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Seven new species of *Paleanotus* (Annelida: Chrysopetalidae) described from Lizard Island, Great Barrier Reef, and coral reefs of northern Australia and the Indo-Pacific: two cryptic species pairs revealed between western Pacific Ocean and the eastern Indian Ocean

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Abstract

Morphological investigation into the paleate genus *Paleanotus* Schmarda 1861 of the family Chrysopetalidae from northern Australian coral reefs, primarily Lizard Island and outlying reefs, included a complex of very small, slender individuals (length < 5 mm). This complex resolved into 7 new species, described herein: *Paleanotus inornatus* n. sp., *P. adornatus* n. sp., *P. chrysos* n. sp., *P. aquifolia* n. sp., *P. latifolia* n. sp., *P. silus* n. sp., and *P. silopsis* n. sp. A key is provided to the new species and *Paleanotus* distinguished from *Treptopale* and *Hyalopale*, two closely related genera. Diagnostic features of the apical structure and shape of the notochaetal main paleae plus median paleae shape and raised rib pattern, differentiates each species from the other. Gametous states are described. Two cryptic species pairs (*Paleanotus silopsis* n. sp. and *P. silus* n. sp.; *Paleanotus aquifolia* n. sp. and *P. latifolia* n. sp.) were identified. In each case one species is restricted to either the NE or NW Australian coast. In each pair the most eastern point for the NW Australian species range occurs at Darwin, western Arnhemland, Northern Territory. Additional material for each species pair extends their respective ranges northwards: NW Australia to Thailand, Andaman Sea, eastern Indian Ocean or NE Australia, Great Barrier Reef to the Philippines, western Pacific Ocean. Cryptic morphology and potential genetic diversity is discussed in *Paleanotus inornatus* n. sp. and *P. adornatus* n. sp. that possess overlapping widespread distribution patterns across northern Australia and Indo-Pacific reefs. The smallest bodied taxon, *Paleanotus chrysos* n. sp. is the only species with a Coral Sea range encompassing Lizard Island, Heron Island and New Caledonia.

Key words: Morphology, taxonomy, crypticism, NE/NW Australia, biogeography

Introduction

Chrysopetalids are small, fragmentable worms possessing distinctive silvery to bright golden coloured paleae (flattened notochaetae) held in tight segmental fans that imbricate down the dorsum. They are found worldwide between 60° N-S and are associated with crevicular habitats from a wide range of marine environments, intertidal to ~5000 m. It is one of the most common polychaete families associated with fringing mainland and off shore coral reefs of the Indo-Pacific and Western Atlantic (Watson 2010). A number of chrysopetalid taxa possess planktonic larvae (e.g., *Paleanotus* Blake 1975; *Arichlidon* Watson *et al.* 2014) and are among primary colonizers in settlement studies on tropical reefs e.g., GBR, western Pacific (Hutchings & Murray 1982); eastern Indian Ocean (Peyrot-Clausade 1974); eastern Pacific (Peyrot-Clausade 1976) and the Caribbean, West Atlantic (CW pers.obs.).

Chrysopetalidae was erected by Ehlers (1864) to contain the paleate genera *Paleanotus* Schmarda, 1861, *Bhawania* Schmarda, 1861, *Chrysopetalum* (Ehlers, 1864) and *Palmyra* (Savigny in Lamarck, 1818); the latter taxon since referred to the family Aphroditidae (Watson Russell 1989). Subsequently a further 10 genera have been described (see Watson Russell 2000; Rouse & Pleijel 2001). Recent genetic investigation has found that the rare families Nautiliniellidae Miura & Laubier, 1989 (inquiline in deep-sea mussels) and Calamyzidae (*Calamyzas amphictenicola* Arwidsson, 1932 parasitic on tube dwelling ampharetids in shallow waters) are derived

chrysopetalids that now both belong within the subfamily Calamyzinae (Hartmann-Schröder, 1971). Two additional subfamilies, Chrysopetalinae Ehlers, 1864 including paleate taxa, and Dysponetinae Aguado, Nygren & Rouse, 2013 erected for spinose taxa, were nominated within the Chrysopetalidae (Aguado *et al.* 2013).

Five genera of the Chrysopetalinae are known from Lizard Island and GBR offshore reefs (*Chrysopetalum*, *Paleanotus*, *Treptopale* (Perkins 1985), *Arichlidon* (Watson Russell 1998), *Bhawania*) and three from GBR inshore reefs (Chrysopetalinae, *Hyalopale* (Perkins 1985), *Paleaequor* (Watson Russell 1986) and the Dysponetinae genus, *Dysponetus* (Levinsen 1879)). These eight chrysopetalid taxa are present across all Indo-Pacific and Western Atlantic coral reefs. Globally there is only one reefal, shallow-water, endemic genus (Chrysopetalinae) known: *Acanthopale* (San Martin 1986) from the Caribbean (CW unpubl.).

Four new paleate chrysopetalid species have been described from the GBR belonging to *Treptopale*, *Arichlidon* and *Paleaequor* (Watson Russell 1986, 1998; Watson 2010; Watson *in* Wei *et al.* 2013). There are a further 30 or so new species from Lizard Island awaiting description, primarily within the genus *Chrysopetalum* (Watson in prep.).

This paper investigates the genus *Paleanotus*, a taxon previously virtually unknown in Australia and in need of revision worldwide. Three species have been described from temperate regions: the type, *Paleanotus chrysolepis* Schmarda, 1861 from Capetown, South Africa, *Paleanotus bellis* (Johnson, 1897) from California, and *Paleanotus intermedius* Orensanz, 1972 from Argentina. The former two species can be commonly found in polluted harbours and hull fouling (CW pers. obs.). A single tropical species *Paleanotus macrophthalmum* (Hartmann-Schröder 1959) has been reported, from El Salvador, eastern Pacific. All nominal species have been examined by the author and the majority share a similar, distinct Atlantic morphology.

Collections of *Paleanotus* at Lizard Island, included many small individuals that initially appeared as one undescribed cryptic complex. The same complex is found across coral reefs of northern, north west Australia and reefs of the Indo-Pacific. It is resolved into seven new species, described herein. Cryptic morphology, potential genetic diversity of the seven species and biogeographic patterns, especially between NE and NW Australia, is discussed.

