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A new species of copepod (Siphonostomatoida: Caligidae) parasitic on the tiger shark *Galeocerdo cuvier* (Péron & Lesueur) from Western Australian waters

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Abstract

A new species of sea-louse (Caligidae, Siphonostomatoida), *Caligus oculicola* n. sp., is described from the eye surface of the tiger shark *Galeocerdo cuvier* from off the northwestern coast of Australia. This copepod is distinguished from its congeners by a combination of characters that include: (i) a bifid, dentiform process of the maxillule; (ii) a sternal furca with a box longer than wide and diverging, truncate tines; (iii) terminal spines 1 to 3 on the last segment of leg 1 exopod, each with serrate margins and an accessory process (accessory process on the spines extending beyond the tip of the spine itself); and (iv) a two-segmented exopod of leg 4 with an armature formula of I-0; III. This is the first description of a caligid copepod collected from a shark host in Western Australian waters. The host-parasite relationships between *Caligus oculicola* and its elasmobranch host are discussed.

Introduction

Although some members of *Caligus* Müller, 1785 have been reported from elasmobranch hosts, this genus is considered predominantly parasitic on marine teleost fishes (Kabata, 1979). The relationship between *Caligus* and elasmobranch species is ill-defined, since reports of *Caligus* collected from elasmobranchs are uncommon, the specific attachment site on the host is infrequently reported, infection parameters are rarely provided, the early infective stages (copepodid and chalimus) have not been found on any elasmobranch, and there is no *Caligus* species that has been repeatedly collected from one particular elasmobranch species. As a consequence, reports of *Caligus* from elasmobranchs are often regarded by parasitologists as ‘accidental’ or ‘fortuitous’ infections, indicating a very loose or ephemeral association between the copepod and its host.

Of the more than 250 recognised *Caligus* species, only 17 have been reported from elasmobranchs (Table 1). It must be emphasised that 13 of the 17 species listed, namely *C. alalongae*, *C. belones*, *C. chelifer*, *C. coryphaenae*, *C. curtus*, *C. elongatus*, *C. latigenitalis*, *C. praetextus*, *C. productus*, *C. punctatus*, *C. quadratus*, *C. rufimaculatus* and *C. willungae*, have been reported in the literature from various teleost hosts as well. Furthermore, *C. chiloscyllii* has been collected from two teleost hosts, the six-lined trumpeter *Pelates sexlineatus* (Quoy & Gaimard) and the barfaced sandsmelt *Parapercis nebulosa* (Quoy & Gaimard), in Shark Bay, Western Australia (Tang, unpublished data). During a biological survey of pelagic sharks conducted in July, 1997 along the Western Australian coastline (Newbound & Knott, 1999), one of us (DRN) collected *Caligus* specimens from tiger sharks *Galeocerdo cuvier* (Péron & Lesueur). These specimens represent a new species, which is described below. In addition, we discuss the host-parasite relationship between this new copepod and its elasmobranch host.

Materials and methods

Tiger sharks were caught along the Western Australian coastline, from west of the Montebello Islands (20°28′25 S, 115°24′24 E) to west of the Peron Peninsula (22°51′75 S, 113°14′89 E), Shark Bay, using set-line fishing with hooks. Sharks were examined for

Table 1. Species of *Caligus* (in alphabetical order) reported from elasmobranch hosts.

Caligus spp.	Host	Reference
C. alalongae Krøyer, 1863	*Mobula rochebrunei* (Vaillant)	Margolis et al. (1975)
C. belones Krøyer, 1863	*Raja batis* Linnaeus [= *Dipterus batis* (Linnaeus)]	Margolis et al. (1975)
C. chelifer Wilson, 1905	*Mustelus canis* (Mitchill)	Benz (1986)
C. chiloscyllii Pillai, 1967	*Chiloscyllium indicum* (Gmelin)	Pillai (1985)
C. coryphaenae Steenstrup & Lütken, 1861	*Isurus oxyrinchus* Rafinesque *Squalus acanthias* Linnaeus	Kabata (1979)
C. curtus Müller, 1785	*Raja batis* Linnaeus [= *Dipturus batis* (Linnaeus)] *R. clavata* Linnaeus *R. fullonica* Linnaeus [= *Leucoraja fullonica* (Linnaeus)] *R. laevis* Mitchill [= *Dipturus laevis* (Mitchill)] *R. maculata* Shaw [= *Narcine maculata* (Shaw)] *R. montagui* Fowler *R. naevus* Müller & Henle [= *Leucoraja naevus* (Müller & Henle)] *R. oxyrhynchus* Linnaeus [= *Dipturus oxyrhynchus* (Linnaeus)] *R. radiata* Donovan [= *Amblyraja radiata* (Donovan)] *Squalus acanthias* Linnaeus	Parker et al. (1968), Kabata (1979)
C. dasyaticus Rangnekar, 1957	*Amphotistius kuhlii* (Müller & Henle) [= *Dasyatis kuhlii* (Müller & Henle)] *Dasyatis akajei* (Müller & Henle) *Dasyatis uarnak* (Forsskål) [= *Himantura uarnak* (Forsskål)] *Pristis* sp.	Pillai (1985)
C. elongatus Nordmann, 1832	*Alopias vulpinus* (Bonnaterre) *Squalus littoralis* Lesueur [= *Carcharias taurus* Rafinesque] *Dasyatis centroura* (Mitchill) *Raja batis* Linnaeus [= *Dipturus batis* (Linnaeus)] *R. brachyura* Lafont *R. clavata* Linnaeus *R. erinacea* Mitchill [= *Leucoraja erinacea* (Mitchill)] *R. laevis* Mitchill [= *Dipturus laevis* (Mitchill)] *R. montagui* Fowler *R. naevus* Müller & Henle [= *Leucoraja naevus* (Müller & Henle)] *R. ocellata* Mitchill [= *Leucoraja ocellata* (Mitchill)] *R. radiata* Donovan [= *Amblyraja radiata* (Donovan)] *Squalus acanthias* Linnaeus	Parker (1969), Margolis et al. (1975), Kabata (1979)
C. furcisetifer Redkar, Rangnekar & Murti, 1949	*Sphyrna blochii* (Cuvier) [= *Eusphyra blochii* (Cuvier)] *Pristis* sp.	Margolis et al. (1975), Pillai (1985)
C. latigenitalis Shiino, 1954	*Mustelus manazo* Bleeker *Rhinobatus schlegelii* Müller & Henle	Margolis et al. (1975)
C. praetextus Bere, 1936	*Dasyatis sabina* Lesueur *Raja eglanteria* Bosc	Margolis et al. (1975)
C. productus Dana, 1852	*Prionace glauca* (Linnaeus)	Benz (1986)
C. punctatus Shiino, 1955	*Triakis scyllium* Müller & Henle	Margolis et al. (1975)
C. quadratus Shiino, 1954	*Rhinobatus schlegelii* Müller & Henle	Margolis et al. (1975)
C. rufimaculatus Wilson, 1905	*Mobula* sp. *Rhinobatus lentiginosus* Garman	Margolis et al. (1975)
C. torpedinis Heller, 1865	*Torpedo* sp.	Margolis et al. (1975)
C. willungae Kabata, 1965	Unidentified elasmobranchs	Margolis et al. (1975)

