalogue for Fishery Purposes, FAO, Rome, 269 pp.
- Cressey, R.F. (1967) Revision of the family Pandaridae (Copepoda: Caligoida). *Proceedings of the United States National Museum*, 121, 1–133.
- Dojiri, M. & Cressey, R.F. (1987) Revision of the Taeniacanthidae (Copepoda: Poecilostomatoida) parasitic on fishes and sea urchins. *Smithsonian Contributions to Zoology*, 447, 1–250.
- Eckert, K.L. & Eckert, S.A. (1987) Growth rate and reproductive condition of the barnacle *Conchoderma virgatum* on gravid leatherback sea turtles in Caribbean waters. *Journal of Crustacean Biology*, 7, 682–690.
- Froese, R. & Pauly, D. (2010) FishBase. World Wide Web electronic publication. Available from <http://www.fishbase.org/> (accessed 23 February 2010)
- Grabda, J. (1973) Contribution to knowledge of biology of *Cecrops latreillii* Leach, 1816 (Caligoida: Cecropidae) the parasite of the ocean sunfish *Mola mola* (L.). *Acta Ichthyologica et Piscatoria*, 3, 61–74.
- Gudger, E.W. (1941) The feeding organs of the whale shark, *Rhincodon typus*. *Journal of Morphology*, 68, 81–99.
- Heegaard, P. (1972) Caliginae and Euryphorinae of the Dana expedition (Crustacea: Copepoda: Caligidae). *Steenstrupia*, 2, 295–317.
- Heller, C. (1865) Crustacean. Reise der Oesterreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. *Zoologischer Theil*, 2, 1–280, pls. 1–25.
- Ho, J.S. & Lin, C.L. (2004) *Sea lice of Taiwan*. The Sueichan Press, Keelung, 388 pp.
- Humes, A.G. & Gooding, R.U. (1964) A method for studying the external anatomy of copepods. *Crustaceana*, 6, 238–240.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
- International Code of Zoological Nomenclature. (1999) *Fourth edition*. The International Trust for Zoological Nomenclature, London, 306 pp.
- Jan, G. (1862) Enumerazione sistematico delle species d'ofidi del gruppo Calamaridae. *Archivio per la Zoolia, l'Anatomia e la Fisiologia*, 2, 1–76.
- Kabata, Z. (1974) Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. *Journal of the Fisheries Research Board of Canada*, 31, 1583–1588.

- Kabata, Z. (1979) *Parasitic Copepoda of British fishes*. The Ray Society, London, 468 pp.
- Kabata, Z. (1981) Copepoda (Crustacea) parasitic on fishes: problems and perspectives. *Advances in Parasitology*, 19, 1–71.
- Kabata, Z. (1982) The evolution of host-parasite systems between fishes and Copepoda. In: Mettrick, D.F. & Desser, S.S. (Eds.), *Parasites – their world and ours*. Elsevier Biomedical Press, Amsterdam, pp. 203–212.
- Kazachenko, V.N. (2001) *Opredelitel' semeĭstv i rodov paraziticheskikh kopepod (Crustacea: Copepoda) ryb: Monografiia*. Dal'nevostochnyi Gosudarstvennyi Tekhnicheskii Rybokhoziaĭstvennyi Universitet, Vladivostok, 253 pp. [in Russian]
- Kensley, B. & Grindley, J.R. (1973) South African parasitic Copepoda. *Annals of the South African Museum*, 62, 69–130.
- Kirtisinghe, P. (1964) A review of the parasitic copepods of fish recorded from Ceylon, with description of additional forms. *Bulletin of the Fisheries Research Station, Sri Lanka (Ceylon)*, 17, 45–132.
- Leigh-Sharpe, W.H. (1933) *Acespadiapomposa* n. g. et sp., a parasitic copepod of *Rhincodon typicus*. *Parasitology*, 25, 480–482.
- Logan, V.H. & Odense, P.H. (1974) The integument of the ocean sunfish (*Mola mola* L.) (Plectognathi) with observations on the lesions from two ectoparasites, *Capsala martinieri* (Trematoda) and *Philorthagoriscus serratus* (Copepoda). *Canadian Journal of Zoology*, 54, 1039–1045.
- Norman, B.M., Newbound, D.R. & Knott, B. (2000) A new species of Pandaridae (Copepoda), from the whale shark *Rhincodon typus* (Smith). *Journal of Natural History*, 34, 355–366.
- Pillai, N.K. (1985) *The Fauna of India. Parasitic Copepods of Marine Fishes*. Zoological Survey of India, Calcutta, 900 pp.
- Rowat, D. & Engelhardt, U. (2007) Seychelles: A case study of community involvement in the development of whale shark ecotourism and its socio-economic impact. *Fisheries Research*, 84, 109–113.
- Shiino, S.M. (1965) On *Cecrops exiguus* Wilson found in Japan. *Report of the Faculty of Fisheries, Prefectural University of Mie*, 5, 381–390.
- Stevens, J.D. (2007) Whale shark (*Rhincodon typus*) biology and ecology: A review of the primary literature. *Fisheries Research*, 84, 4–9.
- Taylor, J.G. (2007) Ram filter-feeding and nocturnal feeding of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Fisheries Research*, 84, 65–70.
- Webb, D.A. (1991) The herbarium of Trinity College, Dublin: its history and contents. *Botanical Journal of the Linnean Society*, 106, 295–327.
- Williams, E.H. & Williams, L.B. (1986) The first association of *Conchoderma virgatum* (Spengler) (Cirripedia: Thoracica) with a euryphorid copepod in the mouth of a fish. *Galaxea*, 5, 209–211.
- Williams, K.L. & Wallach, V. (1989) *Snakes of the World: Synopsis of Snake Generic Names*. Krieger Publishing Co., Malabar, 234 pp.
- Williams, K.L. & Wilson, L.D. (1967) A review of the colubrid snake genus *Cemophora* Cope. *Tulane Studies in Zoology*, 13, 103–124.
- Wilson, C.B. (1907) North American parasitic copepods belonging to the family Caligidae. Parts 3 and 4. A revision of the Pandarinae and the Cecropinae. *Proceedings of the United States National Museum*, 33, 323–490, pls. 17–43.
- Wilson, C.B. (1944) Parasitic copepods in the United States National Museum. *Proceedings of the United States National Museum*, 94, 529–582, pls. 20–34.
- Wright, E.P. (1876) A new genus and species belonging to the family Pandarina. *Proceedings of the Royal Irish Academy*, 2, 583–585, pl. 35.
- Yamaguti, S. (1963) *Parasitic Copepoda and Branchiura of Fishes*. Interscience Publishers, New York, 1104 pp.