Material and methods

Lizard Island is a high continental formation that lies at 14° N in the northern section of the Great Barrier Reef (GBR). It is close to a series of extensive high water submerged reefs situated near to the Outer Barrier at the edge of the continental shelf. Sampled reefs around Lizard Island include North Direction Island, High Rock, deep *Halimeda* reefs at Snake Pit, and coral banks from MacGillivray, Yonge and Day Reefs, in 1–30 metres.

Lizard Island collections include: Pat Hutching's Coral Block settlement study (1976–78); yearly trips by the Northern Territory Museum (NTM) in collaboration with CReefs, a project of the Census of Marine Life (2008–2010); Worm Net 11 expedition (August, 2013) and the Polychaete Workshop (September, 2013). Additional material is from 2008–2010 CReefs expeditions to Heron Island, southern GBR, and Ningaloo Reef, NW Australia; collections made by the NTM in the Northern Territory and Kimberley; WAM and Woodside Kimberley Survey, Western Australia; and museum field work by CW in Indonesia, Philippines and Moorea. Throughout the paper Australian state names are referred as: Queensland (QLD), Northern Territory (NT) and Western Australia (WA) and northern Australia coasts: north eastern (NE); northern (N); north western (NW).

Material examined is deposited in the following institutions: Australian Museum (AM); Museum Victoria (MV); Museum and Art Gallery of the Northern Territory (NTM: note registrations prefaced NTM at MAGNT); Museum of Western Australia (WAM); Swedish Museum of Natural History (SMNH); California Academy of Sciences (CAS); Scripps Institution of Oceanography, Benthic Invertebrate Collection (SIO); Phuket Marine Biological Centre (PMBC). CReefs stations, established during expeditions to Lizard Island, Heron Island and Ningaloo Reef, are prefixed accordingly: LI, HI and NR with the year following e.g., LI-09-XXX. Site information for material collected during the Polychaete Workshop in 2013 is prefaced with an MI QLD number (for details see Ribas & Hutchings 2015, *Zootaxa* 4019).

A generalized *Paleanotus* notochaetal fan and main palea is figured with notochaetal paleael types and ultrastructural details labelled (Fig. 1A, B). A composite plate of main paleae belonging to the seven new species is provided in association with a key to species (Fig. 1C–I). A Leitz compound microscope and AutoMontage software was used to take photos, referred to as 'micropics' in figure captions.



FIGURE 1. A. *Paleanotus* generalized notochaetal fan; B. Main paleae sculptural detail. C–I: Comparative micropics of main palea in *Paleanotus* new species. C. *Paleanotus inornatus* n. sp., NTM W.23684; D. *P. adornatus* n. sp., NTM.W.23660; E. *P. acquifolia* n. sp., NTM W.23440; F. *P. latifolia* n. sp., NTM.W.23710; G. *P. silus* n. sp., NTM.W.23731; H. *P. silopsis* n. sp., NTM W.23186; I. *P. chrysos* n. sp., NTM.W.25641. Abbreviations: b.l = 'broken line'sculpture, c = cilia, gl = gland, h.s = horizontal striae, la = lateral paleae, ma = main paleae, me = median paleae, r.r = raised rib, su1= sub-unit 1 palea.

Chaetal terminology follows Watson *et al.* (2014). Designations of notochaetal paleae are based on position: i.e. lateral group inserts below the acicula; main group above the acicula; the median group at the mid-dorsal line. Abbreviations used: *la* denotes lateral paleae; *ma*, main paleae; *me*, median paleae; *mm*, medial main paleae (main paleae closest to median group); *sul*, sub-unit1 palea (small palea in between lateral and main groups). Ultrastructural details include: *h. s.* horizontal striae; *r. r.* raised ribs; *b. l.* 'broken line' indicates a very finely raised rib, often only visible under high power (Fig. 1A, B). Roman numerals indicate segment number of the anterior end: m.a. denotes median antenna; *l.a.* lateral antennae; *p*, palp; *ca*, caruncle; *n.f.* nuchal fold; *p.i.* paleae insertion; *s*, stylet. Additional structures are: *e*, eggs; *sp*, sperm; *gl*, glands; *o.g.* oil globules; *c*, interamal cilia. An exact number of ribs is drawn in each notochaetal paleae. Neurochaetal types are denoted by position and blade length within the fascicle (e.g., Fig. 4D–H caption).

During collecting and handling *Paleanotus* individuals are more more liable to fragment than to stay entire. Abbreviations associated with these body states and measurement of segment numbers are provided in the Material examined section: E, entire; NE, not entire; L, length; W, width. As the majority of studied material is broken, it is important to give information where possible, e.g., '4: 1, 33E, L: 3.5 mm, W: 0.9 mm' means four specimens were present in a sample of which one was entire with 33 segments with X length and X width; ' 1, 32NE' means one specimen was present of 32 segments and not entire.

Taxonomic account

Key to related genera and new species of Paleanotus

1.	Main paleae mainly symmetrical in shape	Treptopale
_	Main paleae mainly asymmetrical in shape	
2. (1)	Lateral and median notochaetae in form of spines	Hyalopale
_	Lateral and median notochaetae in form of paleae	Paleanotus 3
3. (2)	Median paleae with serrate central raised rib	4
_	Median paleae with multiple ' broken-line' raised ribs	5
4. (3)	Main paleae with 11–14 ribs; 1–2 full length b.l. ribs.	P. adornatus n. sp.
_	Main paleae with 9–12 ribs; multiple b.l. ribs.	. P. aquifolia n. sp.
_	Main paleae with 12–14 ribs; multiple b.l. ribs.	P. latifolia n. sp.
5. (3)	Main paleae with distinct apex; 11–14 ribs.	P. inornatus n. sp.
_	Main paleae with tiny 'snub-nosed' apex; 12–14 ribs	P. silus n. sp.
_	Main paleae with slightly larger 'snub-nosed' apex; 15–17 ribs	P. silopsis n. sp.
-	Main paleae with broad, 'turned-up' apex; 13–15 ribs	P. chrysos n. sp.

Note: Main paleae descriptions and rib counts taken from mid-body chaetigers (Fig. 1C-I).