copepods immediately after retrieval. Copepods were removed from the hosts using fine point forceps, stored in seawater for a 10 h period and then preserved in 80% ethanol. Specimens were later cleared in 85% lactic acid for at least 24 h before measurements were taken with an ocular micrometer. Measurements given are the mean followed by the range in parentheses. Selected specimens were then dissected according to the wooden slide procedure of Humes & Gooding (1964). Drawings were made with the aid of a drawing tube attached to an Olympus BH-2 compound microscope.

Order Siphonostomatoida Burmeister, 1835
Family Caligidae Burmeister, 1835
Genus *Caligus* Müller, 1785

Caligus oculicola **n. sp.**

Material examined

Twenty-seven ♀♀ and 8 ♂♂ collected from the eye surface of tiger sharks *Galeocerdo cuvier* captured in July, 1997 between Exmouth and Shark Bay, Western Australia. Ten ♀♀ and 7 ♂♂ collected from *G. cuvier* captured in September 1998 between Exmouth and Shark Bay, Western Australia. Holotype female (WAM C33229), allotype (WAM C33230), 8 female paratypes (WAM C33231-C33233) and 3 male paratypes (WAM C33234-C33236) deposited in the Western Australian Museum. Four female and 3 male paratypes (BMNH 2004.50-56) also deposited in The Natural History Museum, London.

Etymology: The specific name combines two Latin words: *ocul* meaning eye, and *colus* meaning inhabit. It alludes to the specific infection site of this sea-louse.

Description (Figures 1–4)

Female

Body as in Figure 1A. Total length (excluding setae on caudal rami) 4.37 (4.21–4.68) mm based on 9 specimens. Cephalothoracic shield suboval, 2.98 (2.83–3.23) mm long and 2.42 (2.32–2.60) mm wide (excluding marginal membrane); dorsal surface of shield ornamented with setules; tips of antennae not extending beyond widest margin of cephalothoracic shield; posterior margin of thoracic zone extends beyond posterior limit of lateral zone. Frontal plate well developed with moderate-sized lunules. Fourth pedigerous segment much broader than long, 0.13 (0.12–0.16) × 0.67 (0.62–0.73) mm. Genital complex wider than long, 0.95 (0.85–1.12) × 1.35 (1.19–1.50) mm; dorsal and ventrolateral surfaces ornamented with setules and slightly produced at posterior corners. Abdomen (Figure 1B) 1-segmented, of almost equal length and width, 0.34 (0.24–0.41) × 0.35 (0.31–0.40) mm, narrower anteriorly, ornamented with 6 setules on dorsal surface and 1 pair of setules on ventral surface. Caudal ramus (Figure 1B) longer than wide, 0.21 (0.18–0.24) × 0.15 (0.14–0.17) mm, with strongly slanted anterior border and bearing inner row of setules, 3 short and 3 long pinnate setae and 1 dorsal setule.

Antennule (Figure 1C) 2-segmented; first segment stout, carrying 2 anterodorsal and 27 anteroventral plumose setae; second segment (Figure 1D) short, armed with 1 subapical seta on posterior margin and 11 setae (2 sharing common base) plus 2 aesthetascs on distal margin. Antenna (Figure 1E) 4-segmented; first segment unarmed; second segment with blunt posteriorly-directed process; third segment stout, unarmed; terminal segment a curved claw bearing 2 setae (proximal seta borne on papilla). Postantennal process (Figure 1F) stout, slightly curved, pointed, with 2 basal papillae each bearing single setule and another papilla carrying setule near base of process. Mandible (Figure 1G) separated into 4 parts by 3 annulations; terminal part bears transparent membrane on lateral margin and 12 teeth on medial margin. Maxillule (Figure 1H) consists of papilla bearing 3 setae and wide dentiform process which is bifid terminally; lateral tine wider than medial tine. Maxilla (Figure 2A) 2-segmented and brachiform; proximal segment elongate and unarmed; distal segment slender and elongate with subapical striated membrane (flabellum) and 2 unequal apical elements (calamus and canna); canna approximately two-thirds length of calamus; both elements ornamented with strips of serrate membrane along edges. Maxilliped (Figure 2B) strongly developed, subchelate; corpus long and unarmed; shaft carrying 1 small, subterminal naked seta and 1 small, terminal naked seta on ventral surface; claw curved with conspicuous seta at base. Sternal furca (Figure 2C) with relatively slender box, longer than wide; tines diverging and truncate at tip.

