Caught in speciation? A new host for *Conchodytes meleagrinae* Peters, 1852 (Decapoda, Caridea, Palaemonidae)

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**Abstract**

During fieldwork in 2009 at Ternate, Indonesia, a pair of a pontoniine shrimp species belonging to the genus *Conchodytes* was collected from a bivalve mollusk of the genus *Spondylus*. This constitutes the first record of a species of the genus *Conchodytes* associated with a spondylid host. The specimens can be distinguished from other known *Conchodytes* species based on both morphology and colour pattern. Its COI barcode however, strongly resembles those obtained from three specimens of *C. meleagrinae* and is nested in the *C. meleagrinae* clade of the reconstructed phylogeny. Based on morphology and colouration only the specimens associated with the *Spondylus* bivalve would have been described as a species new to science. The modest conflicting molecular data have lead the authors to fully describe and figure the *Spondylus* associated specimens and compare them with the *Pinctada* associated specimens. Based on the present information it is decided not to give the *Spondylus* associated specimens the status as a distinct species but regard them as host-related (colour)morph of *Conchodytes meleagrinae*.

**Key words:** Palaemonidae, Pontoniinae, *Conchodytes meleagrinae*, new host, phylogeny, Ternate, Indonesia

**Introduction**

The Indo-West Pacific genus *Conchodytes* Peters, 1852, contains ten known species (De Grave & Fransen, 2011; Fransen & Reijnen, 2012), which are all associated with Indo-West Pacific bivalve mollusks: *C. biunguiculatus* (Paulson, 1875); *C. chadi* (Marin, 2011), *C. maculatus* Bruce, 1989; *C. meleagrinae* Peters, 1852; *C. monodactylus* Holthuis, 1952; *C. nipponensis* (De Haan, 1844); *C. philippinensis* Bruce, 1996, *C. placunae* (Johnson, 1967), *C. pteriae* Fransen, 1994a, and *C. tridacnae* Peters, 1852. These species have been recorded to live in association with scallops (Pectinidae: *Amusium* Röding, 1798; *Pecten* O.F. Müller, 1776), windowpane oysters (Placunidae: *Placuna* Lightfoot, 1786), cockles (Cardiidae: *Tridacna* Bruguière, 1797), fan shells (Pinnidae: *Atrina* Gray, 1842; *Pinna* Linnaeus, 1758), pearl oysters (Pteriidae: *Pinctada* Röding, 1798), tree oysters (Isognomoidae: *Isognomon* Lightfoot, 1786), and Cock's comb oysters (Ostreidae: *Lopha* Röding, 1798).

A faunal survey for shallow-water pontoniine shrimps during a research expedition to Ternate and surroundings, revealed a male/female pair of shrimps of *Conchodytes* living in a spiny oyster (*Spondylidae*) of the genus *Spondylus*. This is the first record of a *Conchodytes* living in symbiosis with a species of the bivalve genus *Spondylus*.

**Material and methods**

**Sample collection.** The expedition was organised in around Ternate, northern Moluccas (23 October–18 November, 2009) by the Research Center for Oceanography, Indonesian Institute of Sciences (RCO-LIPI), and Naturalis Biodiversity Center in Leiden, the Netherlands, as part of the Ekspedisi Widya Nusantara (E-Win expedition). The specimens were collected using SCUBA equipment. Live specimens were photographed in their
host with a Nikon D80 digital camera. The specimens were preserved in 70 % ethanol. For data on additional specimens used in the molecular analyses see Fransen & Reijnen (2012: Table I). Platypontonia hyotis Hipeau-Jacquotte, 1971, was selected as outgroup for the molecular analyses. Specimens were observed, measured and illustrated using a Wild M5 dissecting microscope and a Leitz Ortholux II stereomicroscope, both with drawing tubes. Post processing of photographs and illustrations was done in Adobe Photoshop CS6.

**Molecular analysis.** We followed the protocol used by Fransen & Reijnen (2012). Of 648 total aligned sites, 147 were variable and informative for maximum parsimony (MP). The sequences obtained were deposited in GenBank (for accession nos. see ‘Material examined’). The material is deposited in the Naturalis Biodiversity Center collections at Leiden, the Netherlands (formerly Rijksmuseum van Natuurlijke Historie [RMNH]). Abbreviations: pocl., postorbital carapace length.