Family Chrysopetalidae Ehlers, 1864

Chrysopetalinae Ehlers, 1864

Genus Paleanotus Schmarda, 1861

Type-species. Paleanotus chrysolepis Schmarda, 1861

Diagnosis. Elongate body (to 70 segments) with partly retractile anterior three segments in conjunction with flexible nuchal fold. Prostomium with two pairs of large red eyes, single subulate median antenna, two lateral antennae, two short, ovoid palps insert ventrally. Broad, barrel-shaped proboscis with terminal papillae, pair of brown tipped stylets, triangular mouth flap. Segment 1 reduced, achaetous, with two pairs of dorsal and ventral tentacular cirri. Segments 2 and 3 fused in part. Segment 2 biramous with dorsal cirri, small notochaetal fascicle, neuropodia with spinigerous neurochaetae; ventral cirri absent. Segment 3 onwards with all notochaetal and neurochaetal types, dorsal and ventral cirri. Mid-body notopodia with dorsal cirri, lateral, main and median notochaetal paleal fascicles. Main paleae in single fan; paleae broad, asymmetrical with small hooked apices, with

or without raised denticulate ribs. Median paleae interlock in mid-dorsal line forming shallow but distinct convex median ridge. Median palae asymmetrical or symmetrical in shape; with or without raised, denticulate ribs. Midbody neuropodia with short, subulate ventral cirri, falcigerous neurochaetae with blades grading in size from longer in superior position to shorter, slender blades in inferior position. Pygidium quadrate with two small anal cirri. Cilia present inter-ramally; horizontal or 'flower' shaped enlarged glands occur adjacent to dorsal ceratophore in mature specimens.

Remarks. *Paleanotus* was incorrectly synonymised with *Chrysopetalum* by Day (1967). The two genera are clearly distinguished by differences of the anterior end and characteristic notochaetal types. Perkins (1985) recognized *Paleanotus* and *Chrysopetalum* as distinct genera and created two new chrysopetalid genera, *Treptopale* and *Hyalopale* from Florida reefs. These latter two taxa are closely related to *Paleanotus* with similar anterior end configurations and chaetal types. Species of *Paleanotus* are distinguished from *Treptopale* by the possession of predominantly asymmetrical notochaetal paleae and from species of *Hyalopale* with a full complement of paleal notochaetal types (Perkins 1985; key, this paper).

Paleanotus species are found among interstices of coral and rocky reefs; dead shell middens on sand or mud; fouling accretions on wooden platforms or hulls of boats; branchial chambers of molluscs and crustaceans; among *Mytilus*, bryzoan, tunicate and algal encrusting communities on jetty piers; and associated with tubiculous polychaete colonies. *Paleanotus* species possess a pair of stylets with brown-coloured roughened distal tips, like sandpaper, that can rasp away at prey. Habitat and stylet structure indicates both a scavenging and quasi-commensal mode of life (CW, per.obs.).

Paleanotus has a specific arrangement of cirri of the anterior three segments and a degree of retractability of these segments in association with a flexible nuchal fold; a pattern in common with that observed in the majority of Chrysopetalinae taxa. The prostomium appears fused between the anterior three segments with the following cirri pattern: segment 1 with two pairs of cirri; segment 2 with dorsal cirri, notochaetae, neurochaetae but ventral cirri absent; segment 3 with dorsal cirri, notochaetae, neurochaetae and ventral cirri present (Fig. 8A). Retraction of the anterior end makes the position of tentacular ventral cirri variable; anterior, adjacent or slightly posterior to the palps.

Distinctive glands in mature *Paleanotus* males and females are described for the first time. Horizontal, elongate, granular textured glands and 'flower' shaped glands are observed within the notopodia posterior to the dorsal ceratophore; associated oil globules are also found (Figs 2H, I; 4A, I; 6D). Inter-ramal cilia appear longer in mature specimens and parapodial white pigmentation and 'white granules' are seen in the males of one species. These latter structures have been described for mature specimens in the related taxon *Treptopale* (Watson 2010).

Paleanotus inornatus n. sp.

(Figs 1C; 2A-I)

Type material. Holotype: NTM W.25390, Western Pacific Ocean, Australia, Queensland, GBR, Day Reef, 14°28.33'S, 145°31.41'E, CReefs, LI-10-074, clean coralline rubble, 5–10 m, coll. C. Buxton, Sep 2010, (26E, L: 2.2 mm, W: 0.5 mm). Paratypes: NTM W.25391, same locality as holotype (4 NE).

Other material examined. NTM W.23679, Day Reef, 14°26.87'S, 145°29.95'E, Stn. LI-09-048, rubble, 30 m, coll. CReefs, Feb 2009, (4: 30E, L: 2.2mm, W: 0.55 mm; 33E, L: 3.4 mm, W: 0.65 mm; 2NE); NTM W.23692, Yonge Reef, 14°34.38'S, 145°31.13'E, CReefs, LI-10-126, rubble, coll. C. Buxton, Sep 2010, (1, 31E, L: 2.2 mm, W: 0.65 mm); NTM W.23684, MacGillivray Reef, 14°38.87'S, 145°29.19'E, CReefs, LI-10-041, coral rubble, 14–20 m, Aug 2010, (3NE); NTM W.25631, CReefs, LI-10-034, rubble, 14–20 m, Aug 2010, (1E) ; NTM W.23203, North Direction Island, 14°44.62'S, 145°30.72'E, CReefs, LI-08-19, rubble, 2 m, coll. C. Glasby, Apr 2008, (7:1, 23 E, L:3 mm, W: 0.5 mm); NTM W.25632, High Rock, 14°34.38'S, 145°31.13'E, CReefs, LI-10-135, clean coralline rubble, 30 m, coll. C. Buxton, Sep 2010, (4: 1,23E, L: 2.3 mm, W: 0.45 mm); NTM W.23661, Snake Pit, 14°40.20'S, 145°34.04'E, CReefs, LI-10-054, *Halimeda* beds, 30 m, coll. CReefs, Feb 2010, (1 male, 25NE); AM W.23344, Outer Barrier, Cooks Passage, Cod Hole, coral rubble, 10 m, coll. A. Murray, Sep 1995, (1, 31E, W: 0.76 mm, female); NTM W.23712, Coral Sea, Flora Reef, 16°45'S, 147°43.7'E, fine rubble, 42 m, coll. C. Buxton, Oct 2010, (1, 17 NE, W: 0.47 mm); NTM W.23194, Heron Island, CReefs, HI-09-001, North Wistari Reef, 23°27.11S, 151°52.02 E, Nov 2009, (1NE); NTM W.23192, CReefs, HI-09-045, Harry's Canyons, 15 m, rubble, Nov 2009, (1, 26E); NTM W. 23659, CReefs, HI-10-040, 12 m, rubble under overhang, coll. M. Capa, Nov 2010, (1); NTM