Armature on rami of legs 1–4 as follows (Roman and Arabic numerals indicating spines and setae, respectively):

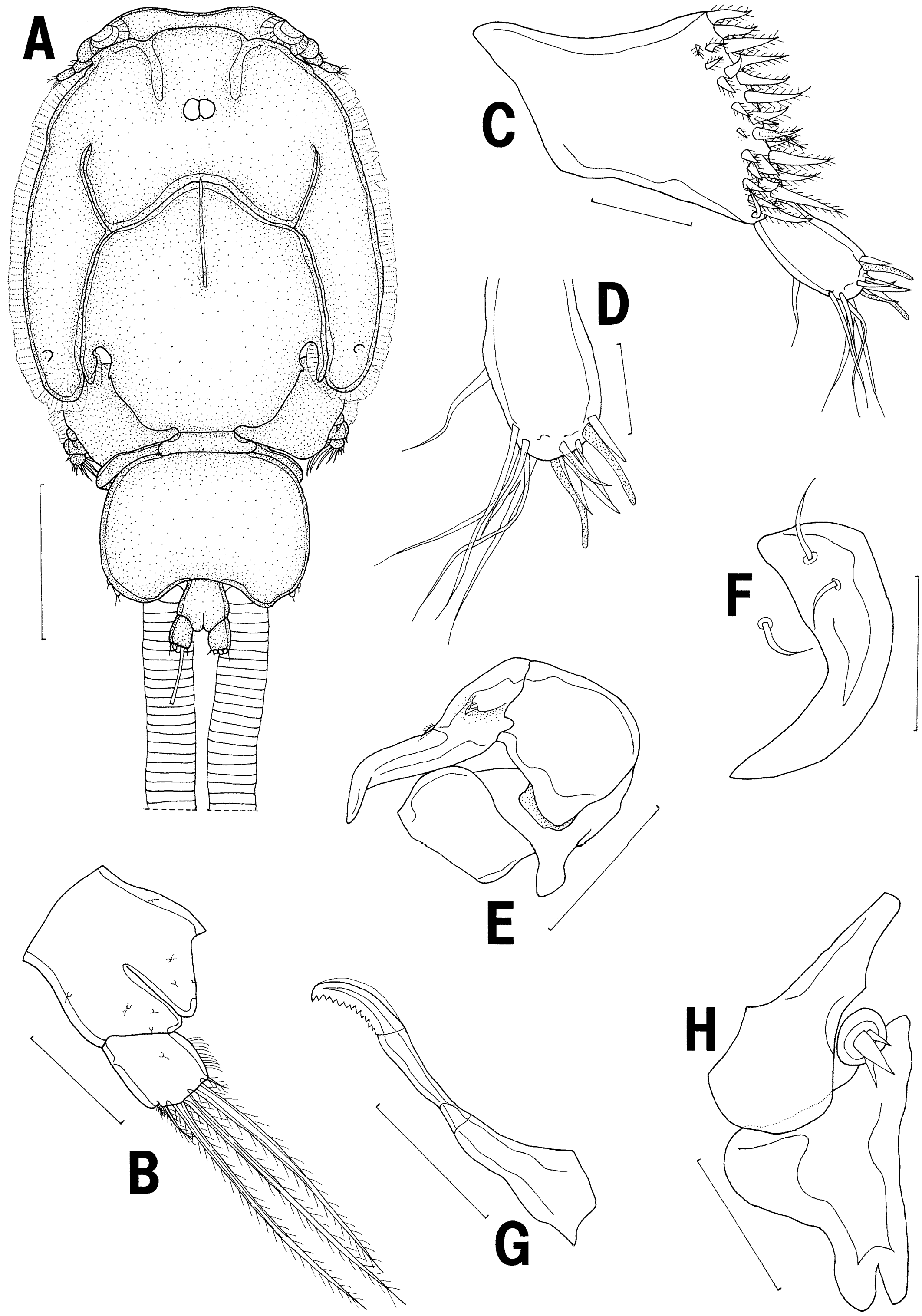

Figure 1. Caligus oculicola n. sp. Adult female: A. habitus, dorsal; B. abdomen and caudal ramus, ventral; C. antennule, ventral; D. second segment of antennule, ventral; E. antenna, ventral; F. postantennal process, ventral; G. mandible, ventral; H. maxillule, ventral. *Scale-bars*: A, 1.00 mm; B, 0.40 mm; C,F-H, 0.10 mm; D, 0.05 mm; E, 0.20 mm.