**Data analysis.** The best-fitting model for sequence evolution (TIM2+I+G) of the COI dataset was determined by jModelTest (vers. 0.1.1., Posada 2008), selected by the AIC (Akaike Information Criterion), and was subsequently applied to the maximum likelihood (ML) analyses with PAUP* (vers. 4.0b10, Swofford 2003) using 2000 bootstrap reiterations. A maximum parsimony (MP) tree was constructed using PAUP* using 2000 bootstrap reiterations with a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping, and 10 randomly added sequence replications.

**Results**

**Palaemonidae Rafinesque, 1815**

**Pontoniinae Kingsley, 1879**

**Conchodytes Peters, 1852**

**Conchodytes meleagrinae Peters, 1852**

(Figs 1–7)

**Material examined.** 1 ovigerous female (pocl. 7.4 mm) (RMNH.CRUS.D.53203), 1 male (pocl. 4.8 mm) (RMNH.CRUS.D.53202) (GenBank accession no. KF638630): Indonesia, northern Moluccas, Halmahera mainland, Pasir Lamo (W side), 0°53'20.5"N 127°27'34.2"E, 12 m depth, exposed at low tide, shallow reef flat in front of Halmahera, sandy slope with corals, in *Spondylus* spec., 8.xii.2009, collected by Bastian T. Reijnen, Ternate 2009 Expedition stn TER.26.

**Material of *C. meleagrinae* for comparison.** 1 male pocl. 5.0 mm, 1 ovigerous female pocl. 6.8 mm (RMNH.CRUS.D.53211): stn TER.04, Indonesia, Ternate, Sulamadaha Beach, 0°51'47.6"N 127°20'4.1"E, shallow sandy area with coral gardens, 5 m depth, in *Pinctada margaritifera*, 26.x.2009, collected by C.H.J.M. Fransen, photo TER.04-0090-93.—1 male pocl. 5.5 mm, 1 ovigerous female pocl. 7.2 mm (RMNH.CRUS.D.53510): stn TER.41, off Halmahera mainland, Teluk Dodinga; Karang Luwelue E, 0°46'32.8"N 127°33'43.4"E, sloping sandy bottom with coral patches, in *Pinctada margaritifera*, few m depth, 15.xi.2009, collected by C.H.J.M. Fransen, photo TER.41-0108.—1 male pocl. 5.5 mm, 1 ovigerous female pocl. 7.5 mm (RMNH.CRUS.D.53816): stn SEM.09: Malaysia, Sabah, Semporna area, Ligitan Reef 1 S/Yoshi Point, 04°14'05.8"N 118°33'26.7"E, 5 m depth, in *Pinctada margaritifera*, 1.xii.2010, collected by S.E.T. van der Meij.—1 male pocl 6.7 mm, 1 ovigerous female pocl 6.4 mm (RMNH.CRUS.D.53871) (GenBank accession no. KF638631): stn SEM.30, Malaysia, Sabah, Semporna area, S Kulapuan Isl., 04°30'41.3"N 118°51'58.4"E, few m depth; in *Pinctada margaritifera*, 9.xii.2010; collected by B.T. Reijnen.—1 male pocl 6.7 mm, 1 ovigerous female pocl. 6.4 mm (RMNH.CRUS.D.53834): stn SEM.38, Malaysia, Sabah, Semporna area, Boheydulang Isl., outer reef lagoon, 04°34'01.8"N 118°45'27.5"E; 12 m depth; in *Pinctada margaritifera*, 11.xii.2010, collected by C.H.J.M. Fransen, photo 945-955.—1 male (pocl 4.9 mm), 1 ovigerous female (pocl 7.0 mm) (RMNH.CRUS.D.53348): Santo stn FR3, Vanuatu, Santo, S Segond Channel, Belmont lagoon entrance, Brickstock Point, -15.36239 167.06320, 11.ix.2006, 3–32 m depth, in *Pinctada margaritifera* on sandy *Halimeda* slope with patches of coral, photo by Tin-Yam Chan.
FIGURE 1. Conchodytes meleagrinae Peters, 1852 from Spondylus spec. Ovigerous female, pocl. 7.5 mm (RMNH.CRUS.D.53203). Scale bar = 4 mm.

Description. Body subcylindrical (Fig. 1). Carapace smooth. Rostrum short, stout, thickened, toothless; anterior border bluntly rounded in lateral view, reaching distal margin of distal segment of antennular peduncle in male (Fig. 2A) and halfway distal segment in female (Fig. 2C), with few tiny setae; depressed, oblong triangular in dorsal view, without dorsal carina; ventral margin distally concave (Fig. 2B). Supraorbital, hepatic and antennal spines absent; inferior orbital angle produced, angular; anterolateral angle of carapace slightly produced, bluntly subrectangular (Fig. 2B, D).