W.3021, Arafura Sea, NT, Channel Island, Darwin, washings Halimeda, 0.1 m, coll. C. Watson, Oct 1985, (1, 22NE, L: 3.4 mm, W: 0.66 mm); NTM W.25787, Indian Ocean, WA, Kimberleys, Stn. 127-146 K13, 14 m, coll. L. Avery, Sep 2013, (1, 36E); NTM W.23187, Ningaloo Reef, off northern passage near Tantabiddi, 21°51.15'S, 113°2.04'E, CReefs, NR-08-3B, coll. N. Bruce, June 2008, (fragment); NTM W.23453, CReefs, NR-10-021, coral blocks, 30 m , coll. Merrick, May 2010, (1NE); NTM W.23654, Outer Ningaloo Reef, 22°39.33'S, 113°37.00'E, CReefs, NR-09-004, May 2009, (1NE); NTM W.23726, Norwegian Channel, Stn. CReefs, NR-10-021, coral blocks, 30 m, coll. Merrick, May 2010, (1NE); AM W.33493, North end of Long Island, Stn.WA 522, 28°27.9'S, 113°46.3'E, dead coral substrate covered in coralline & brown algae, 5–6 m, coll. C. Bryce, May 1994, (1); AM W.33491, Goss Passage, 28°25.5'S, 113°47'E, Stn. 526, dead coral substrate embedded in fine sediment at base of reef slope, 33 m, coll. P. Hutchings, May 1994, (3: 1, 39E); AM W.36171, Dampier Archipelago, Legendre Island, Stn. WA 645, 14 m, Aug 2000, coll. P. Hutchings & L. Avery, (1NE); AM W. 36168, Angel Island, Stn. WA 642, dead coral, 14 m, Aug 2000, coll. P. Hutchings & L. Avery, (1NE); NTM W.7573, New Guinea, Madang, Sandy Bay behind Wongat Island, 5°10'S, 145°50'E, Stn. 99, coral rubble in sand, 3-6 m, coll. J.R. Hanley, 19 Oct 1991, (1, 45E, male, L: 6 mm, W: 0.7 mm); NTM W.25261, Indonesia, Flores, Maumere, 8°35'S, 112°13'E, Halimeda and rubble, 3-6 m, coll. B. Russell, Nov 1991, (fragments); NTM W.25620, Philippines, Luzon, Batangas province, Batangas Bay, Sombrero Island, 13°41.91'N, 120°49.37'E, coral blocks, 20 m, coll. G. San Martin, 9 Dec 2010, (1, 19 E, L: 2.2 mm, W: 0.7 mm, plus fragments); CAS 185685, Bonito Island, 13°63'N, 120°95'E, coral rubble, 1-15 m, coll. C. Piotrowski, 16 May 2011, (1E, ovigerous female).

Paleanotus inornatus species complex

AM W.23352, Tasman Sea, NSW, Middleton Reef, Stn. 8, 15 m, coll. P. Hutchings, Dec 1987, (2 NE); AM W.23354, Elizabeth Reef, Stn. 43, reef flat, Dec 1987, coll. P. Hutchings, (2E); AM W.38737, southern NSW, Tathra, Little Kianinny Gutter, Stn. NSW 2397, in algae *Delicea pulchra*, Mar 2004, coll. AM team, (1, 19E, L: 1.5 mm, W: 0.49 mm); AM W.38736, Stn. NSW 2388, Guerilla Bay, in algae *Dilophus intermedius*, Mar 2004, (5); NTM W.23464, Eastern Pacific Ocean, French Polynesia, Moorea, Stn. 487, outer reef between Opunohu Bay & Motus Islands, 15–18 m, coll. J. Moore, Oct 2010, (1NE, ovigerous female).

Description. (based on holotype and other material where noted). Slender, pale to white bodied with dark gut (gut often red when alive, blackish/green when preserved). Flat dorsum with paleael notochaetae silvery sometimes with pale golden shine; neuropodia tucked under notopodia. Live eye colour bright red. Notopodia of chaetiger 1 with 2–4 short paleae with broad tips; same shape as lateral paleae down body.

Notochaetae of mid-body notopodium composed of 2 lateral paleae either both with broad symmetrical tips or superior one slightly pointed; posterior one always broad-tipped with 5–7(8) ribs. Subunit 1 paleae number 1–2; slender, short, pointed distally, with 5–6 ribs (Fig. 2A, H, I). Main paleae rounded distally with very fine serration on brow leading to small apical space and apice. Ribs number 11–13, 14 (15) including about 5 fine, b.l. ribs, most visible basally; very finely spaced horizontal straie. Dorsal cirri, slender, subulate (Figs 1C, 2A, I). Broad median paleae (particularly distally), number 3, with 10–12 ribs; very finely raised 4–7 b.l. ribs present, central raised rib absent (Fig. 2B, H).

Neurochaetae of mid-body neuropodium composed of 2 long, slender superior falcigers, 2–3 shorter long falcigers (Fig. 2D); 10 mid- superior, medium length falcigers with longer basal serration; 10 shorter falcigers mid-inferior position; 10 inferior shortest falcigers; total number about 35. Ventral cirri subulate (Fig. 2A, C–G).

Remarks. *Paleanotus inornatus* n. sp. is a small species characterized by broad, distally rounded main paleae and distinctive, broad median paleae that lack distinct raised ribs. These features are present in all northern Australian reefal material: GBR, QLD; Darwin, NT; Kimberley and Ningaloo Reef, WA. Majority of mature specimens attain a length to 4 mm, width to 0.6 mm and to 36 segments entire. One New Guinea male specimen was larger at 45 segments (length 6 mm, width 0.7 mm).

Material from N and NW Australia possess slightly different shaped median paleae group in comparison to that from NE Australia. The tallest median palea is more slender and the shortest is broader compared to the median paleae group of GBR specimens (cf Fig. 2B & 2H); there is also displayed a more obvious 'broken line' pattern. The rib numbers of the median and all paleae groups are in the same range between specimens from western and eastern Australian coasts. It is possible West Australian coast *P. inornatus* n. sp. material is a different species, but until comparative DNA work is undertaken there is only one species identified.