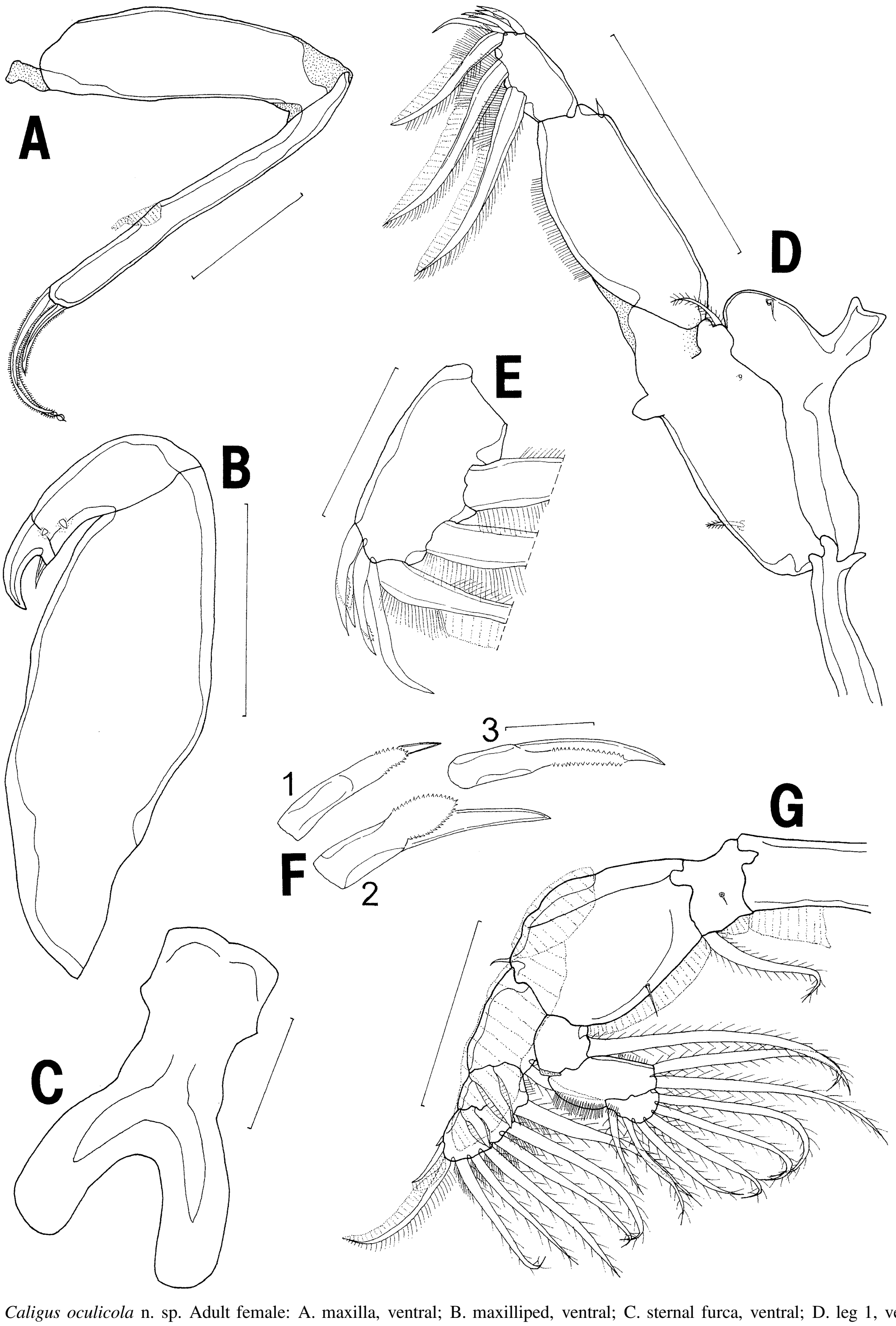

Figure 2. Caligus oculicola n. sp. Adult female: A. maxilla, ventral; B. maxilliped, ventral; C. sternal furca, ventral; D. leg 1, ventral; E. terminal exopodal segment of leg 1, ventral; F. serrate apical spines (1, spine 1; 2, spine 2; 3, spine 3), each with an accessory process, on second exopodal segment of leg 1, dorsal; G. leg 2, ventral. *Scale-bars*: A,B, 0.20 mm; C,E, 0.10 mm; D, 0.30 mm; F, 0.025 mm; G, 0.40 mm.

	Exopod	Endopod
Leg 1	I-0; III, 1, 3	vestigial
Leg 2	I-1; I-1; II, 1, 5	0–1; 0–2; 6
Leg 3	I-0; I-1; III, 4	0–1; 6
Leg 4	I-0; III	absent

Leg 1 (Figure 2D) sympod with 1 anterolateral setule, 1 mid-lateral and 1 inner pinnate seta, and small integumental pore on mid-ventral surface; first segment of exopod with small distolateral spine and row of setules on posterior margin; second exopodal segment (Figure 2E) bears 3 apical spines (first spine positioned dorsal to second), 1 long naked seta and 3 large posterior, pinnate setae; each apical spine (Figure 2F) bears serrate margins and accessory process; accessory process on spines extends beyond tip of spine itself; first spine shorter than second and third; each posterior seta with dense proximal fringe of setules and distal striated membrane on outer edge, and short proximal setules and long distal setules on inner edge. Endopod represented by small, unarmed lobe. Leg 2 (Figure 2G) coxa bears 1 large plumose seta on posterior margin and 1 setule on ventral surface; basis with small naked seta on outer edge, long setule on posterior margin and striated membrane along posterior edge; striated membranes cover outer margin of basis and exopod segments. Exopod (Figure 3A) 3-segmented; first and second segments each with 1 large outer spine, 1 inner plumose seta and row of setules on inner margin; both spines with flange on outer and inner margins and extending diagonally across ventral surface of second and third segments; seta on second segment with fringe of dense setules on proximal outer edge; terminal segment with 1 small outer spine, 1 spine with striated membrane along inner margin, 1 long terminal seta with striated membrane along outer margin and setules on inner margin, and 5 plumose setae with fringe of dense setules on proximal outer edge. First endopodal segment with long plumose seta (Figure 2G); second endopodal segment with several rows of setules on outer margin and row of setules and 2 plumose setae on inner margin; last endopodal segment with patch of setules on outer surface and 6 plumose setae. Leg 3 (Figure 3B) sympod with small adhesion pad on anterolateral corner, striated marginal membranes, 1 medial pinnate seta and 2 medial setules. Large spine on first exopodal segment (Figure 3C) with lateral flange; spine terminally situated on basal swelling which carries striated membrane along apical and outer margins and 1 ventral setule. Second exopodal segment (Figure 3B) with outer row of setules, 1 short outer spine and 1 inner plumose seta; last segment with 3 outer spines and 4 plumose setae. First endopodal segment expanded laterally into velum and bearing 1 inner plumose seta; second segment with row of outer setules and 6 plumose setae. Leg 4 (Figure 3D) sympod bears 1 pinnate seta on outer distal corner; first exopodal segment bears naked spine, one-third length of second exopodal segment; pectinate membrane near base of each spine on second exopodal segment; 3 spines, with innermost spine longer than middle spine and outermost spine one-half length of middle spine; middle and innermost spines curved distally. Leg 5 (Figure 3E) represented by 2 setiferous lobes; anterior lobe with 1 pinnate seta; posterior lobe bears 2 unequal pinnate setae.