Abdomen (Fig. 1) smooth. Pleura of first three segments large, broadly rounded; fourth segment small and rounded, fifth very small and rounded. Telson (Fig. 3A, B) almost twice as long as sixth abdominal segment, slightly more than twice as long as proximal width; posterior border without median process, equal to about 0.4 of anterior width; two pairs of large submarginal dorsal spines equal to 0.14 of telson length, arising from distinct fossae and with swollen bases, at 0.18 and 0.68 of the telson length; posterior margin (Fig. 3C) with three pairs of spines, lateral spines small, marginal, arising slightly proximally of intermediate spines, intermediate spines large, about as large as dorsal spines, submedian spines as long as intermediate spines, more slender, setulose.

Eyes with globular, well pigmented cornea, without accessory pigment spot, diameter subequal to width of cylindrical stalk; stalk twice as long as distal width.

Antennule (Fig. 3D) with peduncle and flagella short; proximal segment about as long as central width, lateral border bluntly angulate, medial border straight with few plumose setae, distolateral angle with acute tooth, stylocerite large, broad, distally rounded with few short setae, statocyst conspicuous, with granular statolith, ventral median border with distinct short acute tooth; intermediate segment short, twice as wide as long; distal segment about as wide as long; upper flagellum short, biramous, with five proximal segments fused bearing aesthetascs, short free ramus unisegmented or indistinctly two-segmented, longer free ramus with four segments; lower flagellum short with 10 segments.

Antenna (Fig. 3E) with basicerite short, laterally unarmed, obscured by anterolateral angle of carapace, with conspicuous papilliform process medially; carpocerite extending beyond lamella of scaphocerite; flagellum slightly more than twice length of carpocerite; scaphocerite with lamella about 1.6 times longer than central width, medial border broadly rounded, lateral margin convex with large distal tooth slightly sinuous medially, extending well beyond anterior edge of lamella.

Epistome with distally triangular; labrum oval.
Alae of paragnath with large subcircular distal lobes, with small submedian ventral lobes; corpus long, with long median groove, bordered by non-setose carinae.

Second to fourth thoracic sternites unarmed, fifth with lateral plates posteromedial of second pereiopods.

Mandible (Fig. 3F) without palp; molar process (Fig. 3G) stout, minutely denticulate distally, with distal end truncate, with strong blunt teeth, tessellate protuberance and dense setal brushes; incisor process slender, with four distal teeth on both right and left mandible.

Maxillula (Fig. 4A) with bilobed palp, lower lobe with small seta ventrally; upper lacinia broad, with about 15 spines in double row medially, distoventral margin densely setose; lower lacinia broadly triangular, densely setose distoventrally and marginally, without spines.

Maxilla (Fig. 4B) with broad palp, proximal lateral border with row of plumose setae, subdistal medial border with few plumose setae; basal endite simple, distally produced and narrow, as long as palp, medial border with a dense fringe of long, slender, finely plumose setae; coxal endite obsolete; scaphognathite slightly more than three times longer than wide, with broad anterior and posterior lobes.

First maxilliped (Fig. 4C) with simple palp with few subdistal plumose setae; basal endite large and broad, fringed with many simple and finely serrulate setae; coxal endite obsolete; exopod with caridean lobe, flagellum broad with several long plumose setae in distal half, epipod bilobed.