FIGURE 2. *Paleanotus inornatus* n. sp. A. Notopodium in part and neuropodium, NTM W.23684: MacGillivray Reef, GBR; B. Median paleae and medial main paleae, NTM W.25390: Day Reef, GBR; C–G: Neurochaetal types, NTM W.23684: MacGillivray Reef, GBR; H. Male, notopodium and neuropodium (neurochaetae omitted), NTM W.23726: Ningaloo Reef, WA; I. Ovigerous female, notopodium, CAS 185685: Philippines. Abbreviations: e = egg, gl = gland, la = lateral paleae, me = median paleae, sp = sperm. Scale bars: $B = 30 \mu m$, $C-G = 10 \mu m$, $H = 100 \mu m$.

Examined material of *P. inornatus* n. sp. from the Western Pacific (New Guinea, Indonesia and Philippines) and Eastern Pacific (Moorea) exhibit main and median paleae shape and paleal rib numbers similar to those of the GBR. Females possessing typical 'flower' glands, large eggs and oil globules are observed in GBR, Philippine and Moorea specimens (Fig. 21).

In comparison to other *Paleanotus* species described in this paper *P. inornatus* n. sp. forms the most widespread Indo-Pacific cryptic complex. Individuals examined from the Red Sea and Eastern Mediterranean reefs are being described as a new species (Watson & Chatzigeogiou, submitted) and it has been recorded from Moorea in the eastern Pacific. *Paleanotus inornatus* species complex is found from eastern Australian localities at Middleton and Elizabeth Reefs, Tasman Sea and southern NSW. Tropical chrysopetalid fauna may be recorded in these latter areas (e.g., *Treptopale homalos* from Middleton Reef by Watson 2010).

Paleanotus inornatus n. sp. is commonly found sympatrically with, and has some morphological similarity to, *P. adornatus* n. sp. Both possess similar sized small bodies and number of segments, translucent to silvery/pale golden coloured paleae with a dark gut often showing through and a flat dorsum with neuropodia tucked under notopodia. Observation of chaetal differences between the two species reveal *Paleanotus inornatus* n. sp. possess lateral paleae with broader tips; broader, rounded main paleae with slightly higher rib number (11–14 (15)) vs 11–13 (14)); finer horizontal striae, and very 'clean, smooth' paleael surface with little ornamentation. *Paleanotus inornatus* n. sp. also possesses much broader median paleae with multiple broken line ribs compared with the pointed apices and single, overt raised rib in *P. adornatus* median paleae (cf Figs 2B & 3C).

Etymology. The specific name, *inornatus*, comes from the Latin and refers to the 'unadorned' median paleae group possessing only a faint 'broken line' type of sculpture, lacking raised and ornamented ribs.

Habitat / **Distribution.** *Paleanotus inornatus* n. sp. is found primarily from a rubble habitat in coral reefs of the northern and southern GBR, northern Australia, NW Australia and New Guinea, Indonesia and the Philippines; intertidal to 42 m. *Paleanotus inornatus* species complex includes material examined from Moorea, eastern Pacific; reefs of the Tasman Sea and temperate, mainland rocky coasts of NSW.

Paleanotus adornatus n. sp.

(Figs 1D; 3A–G)

Type material. Holotype: NTM W.23677, Western Pacific Ocean, Australia, Queensland, Great Barrier Reef, MacGillivray Reef, 14°39.41'S, 145°29.68'E, CReefs, LI-09-034, coral rubble, 2–12 m, coll. C. Watson, Feb 2009, (27E, L: 3.0 mm, W: 0.75 mm). Paratypes: NTM W.25634, same locality, (4, NE).

Other material examined. NTM W.23451, MacGillivray Reef, 14°26.87'S, 145°29.95'E, CReefs, LI-10-028, rubble, 24 m, coll. M. Capa, Aug 2010, (1NE); NTM W.23687, Day Reef, 14°28.33'S, 145° 31.41'E, CReefs, LI-10-074, clean coralline rubble, 5-10 m, coll. C. Buxton, Sep 2010, (6); NTM W.25635, Day Reef, 14°26.87'S, 145°29.95'E, CReefs, LI-09-048, rubble, 30 m, coll. CReefs, Feb 2009, (1); NTM W.23689, Yonge Reef, north front, 14°34.38'S, 145° 31.13'E, CReefs, LI-10-126, coarse sand, 25 m, coll. C. Buxton, Sep 2010, (1, 35E, L: 3.5 mm, W: 0.7 mm); AM W.47532, Lizard Island, Stn. 76 B-06.15.2, coral block study, coll. P. Hutchings, 1976, (1NE); NMV F.214513, Coral Sea, wreck of HMS Pandora, 11°21.25'S, 143°59.17'E, Stn. NQ 18, 1982, (1E); AM W.23349, North West Ruby Reef, 15°44'S, 145°47'E, rubble from bommie, 9–14 m, coll. I. Loch, Dec 1984, (1, 19E); NTM W.25636, Flora Reef, 16°45'S, 147°43'E, fine rubble, 42 m, coll. C. Buxton, Oct 2010, (1, 13NE, W: 0.7 mm); NTM W.25633, Heron Island, Harrys Bommie, 23°27.62'S, 151°55.77'E, CReefs, HI-10-051, sand & rubble, 12-16 m, coll. C. Buxton, Nov 2010, (2); NTM W.23463, CReefs, HI-10-020A, rubble, coll. C. Buxton, Nov 2010, (1, 19NE, L: 1.00 mm, W: 0.5 mm); NTM W.23191, Heron Channel, Sykes Reef, 23°25.94'S, 151°2.02'E, CReefs, HI-09-018, Nov 2009, (1NE); NTM W.23660, Heron Channel, CReefs, HI-10-055, 23°26.98'S, 151°54.75'E, sand, 30 m, coll. C. Buxton, Nov 2010, (4, NE); NTM W.3021, Arafura Sea, NT, Darwin, Channel Island, Halimeda, LWS, Oct 1985, coll. P. Alderslade, (1, 22E, L: 3.4 mm, W: 0.66 mm); NTM W.13179, Channel Island, under bridge 0.1 m, Halimeda & coral rubble, coll. C. Watson, Dec 1986, (1, 25E, L: 2.1 mm, W: 0.74 mm); AM W.23709, WA, Kimberley, Adele Island, 15°31.7'S, 123°11.61'E, Stn.3 K09, subtidal, 14 Oct 2009, coll. WAM & Woodside Kimberley Survey, (fragments); AM W.47531, Angel Island, Dampier, Stn. WA639, coll. P. Hutchings & L. Avery, 4 Aug 2000, (1, 18NE); NTM W.23725, Outside Channel South, Ningaloo Reef, 22°42.33'S, 113°37'E, CReefs, NR-10-008, 18 m, May 2010, (1, 17NE); NTM W.23187, Ningaloo Reef, off northern passage near Tantabiddi, 21°51.15'S, 113°2.04'E, CReefs, NR13B, coll. N. Bruce, June 2008, (1NE);