Male

Body as in Figure 3F. Total length 4.20 (3.97–4.52) mm based on 7 specimens. Cephalothoracic shield 2.89 (2.69–3.04) mm long, 2.37 (2.16–2.59) mm wide. Fourth pedigerous segment much wider than long, 0.14 (0.10–0.18) $\times$ 0.64 (0.58–0.70) mm. Genital complex slightly wider than long, 0.71 (0.63–0.99) $\times$ 0.86 (0.72–1.40) mm, with dorsal surface ornamented with setules. Abdomen (Figure 4A) 1-segmented, with length and width subequal, 0.35 (0.32–0.41) $\times$ 0.35 (0.33–0.38) mm, ornamented with 6 setules on dorsal surface and 1 pair of setules on ventral surface. Caudal ramus longer than wide, 0.23 (0.19–0.26) $\times$ 0.16 (0.15–0.18) mm.

Antenna (Figure 4B) 3-segmented; proximal segment relatively slim, with corrugated surface on outer distal margin; second segment robust, bearing 3 corrugated adhesion pads; last segment forming claw and equipped with 2 setae. Dentiform process of maxillule (Figure 4C) bifid as in female, but lateral tine is less than one-half length of medial tine. Maxilliped (Figure 4D) with corrugated protrusion in myxal area; shaft with small, terminal cuticular protrusion; claw slightly curved, bearing basal seta. Legs 5 and 6 (Figure 4E) composed of relatively large conical lobes; leg 5 bears minute setule, 2 subterminal dorsal pinnate setae and 1 apical pinnate seta; leg 6 bears 1 minute, naked seta and 2 unequal apical pinnate setae.

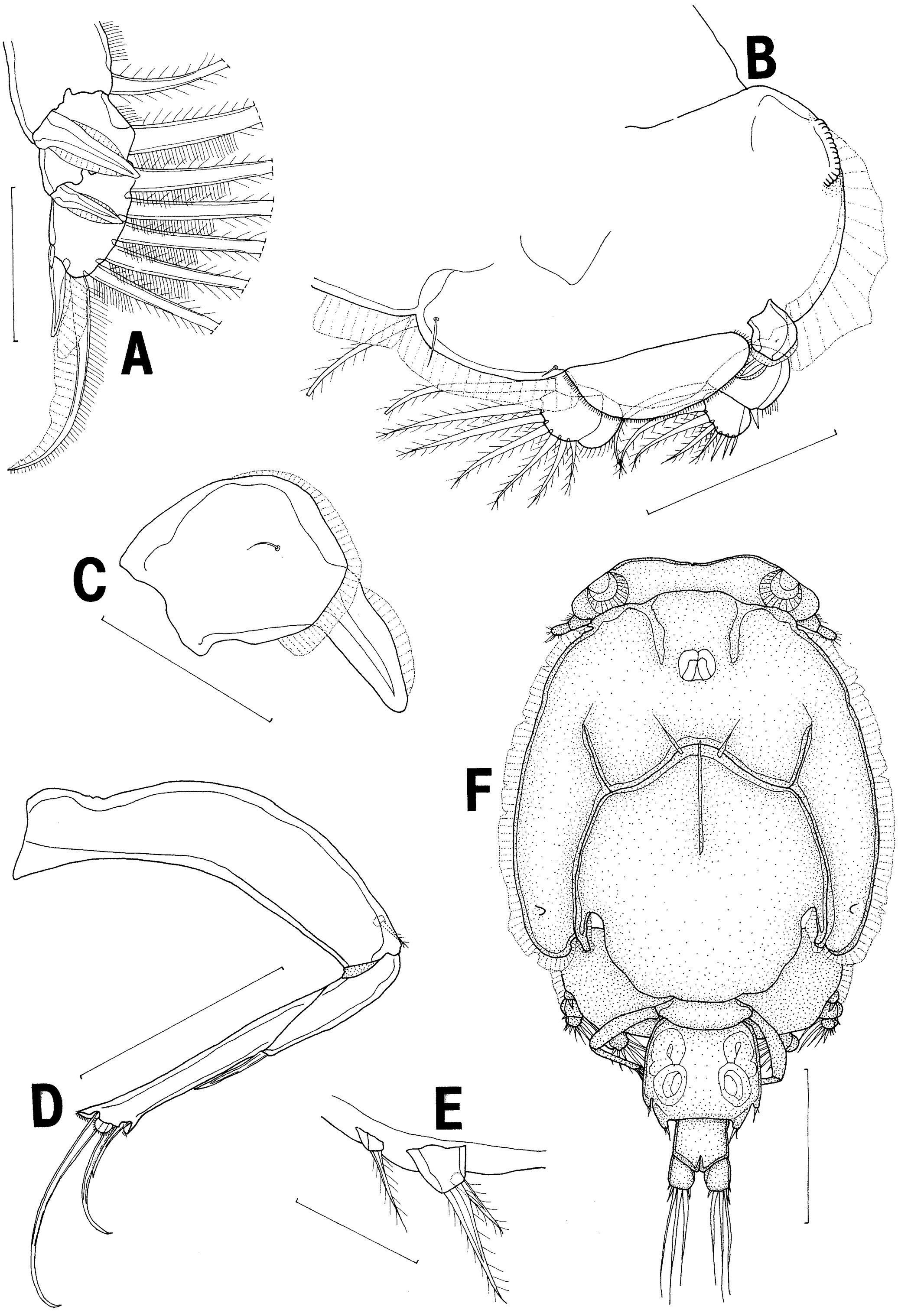

Figure 3. *Caligus oculicola* n. sp. A-E. Adult female: A. leg 2 exopodal segments, ventral; B. leg 3, ventral; C. first exopodal spine of leg 3, ventral; D. leg 4, ventral; E. leg 5, ventral. F. Adult male: habitus, dorsal. *Scale-bars*: A, 0.20 mm; B, 0.40 mm; C,E, 0.10 mm; D, 0.30 mm; F, 1.00 mm.