Second maxilliped (Fig. 4D) with dactylar segment narrow, with numerous finely serrulate spiniform setae medially; distomedial lobe of propod produced, rounded with simple marginal setae; carpus distomedially angular; ischium and basis fused; exopod with small lateral lobe proximally, bearing few plumose setae in distal fourth; coxae not produced medially, with subrectangular epipod not bearing a podobranch.
Third maxilliped (Fig. 4E) with ischiomerus semi-fused with basis; basal segment triangular, ischiomerus about twice as long as wide, both segments with dense cover of long slender simple setae ventrally and medially; penultimate segment about twice as long as width, about 0.3 times ischiomeral length; distal segment as long as penultimate segment, tapering distally, with several rows of serrulate setae medially; exopod slightly longer than ischiomeral segment with distal half fringed by plumose setae; coxal segment not produced medially, with oval lateral plate, without epipod or arthrobranch.
First pereiopods (Fig. 4F) slender, extending beyond scaphocerite with chela and distal half of carpus; chela with palm as long as fingers; fingers slender, with several rows of finely serrulate setae, cutting edges entire, tips of fingers hooked; carpus 1.4 times as long as chela, slightly widening distally; merus as long as carpus, slightly bent; ischium short, about 0.4 times merus length with row of plumose setae along lateral border; basis about as long as ischium; coxa robust with conspicuous setose ventromedial process.
Second pereiopods (Fig. 4G, H) similar, subequal; palm 2.2 times longer than deep, compressed; dactylus 0.5 times palm length, with blunt denticulate tooth in proximal part of cutting edge, distal part entire, tip strongly hooked, dorsal margin rounded, not carinate; fixed finger with blunt denticulate tooth just proximal of tooth on dactylus and blunt denticulate tooth just distal of tooth on dactylus, distal part of cutting edge entire, tip strongly hooked; carpus short and stout, expanding distally, 1.5 times longer than distal breadth, unarmed, about 0.3 times chela length; merus short and stout, about as long as carpus; ischium short and stout, with small distomedial protuberance, slightly shorter than merus; basis and coxa stout, without armature.
Ambulatory pereiopods (Fig. 5A–C) robust, similar. Dactylus of third to fifth pereiopods (Fig. 6A–C) similar. Third pereiopod with strongly curved, simple unguis; corpus strongly compressed, ventral border with large acute strongly recurved distal accessory tooth, dorsal border with row of simple short setae, basal protuberance with
straight proximal margin, without proximal tooth, densely covered with simple setae along entire margin; propodus about 5.5 times longer than wide, unarmed; carpus 0.55 propodus length, unarmed; merus 0.9 times as long as propodus, unarmed; ischium, basis and coxa without special features.

Uropods (Fig. 3A, B) with protopod postolaterally blunt; exopod with lateral border convex (Fig. 6D), with small mobile spine posteriorly, without posterolateral tooth; endopod extending well beyond exopod, slightly overreaching telson.

First male pleopod (Fig. 5D) with endopod (Fig. 5E) half exopod length, medially concave, distally rounded with long plumose setae on distal half of lateral and distal fourth of medial border, concave medial border with double row of short simple setae. Endopod of male second pleopod (Fig. 5F) slightly shorter than exopod, with appendix masculina (Fig. 5G) subcylindrical, slightly shorter than appendix interna, with about 16 long simple setae in distal half; appendix interna slender with few distal cincinnuli.

Female larger in size than male, with relatively smaller second pereiopods and rostrum broader at base. Ova numerous, length about 1.0 mm.

**Size.** Ovigerous female pocl. 7.4 mm; male pocl. 4.8 mm.

**Colour.** Translucent reddish with dense cover of white chromatophores (Fig. 7).

**Host.** *Spondylus* aff. *violascens* Lamarck, 1818 or *Spondylus regius* Linnaeus, 1758 (Mollusca, Bivalvia, Pectinoidea, Spondylidae) (see Lamprell, 2003; Finet & Lamprell, 2008). The bivalve was found loose on coral rubble, both valves were similar in size and form, the mantle and gills were orange in colour. This is the first record of a *Conchodytes* species from a *Spondylus* host. *Spondylus* species have been recorded as host of a few pontoniine shrimps. Namely, in the Indo-West Pacific *Anchiopontonia hurii* (Holthuis, 1981), *Paranchistus nobilii* Holthuis, 1952, *P. spondylis* Suzuki, 1971 (see Fransen, 1994b) and *Cainonia medipacifica* (Edmondson, 1935) (see Fransen 2002, as *Dactylonia medipacifica*) and in the Atlantic *Pontonia manningi* Fransen, 2000. The original description of *Conchodytes meleagrinae* by Peters (1852) is based on a male/female pair from Ibo Island off Mozambique collected from the pearl oyster *Pinctada margaritifera* (Linnaeus, 1758). It has subsequently been recorded...
throughout the Indo-West Pacific from East Africa to Hawai‘i. Most of the records mention *P. margaritifera* as host whereas few refer to *P. maxima* (Jameson, 1901) and *P. radiata* (Leach, 1814) as host species (see Holthuis, 1986; De Grave, 1999).