NTM W.25643, Western Pacific Ocean, Philippines, Luzon, Batangas Bay, Sombrero Island, coral blocks, 17 m, coll. G. San Martin, Dec 2010, (1NE, ovigerous female); CAS 189079, Maricaban Island, Bethelhem, 13°67'N, 120°.84'E, 21 m, coll. C. Piotrowski, May 2011, (1NE); NTM W.25642, Eastern Indian Ocean, Andaman Sea, Thailand, West Ko Similan, 8°38'N, 97°38'E, from live *Montipora* corals, coll. A. Nateewathana, 15 Feb 1981, (1, 33E, L: 3.4 mm, W: 0.6 mm).

Paleanotus adornatus species complex

Broad median type

NTM W.25644, QLD, GBR, North Direction Island, 14°44.62'S, 145°30.72'E, CReefs, LI-08-019, coll. C. Glasby, Apr 2008, (1NE); SIO A3629, Indonesia, West Papua, Raja Ampat, Chicken Reef , coll. G. Rouse, 2013, (1E); NTM W.13177, Flores, Maumere, reef off Sao Wisata, coral rubble with encrusting sponges, algae, silty sand, 2.5 m, coll. C. Watson, Aug 1987, (3: 14 NE, 11E, 21NE, W: 0.72 mm); NTM W.13178, Maumere, rubble, algae, sand sample, 24–27 m, coll. B. Russell, Nov 1991, (fragments).

Temperate type

AM W.33487, Geordie Bay, WA, 31°59.5'S, 115°35'E, algae, 10 m, coll. R. Springthorpe, 20 Dec 1983, (1); AM W.23350, Cathedral Rock, Rottnest Island, 32°015'S, 115°27'E, foliose red algae, 6 m, coll. R. Springthorpe, 1983, (1, 34E); NTM W.5124, Albany, North of Geak Point, Stn. RH88-10, 34°58'S, 117°54'E, *Posidonia* roots & fine sand, coll. C. Erseus, Jan 1988, (4: 1, 33E, L: 3.5 mm, W: 0.9 mm).

Description. (based on holotype and other material where noted). Live body colour whitish with transparent to silvery or pale golden coloured main paleae main covering dorsum; dark red eyes; red pigment in gut plus red spot on ventrum, base of neuropodia. Neuropodia extend little past notopodia.

Notochaetae of mid-body notopodium composed of 2 laterals, broadly pointed distal tips, 5–7 (8) ribs; 1–2 short, pointed subunit 1 paleae, with 4–6 (7) ribs (Fig. 3A, D). Main paleae with 11–13 (14) ribs; 1–2 dominant full length finely raised ribs (close to straight margin), plus light, part- length b.l. ribs especially visible basally. Main paleae with slight sloping brow, elevated apices, widely spaced horizontal striae; dorsal cirri 3/4 L of main paleae (Figs 1D; 3A–G). Median paleae neatly 'tuck in' to main paleae group; number 3, slender, pointed distally, with (8) 9–11 ribs, distinct raised central rib; other lightly raised ribs may be present basally (Fig. 3C, D–E).

Neurochaetae of mid-body neuropodium composed of 2 long superior falcigers, 2 shorter falcigers with basal serration; 12 mid-group, medium length falcigers with basal serration; 6–8 inferior group shorter, slender falcigers; total number about 20–25.

Remarks. The small species *Paleanotus adornatus* n. sp. is described from coral rubble collected from the northern and southern GBR. The largest GBR specimen is 35 segments entire, length 3.5 mm and width 1.0 mm. The species is characterized by main paleae with a slight sloping convex margin, a 'clean' dorsal surface with 1-2 full length finely raised ribs and widely spaced horizontal striae (Figs 1D; 3A-E).

The species is recognizably present in South-East Asia (Indonesia and Philippines), across NW Australia and north to the Andaman Sea, Thailand. *Paleanotus adornatus* n. sp. from GBR to the Philippines possess median paleae with narrow, pointed apices and one prominent central raised rib. Darwin, NW Australian and Thailand material is similar but with slightly broader and less pointed median paleae (cf Fig. 3C–D and 3E).

Paleanotus adornatus n. sp. and *P. inornatus* n. sp. are small, similar looking, pale-bodied species with transparent to pale gold paleae and a dark gut showing through. Both species are commonly found sympatrically in coral rubble. The most obvious difference between them is the more pointed median paleae with a distinct raised central rib in *P. adornatus* n. sp. contrasting with very broad median paleae lacking raised ribs in the latter (detailed comparison in Remarks *P. inornatus* n. sp.).



FIGURE 3. *Paleanotus adornatus* n. sp. A–C: NTM W.23677: Lizard Island, GBR. A. Lateral group and main paleae; B. Micropic of main palea; C. Median and medial main paleae; D. Micropic of notopodium, NTM W.23660: Heron Island, GBR; E. Micropic of notopodium, AM W.7531: Dampier, WA. F–G: *P. adornatus* broad form. F. Micropic of notopodium and neuropodium, NTM W.25644: North Direction Island, GBR; G. Micropic of notopodium and neuropodium, SIO A3629: Indonesia, West Papua, Raja Ampat. Abbreviations: me = median paleae, mm = medial main paleae. Scale bars: A, C = 100 μ m.

Paleanotus adornatus n. sp. can be confused with *Paleanotus aquifolia* n. sp. especially in preserved material from NE Australian reefs. The colouration is different in the live animals: *P. adornatus* n. sp. has transparent to pale gold paleae and a white body with dark red piment in the gut and dark red eyes. Paleal fans lie flat across the dorsum and neurochaetae extend a small way beyond notopodia. *Paleanotus aquifolia* n. sp. has a yellow body, dark maroon eyes and a more distinct golden shine to paleal fans that appear less flattened; neurochaetae extend out beyond dorsum. The two species may be found sympatrically although the micro-habitat differs: *P. adornatus* n. sp. is commoner in cleaner coral substrates and *P. aquifolia* n. sp. from sedimented coral rubble and sandy gravels.