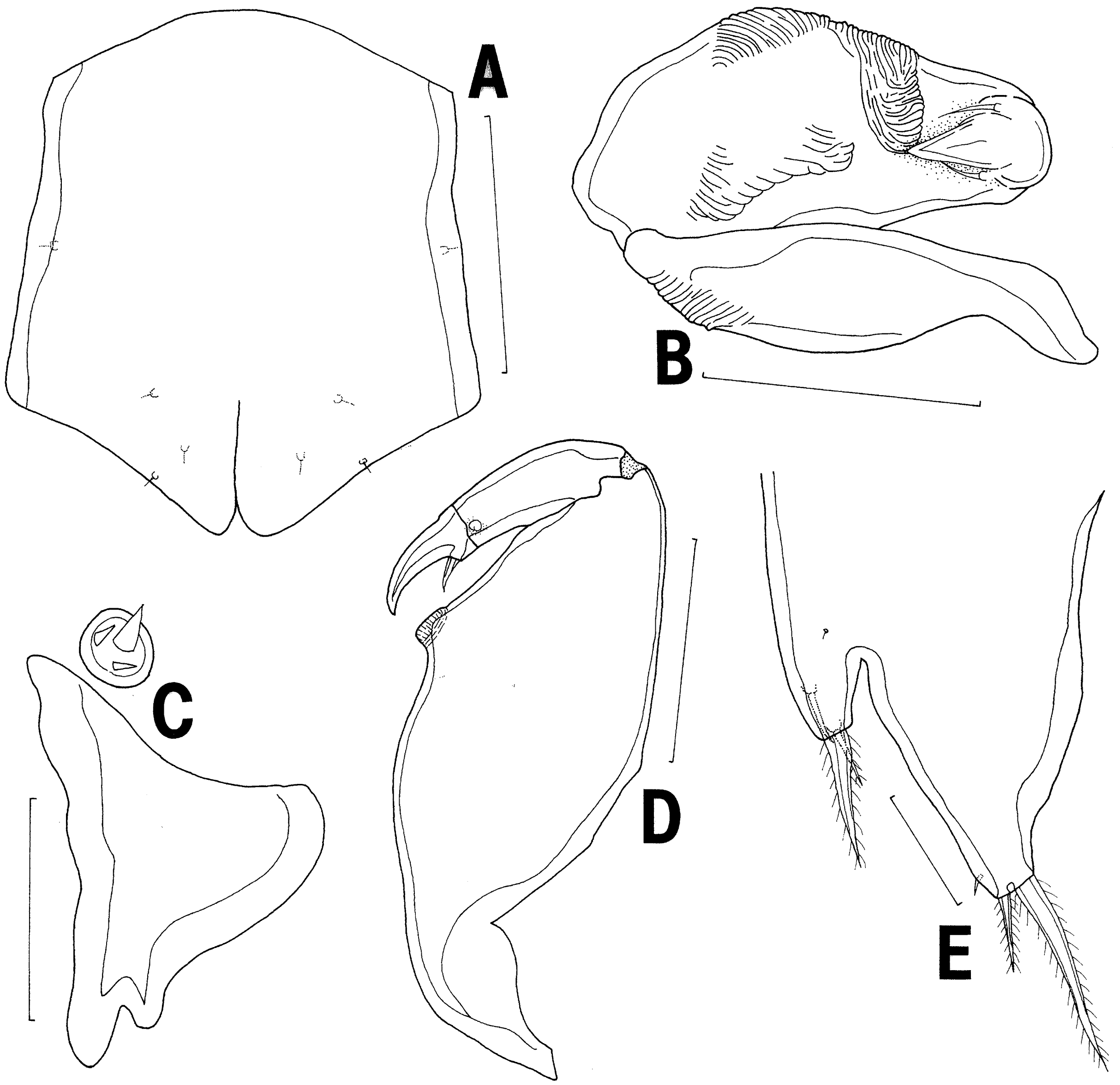

Figure 4. *Caligus oculicola* n. sp. Adult male: A. abdomen, ventral; B. antenna, ventral; C. maxillule, ventral; D. maxilliped, ventral; E. legs 5 and 6, ventral. *Scale-bars*: A,B,D, 0.20 mm; C,E, 0.10 mm.