FIGURE 9. Conchodytes meleagrinae Peters, 1852 from Pinctada margaritifera (Linnaeus, 1758). Ovigerous female, right third pereiopod, dactylus, lateral view. A, RMNH.CRUS.D.53211; B, RMNH.CRUS.D.53871; C, RMNH.CRUS.D.53816. Scale bar = 0.24 mm.
Morphological comparison. The specimens obtained from the Spondylus host were compared with material of C. meleagrinae obtained from specimens of Pinctada margaritifera. The specimens from the Spondylus host differ from C. meleagrinae specimens associated with Pinctada in having: 1) the merus and carpus of the first pereiopod of equal length while the carpus is distinctly shorter in C. meleagrinae from Pinctada; 2) the dactylus of the ambulatory pereiopods with the flexor margin broadly rounded while forming a protuberance with a straight edge often provided with a more or less developed proximal blunt tooth in C. meleagrinae from Pinctada (Fig 9); 3) the flexor margin of the ambulatory dactylus with a dense cover of setae over its entire surface, whereas the covered surface is much smaller and the number of setae much lower in C. meleagrinae from Pinctada (Fig 9); 4) a smaller distance between the accessory tooth and unguis of the dactylus of the ambulatory pereiopods than in C. meleagrinae from Pinctada (Fig 9); 5) the angle between the unguis and the accessory tooth of the dactylus of the ambulatory pereiopods about 15° while this angle is much larger, ca. 40°, in C. meleagrinae from Pinctada (Fig 9); and 6) the dense cover of large white chromatophores over its entire body while the C. meleagrinae from Pinctada have scattered large red chromatophores interspersed with many small white chromatophores (Fig 8).

The specimens associated with Spondylus differ, together with C. maculatus, from all other species of Conchodytes in the absence of a distinct angular basal protuberance on the dactylus of the ambulatory pereiopods. They differ from C. maculatus in: 1) the rounded dorsodistal margin of the dactylus of the second chelae, whereas it is distinctly carinate in C. maculatus; 2) the distinct tooth on the distolateral angle of the antennular peduncle proximal segment, not rounded as in C. maculatus; 3) in having the rounded dactylar flexor margin of the ambulatory pereiopods with a dense cover of setae over its entire surface, whereas the covered surface is much smaller and the number of setae much less in C. maculatus; and 4) in having a smaller distance between the accessory tooth and unguis of the ambulatory pereiopods than in C. maculatus.
**TABLE 1.** Genetic divergences (%) among specimens analysed.

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Genetic comparison. The COI sequence of a specimen associated with the Spondylus host is similar to of the C. meleagrinae associated with Pinctada hosts (Table I) and therefore clusters within the C. meleagrinae clade (Fig. 10). The divergence between the Spondylus associated and the genetically most similar Pinctada associated specimens is 1.08 %. The maximal intraspecific divergence in C. meleagrinae is 8.65 %.

Discussion

No genetic divergence in the COI marker could be found between the Spondylus associated specimen and the Pinctada associated specimens, the morphological differences however are distinct. The variation in the dactyl of the ambulatory pereiopods among the Pinctada associated specimens is very small, whereas the differences between these and the specimens from the Spondylus is distinct. The colour pattern in the Pinctada associated specimens is constant and clearly different from that of Spondylus associated specimens. These differences in morphology and colouration, combined with the different host association, would suggest these specimens belong to a distinct species. Similar cases where morphological divergence was observed without molecular support from the COI marker have been observed before, viz. in freshwater atyid shrimps (Rintelen et al., 2007a, 2007b). Therein the incongruence between morphology and molecular data is interpreted as an indication of a recent origin of the species, suggesting incomplete lineage sorting and/or introgression (Funk & Omland, 2003). This could be going on here as well and the Spondylus associated specimens might deserve specific status. Based on the meagre information presently available it is decided not to give the Spondylus associated specimens the status as a distinct species but regard them as a host-related (colour)morph of Conchodytes meleagrinae. When more Spondylus associated specimens become available it might be possible to shed more light on its taxonomic status.

Acknowledgements

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The Semporna Marine Ecological Expedition was jointly organized by WWF-Malaysia, Universiti Malaysia Sabah's Borneo Marine Research Institute, Naturalis Biodiversity Center and Universiti Malaya's Institute of Biological Sciences. Research permission was granted by Economic Planning Unit, Prime Minister's Department, Economic Planning Unit Sabah, Sabah Parks and Department of Fisheries Sabah. Dr. Bert W. Hoeksema acted as expedition leaders for the biodiversity theme.

The SANTO 2006 Global Biodiversity Survey was initiated by the Muséum national d'Histoire naturelle, Paris (MNHN), Institut de Recherche pour le Développement (IRD) and ProNatura International. Dr. Philippe Bouchet acted as expedition leader for the marine theme (Bouchet et al., 2011).

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Fransen, C.H.J.M. (1786) A catalogue of the Portland Museum, lately the property of the Duchess Dowager of Portland, deceased:


Latreille (Crustacea: Decapoda: Caridea: Palaemonidae).


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