Overall the shape of lateral, main and median paleae of *P. adornatus* n. sp. is marginally broader compared to those of *P aquifolia* n. sp. However the numbers of ribs of laterals, main and median paleae partially overlap in *P. adornatus* n. sp. *and P aquifolia* n. sp. lateral paleae ribs 5-7 vs 4-5(6); main paleae ribs 10-13(14) vs 9-11(12); median paleae ribs 9-11 vs 7-9(10). *Paleanotus adornatus* n. sp. main paleae appear more 'clean' with only two finely raised ribs and wider spaced horizontal striae in comparison to *P. aquifolia* n. sp. with many broken line raised ribs. Comparing the distal third of the main paleae between the two species, one can see the brow of *P. adornatus* n. sp. is broader and in *P. aquifolia* n. sp. the brow is more sloping and narrower (Fig. 1D & 1E).

Paleanotus adornatus n. sp. and *P. latifolia* n. sp. both possess long, pointed median paleae with a raised central rib. Both species are found on the NW Australian coast but do not occur sympatrically. Comparing the distal third of the main paleae between the two species, one can see clearly the different shape of the main; lateral paleae shape is also different (cf Fig. 1D & 1F).

Paleanotus adornatus species complex includes both tropical and temperate forms. The tropical 'broad median type' observed from GBR and Indonesia possesses broader paleael types, especially median; main and median also have more overt finely raised ribs (Fig. 3F, G). The paleael rib ranges are similar across all mentioned material.

Paleanotus adornatus species complex 'temperate type' occurs from three localities in SW Western Australia. Specimens possess similar shaped main and median paleae with central raised rib, to the tropical *Paleanotus adornatus* n. sp. However the temperate group have mustard coloured bodies and gold paleae in comparison to pale bodied and transparent silvery main paleae of the latter; plus the main paleae lack the two full length finely raised ribs and the median paleae appear comparatively longer. Future DNA analysis of these *P. adornatus* forms will likely prove new undescribed species are present.

Etymology. The specific name, *adornatus*, is from the Latin meaning 'adorned' and refers to the median paleae group, possessing a single, central raised and ornamented rib, and the main paleae with 1–2 full length lightly raised ribs.

Habitat / **Distribution**. *Paleanotus adornatus* n. sp. is found from coarse sand, coral rubble habitats of NE Australian reefs (Lizard Island, Heron Island, inshore GBR reefs); Philippines; N and NW Australia and Andaman Sea, Thailand in depths of 1–42 m.

Paleanotus aquifolia n. sp.

(Figs 1E; 4A-I)

Type material. Holotype: NTM W.25615, Western Pacific Ocean, Australia, QLD, GBR, MacGillivray Reef, 14°39.41'S, 145°29.68'E, CReefs, LI-09-034, coral rubble, 2–12 m, coll. C. Watson, Feb 2009, (29E, L: 3.0 mm, W: 0.7 mm). Paratypes: NTM W.125710, same locality as holotype, (3: 1, 39E, L: 5.2 mm, W: 0.7 mm).

Other material examined. NTM W.23451, MacGillivray Reef, 14°39.41'S, 145°29.68'E, CReefs, LI-10-028, coral rubble, 24 m, coll. M. Capa, Aug 2010, (2); NTM W.23440, Martin Reef, 14°38.73'S, 145°27.2'E, CReefs, LI-10-140, rubble & sediment, 18 m, coll. L. Avery, Aug 2010, (1, 44NE, W: 1.1 mm, ovigerous female); NTM W.23686, Martin Reef, CReefs, LI-10-035, silty sand & rubble, 5 m, coll. C. Watson, Sep 2010, (1, 33NE); NTM W.23204, Lizard Island, North Point, 14°38.73'S, 145°27.2'E, CReefs, LI-08-20, rubble, 2 m, coll. C. Watson & N. Bruce, Apr 2008, (1, 32NE, L: 4 mm, W: 0.8 mm); NTM W. 23449, North Direction Island, CReefs, LI-10-009, sand & rubble, 7–8 m, coll. M. Capa, Aug 2010, (1, 21NE, male, W: 0.9 mm); NTM W.23675, High Rock, 14°34.38'S, 145°31.13'E, CReefs, LI-10-135, clean coralline rubble, 30 m, coll. C. Buxton, Sep 2010, (1, 26E, L: 2.5 mm, W: 0.7 mm); NMV F.214514, Coral Sea, wreck of HMS *Pandora*, 11°21.25'S, 143°59.17'E, Stn. NQ 18, 1982, coll. G. Poore & H. Lew Ton, (1, 28NE, L: 5 mm); MV F.125884, Fantome Island, 18°40'S, 146°31'E, Stn NQ14, coral rubble, 9 m, coll. G. Poore & H. Lew Ton, Dec 1982, (1, 26NE); NTM W.23646, CReefs, HI-10-

051, sand & rubble, 12–16 m, coll. C. Buxton, Nov 2010, (3:1, 17E, L: 1.00 mm, W: 0.5 mm; 2 NE); NTM W.23655, Harry's Bommie, CReefs, HI-10-002, dead coral, 10 m, Nov 2010, (1E, W: 0.5 mm); NTM W.25617, Philippines, Luzon, Balayan Bay, Batangas, Sombrero Island, coral blocks, 17 m, coll. G. San Martin *et al.*, Dec 2010, (1, ovigerous female); NTM W.25843, same locality, coral & sponges, 1–2 m, coll. C. Watson, Dec 2010, (1, 35E, ovigerous female).

Description. (based on holotype and other material where noted). Live colour yellow body, prostomium with two pairs of dark maroon eyes. Paleal fans appear less flattened; with distinct golden shine. Neurochaetae extend out a little from paleal fans. Notochaetae of mid-body notopodium composed of 2 (3) slender, pointed laterals with 4-6 ribs; 1 small pointed, su1 palea often present with 4–5 ribs (Fig. 4A, C, I). Main paleae number to 10, with 9, 10–12 ribs with up to 9 b.l. ribs, 2 often full length. Long, narrow- shaped main paleae possess pointy apices with small hoods; sloping brow with distinct finely raised margin serration (Figs 1E; 4B, C, I). Median paleae number 3 with 7–9 (10) ribs and central raised rib; pointed distal tips (Fig. 4A, B); dorsal cirri 2/3 length of main.