Discussion

Taxonomy

The most distinctive characteristic of *Caligus oculicola* n. sp. is the bifid nature of the dentiform process of the maxillule. The maxillule in *Caligus* species is typically composed of two separate parts, a setiferous papilla and a triangular, sclerotised process, both parts representing an originally biramous appendage (Dojiri & Cressey, 1991). However, the female of some species, such as *C. aesopus* Wilson, 1921, *C. alatus* Heegaard, 1943, *C. bicycletus* Heegaard, 1945, *C. brevicaudus* Pillai, 1963, *C. chorinemi* Krøyer, 1863, *C. constrictus* Heller, 1865, *C. cordyla* Pillai, 1963, *C. cornutus* Heegaard, 1962, *C. equulae* Ho & Lin, 2003, *C. hobsoni* Cressey, 1969, *C. kurochkini* Kazachenko, 1975, *C. platurus* Kirtisinghe, 1964, *C. randalli* Lewis, 1964, *C. robustus* Bassett-Smith, 1898, *C. rotundigentialis* Yü, 1933 and *Caligus* sp. 1 of Byrnes (1987), possess a maxillule with a secondary process (tine) on the sclerotised process. The secondary process in these species is basal, medial or subterminal, whereas it is positioned terminally in the species described here. Nonetheless, *C. alatus* can be distinguished from *C. oculicola* by having a wider cephalothoracic shield, a longer genital complex, a sternal furca with a box nearly as wide as long and pointed tines, and spines 2 and 3 on the terminal segment of leg 4 nearly equal in length. *C. aesopus*, *C. bicycletus*, *C. brevicaudus*, *C. chorinemi*, *C. cordyla*, *C. equulae* and *C. kurochkini* can be easily distinguished from the new species by possessing an accessory process at the base of the postantennal process and a 3-segmented fourth leg. *C. constrictus*, *C. cornutus*, *C. robustus* and *C. rotundigentialis* differ from the new species by having a 3-segmented fourth leg and a 2-segmented abdomen. *C. hobsoni* is differentiated from *C. oculicola* by possessing an accessory process at the base of the postantennal process, a 2-segmented abdomen and a 2-segmented fourth leg with an armature formula of I-0; I, III. *C. platurus* varies from *C. oculicola* by having a sternal furca with a stout box and short tines bearing lateral flanges, a 3-segmented fourth leg and a wider abdomen. *C. randalli* differs from the new species by possessing a longer genital complex and abdomen, a longer second segment of the antennule, an irregular surface on the inner margin of the maxilliped, a longer endopod on leg 1 and a 3-segmented leg 4. *Caligus* sp. 1 of Byrnes (1987) can be distinguished from the new species by possessing a sternal furca with a box as wide as long and nearly parallel tines, elements 1 to 3 on the distal segment of leg 1 exopod are simple with only elements 2 and 3 bearing an accessory process, and a 2-segmented leg 4 with an armature formula of I-0; I, III.

The present species closely resembles *C. buechlerae* Hewitt, 1964 and *C. fortis* Kabata, 1965, both of which possess a bifid maxillule. So far, *C. buechlerae* has been found on *Tripterygion* sp., *Parapercis colias* (Forster) and *Scorpaena papillosus* (Schneider & Forster) in New Zealand waters only (Hewitt, 1964; Jones, 1988), whilst *C. fortis* has been collected from *Carangoides emburyi* (Whitley) [= *Carangoides fulvoguttatus* (Forsskål)] in Australia (Kabata, 1965) and *Caranx* sp. from Trivandrum, India (Prabha & Pillai, 1984). *Caligus buechlerae* can be distinguished from *C. oculicola* by having a postmaxillulary process, a sternal furca with distally rounded tines and the inner margins of the tines curved, element 1 on the distal segment of leg 1 exopod simple, and a 2-segmented leg 4 with an armature formula of I-0; I, III. The male of the new species lacks the following features found in the male of *C. buechlerae*: a simple dentiform process on the maxillule; a postmaxillulary process; a medial protuberance on the corpus of the maxilliped; and a short, stout abdomen. *C. fortis* can be separated readily from *C. oculicola* by the possession of a suborbicular cephalothorax, an antennule with a long and slender second segment, an accessory process at the base of the postantennal process, a maxillule with a sharper and shorter medial tine relative to the lateral tine, a 3-segmented fourth leg, and a wide, trapezoid-shaped abdomen. Thus, the combination of the following features distinguishes *C. oculicola* from all other congeners: (i) maxillule with terminally bifid dentiform process; (ii) box of sternal furca longer than wide and with diverging, truncate tines; (iii) terminal spines 1 to 3 on last segment of leg 1 exopod each with serrate margins and an accessory process (accessory process on spines extending beyond the tip of the spine itself); and (iv) armature formula of leg 4 exopod I-0; III.

Host-parasite relationships

Pre-adult and adult caligids can move over the entire body surface of their hosts, as well as readily detach from one host and attach to another host (Kabata, 1981). As might be expected, it is not unusual to find a caligid infecting a host that does not represent its preferred host. In this study, we consider the association between *C. oculicola* and its shark host as genuine for several reasons. First, Newbound & Knott (1999) collected *C. oculicola* on numerous occasions throughout the month of July, 1997. The copepod was prevalent on 35% of the tiger sharks examined, with a mean intensity of 3.5. In contrast, Boxshall (1974) and Henderson et al. (2002) reported a prevalence of 3% and 0.4%, respectively, for *C. curtus* Müller, 1785 on the spiny dogfish *Squalus acanthias* L. in the Atlantic Ocean. Moreover, the prevalence and mean intensity recorded for *C. oculicola* are similar to, or significantly greater than, those reported for other congeners infecting wild populations of teleost fishes (Boxshall, 1974; Arai et al., 1988; Moser & Hsieh, 1992; Rohde et al., 1995). Newbound & Knott (1999) also found that *C. oculicola* was more prevalent and had a higher mean intensity than most of the pandarids, a group of copepods considered to be exclusive parasites of elasmobranchs, collected on the tiger shark. This suggests that the association between

C. *oculicola* and its shark host is authentic rather than just coincidental. Furthermore, since *Caligus* species are known either to be easily dislodged from the host during capture and handling, or to detach from their hosts soon after the hosts are captured, the aforementioned infection parameters for *C. oculicola* are merely conservative estimates, or indicates that this copepod attaches more firmly to the host relative to its congeners (G.W. Benz, pers. comm.). It appears that the former is more plausible, since *C. oculicola* does not possess any specialised features that would allow it to anchor more firmly to the host than its congeners. However, it should be noted that one of us (DRN) observed *C. oculicola* crawling underneath the nictitating membrane of the hosts' eye, so the likelihood of this copepod being dislodged during handling may be reduced.

Second, *C. oculicola* was found exclusively on the external surface of the hosts' eyes, a microhabitat that serves as an ideal attachment site for this copepod. The suborbicular or oval-shaped cephalothorax of *Caligus*, which is formed by the fusion of the cephalosome with the first three pedigerous somites, acts as a suction cup used in adhering to the host. The suction efficiency and seal of the cephalothorax is enhanced by a frontal plate on the anterior margin of the cephalothorax, a pair of sucking discs (lunules) on the frontal plate, transparent membranes along the outer margins of the cephalothorax, and the expansion of the interpodal bar and sympod of the third leg to form a large ventral apron at the posterior end of the cephalothorax. Moreover, the downward pressure created by the suction facilitates the insertion of the antennal claws into host tissue, thereby anchoring the copepod to the host more securely (Kabata, 1979). Clearly, this arrangement is best suited for a relatively flat, smooth surface, such as the eye, rather than an irregular surface not unlike the placoid scales covering the body surface of elasmobranchs. In fact, Kabata & Hewitt (1971) showed that *Lepeophtheirus salmonis* (Krøyer, 1838), a caligid copepod that is morphologically identical to *Caligus* except for the absence of lunules on the frontal plate, was unable to attach to strips of coarse sandpaper.

It is worth noting that caligiform copepods other than *Caligus*, notably representatives of the family Pandaridae, are better adapted to living on the general body surface of elasmobranchs. The pandarid cephalothorax superficially resembles that of *Caligus*; however, only the first pedigerous somite is incorporated into the cephalothorax. Since the third leg is not modified into an apron in pandarids, it is not surprising that the adhesive power of the pandarid cephalothorax is comparatively weaker than that of *Caligus.* Consequently, pandarids have developed unique mechanisms for attaching to the external surface of their elasmobranch hosts. For instance, members of *Pandarus* Leach, 1826 use their chelate maxillipeds as the primary attachment organs by grasping placoid scales (Benz, 1992), *Perissopus oblongatus* (Wilson, 1908) attaches to its shark host by inserting its toothed antennae between the placoid scales and into the host flesh, and *P. dentatus* Steenstrup & Lütken, 1861 cements the myxal pad of the maxilliped directly to host placoid scales (Benz, 1993). Moreover, most pandarids possess accessory attachment structures in the form of relatively large adhesion pads on their ventral surface, which function as friction devices to help secure themselves on their hosts (Cressey, 1967a; Benz, 1992).

In addition to serving as a suitable attachment site, the eye provides an appropriate grazing substrate for *C. oculicola.* A caligid copepod typically feeds by orienting its relatively short mouth tube, formed from the partial fusion of the labrum and labium, perpendicular to its body and then applying it to the surface of the host. Lateral and medial movements of the dentiferous strigil located at the tip of the labium lacerate host tissue, whilst membranes at the distal end of the labrum and labium prevent dislodged host tissue from exiting the mouth tube. Host tissue is initially conveyed into the mouth tube by the mandibles and is carried further into the mouth by peristaltic pressure waves generated by sequential contraction of various muscles in the labrum (Kabata, 1974; Boxshall, 1990). It is unlikely *C. oculicola* can feed in this manner on the raised and tightly packed placoid scales of the host but can readily do so on the flat surface of the eye. In contrast, pandarids and certain euryphorids (e.g. *Alebion* Krøyer, 1863) are capable of feeding between the raised placoid scales of their elasmobranch hosts because their mouth tube and mandibles are relatively longer and slimmer than those present in *Caligus.* Whether *C. oculicola* feeds exclusively on eye tissue or on the mucus layer covering the eye surface remains to be determined. It should be noted that *C. oculicola* is not the only siphonostomatoid copepod reported from shark eyes. The lernaeopodid copepod *Ommatokoita elongata* (Grant, 1827) has been reported to infect the eyes of two species of squaliform sharks, the Pacific sleeper shark *Somniosus pacificus* Bigelow & Schroeder and the Greenland shark *Somniosus microcephalus* (Bloch & Schneider) (Benz et al., 1998).

Attachment of *O. elongata* to the host eye using its bulla and modified maxilla, as well as the feeding habits of the copepod, has been shown to cause extensive damage to the cornea, lens and iris (Borucinska et al., 1998; Benz et al., 2002).

Newbound & Knott (1999) reported a prevalence of 11.1% and a mean intensity of 3.5 for *C. oculicola* on the thickskin shark *Carcharhinus plumbeus* (Nardo); however, these values were later determined to be incorrect. Of 18 thickskin sharks examined in their study, only one specimen of *C. oculicola* was actually removed from one thickskin shark. Thus, the prevalence and mean intensity of *C. oculicola* on the thickskin shark is amended to 5.5% and 1, respectively. Since *C. oculicola* was not collected again after inspection of 120 additional thickskin sharks (Newbound, unpublished data), we consider the collection of this copepod from the thickskin shark as a fortuitous infection. Interestingly, the parasitic copepod fauna of the tiger shark, a highly migratory and cosmopolitan shark species found in tropical and temperate seas, has been extensively studied worldwide (Lewis, 1966; Cressey, 1967b, 1970; Benz, 1986; Rokicki & Bychawska, 1991), yet this copepod had never been encountered until now. In addition, *C. oculicola* has not been collected south of Shark Bay, or from eleven other shark species: 66 *Carcharhinus obscurus* Lesueur, eight *C. albimarginatus* (Rüppell), 17 *C. brevipinna* (Müller & Henle), four *C. falciformis* (Müller & Henle), one *C. leucas* (Müller & Henle), four *C. limbatus* (Müller & Henle), 14 *C. melanopterus* (Quoy & Gaimard), two *C. amblyrhynchos* Bleeker,104 *Rhincodon typus* Smith, six *Sphyrna lewini* Griffith & Smith and two *Hemigaleus microstoma* Bleeker (Newbound, unpublished data). This indicates that *C. oculicola* is highly host specific to the tiger shark and is restricted (endemic) to the northwestern coast of West Australia, which further suggests that the tiger sharks from northwestern Australia represent populations distinct from those elsewhere.

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