Neurochaetae of mid-body neuropodium composed of 2 superior very long falcigers with fine serration; 2 midsuperior long falcigers (not much shorter than superior) with long serrations especially basally; about 6–8 midgroup falcigers with basal serrations; 4–6 inferior-group falcigers with long, slender blades; ventral cirri subulate (Fig. 4C, D, H, I).

Remarks. *Paleanotus aquifolia* n. sp. is characterized by long, narrow main paleae with a distinct sloping brow; comparatively narrower lateral and sub-unit 1 paleae and robust neurochaetal types. Chaetal morphology and body measurements are similar between Lizard Island localities, reefs off Townsville and Heron Island, GBR. *Paleanotus aquifolia* n. sp. is found only along the NE Australian coast and the Philippines.

The Philippine female has large eggs in clusters stuck interamally and on the dorsal main paleae (220 μ m diameter). Four eggs take up most of the body cavity and have similar measurements to that of the Lizard Island ovigerous specimen. Numbers and shapes of paleae types and rib numbers are also exactly the same as those found in GBR material. A Lizard Island male individual was observed to have sperm in lumps attached to the ventrum plus copious oil globules. As observed in other *Paleanotus* species the inter-ramal cilia appear particularly long in mature individuals and inter-ramal glands are enlarged (Fig. 4 A, C, I).

On the NE Australian coast *P. aquifolia* n. sp. can be confused with *P. adornatus* n. sp. as the numbers of ribs of laterals, main and median overlap. The narrow, pointed shape of the main and median paleae and longer, slender articles of the neurochaetal falcigers distinguish *P. aquifolia* n. sp. from *P. adornatus* n. sp. (full comparison under *P. adornatus* n. sp. Remarks).

Paleanotus aquifolia n. sp. from GBR appears most similar to *Paleanotus latifolia* n. sp. from NW Australian coast (Darwin to Ningaloo Reef). Both species possess a similar body and eye colouration and are found in coral rubble with a predominantly silty sand component. Morphological similarities shared between east and west coast species include possession of comparatively narrower lateral paleae and robust apices forming a peak in main and median paleae. In both species the neurochaetae include robust, mid-superior falcigerous blades almost the same length as those of superior falcigers (cf Figs 4D, E & 5D, E).

Paleanotus aquifolia n. sp. appears to be a slightly larger species (largest 44 E, length 5.6 mm, width to 1.1 mm) compared to *Paleanotus latifolia* n. sp, (largest 28E, length 4.4 mm, width to 0.7 mm). The main paleae shape is different in each species. Main paleae brow of *Paleanotus aquifolia* n. sp. is narrow and sloping compared to the brow of *P. latifolia* n. sp. which is rounded to sloping with distinctive close-set brow serration and apices slightly more centred (Fig.1E cf 1F). There are also differences in numbers of paleae types and ribs. Lateral paleae number is less in *P.aquifolia* n. sp. compared to *latifolia* (2 vs 2–3); main paleae rib numbers less (11–13 vs 12–14); 1 very small sub unit1 palea (1–2 ribs) vs often 2 broad sub unit 1 paleae with up to 7 ribs (cf Figs 4I & 5A).

Paleanotus aquifolia n. sp. occurs in more sandy micro-habitats in clear water coral reefs of the NE coast and *P. latifolia* n. sp. in muddier coral reef areas in sediment laden waters of the N and NW Australian coasts.

Etymology. Species name *P. aquifolia* n. sp. is from a Latin compound noun, meaning 'pointed leaf'. It refers particularly to the shape of the pointed apices of main and median paleae.

Habitat / Distribution. *Paleanotus aquifolia* n. sp. is recorded from the Western Pacific Ocean: NE Australia, Great Barrier Reef (north and south), and the Philippines, South-east Asia. Habitat is predominantly coral rubble and sediment; depth 2–30 m.



FIGURE 4. *Paleanotus aquifolia* n. sp. A–B: NTM W.23449: North Direction Island, GBR. A. Notopodium and neuropodium (neurochaetae omitted); B. Median and main paleae detail; C. Ovigerous female, notopodium, NTM W.23440: Martin Reef, GBR. D–H: Neurochaetal types. D. Superior; E. Mid-superior; F–G. Mid-group; H. Inferior group; I. Micropic, notopodium in part & neuropodium; NTM W.25843: Philippines. Abbreviations: c = cilia, e = egg, la = lateral paleae, me = median paleae, mm = medial main paleae, o. g = oil globules, sp = sperm, su 1 = sub-unit 1 palea. Scale bars: A = 200 μ m, B = 30 μ m, C =100 μ m, D–H = 30 μ m.

Paleanotus latifolia n. sp.

(Figs 1F; 5A–K)

Type material. Holotype: NTM W.23654, Eastern Indian Ocean, WA, Outer Ningaloo Reef, 22°39.33'S, 113°37.00'E, CReefs, NR-09-004, coll. CReefs team, May 2009, (1, 27E, L: 2.6 mm, W: 0.7 mm).

Other material examined. NTM W.23188, Ningaloo Reef, off northern passage near Tantabiddi, CReefs, NR-08-9B, 21°51.40'S, 114°15'E, coll. N. Bruce, June 2008, (fragment); NTM W.23189, CReefs, NR-08-9A, coll. N. Bruce, June 2008, (1NE); NTM W.23725, Outside Channel South, Ningaloo Reef, 22°42.33'S, 113°37'E, CReefs, NR-10-008, 18 m, May 2010, (1, 17NE, anterior end); NTM W.23491, Ningaloo, CReefs, NR-08-48, (fragment); NTM W.25836, Ashmore Reef, 12°17.76'S, 123°1.63'E, Stn. K13 134-75, 3 m, 2013, coll. L. Avery, (1NE); NTM W.23709, Kimberley, Adele island, 15°31.7'S, 123°11.61'E, Stn. 3 K09, subtidal, Oct 2009, WAM & Woodside Kimberley Survey, (1, 17NE,W: 0.7 mm); NTM W.23710, Stn. 2 K09, 11-14 m, same collector, Oct 2009, (fragments); NTM W.25627, Stn.93 K12, coll. J. Finn, Oct 2012, (1, 31E); NTM W.25628, Stn.110 K12, 14°05'S, 125°36'E, coll. J. Finn, Oct 2012, (1, 24E, ovigerous female, L: 2.5 mm, W: 0.6 mm); NTM W.13179, Arafura Sea, NT, Darwin, Channel Island, 12°33'S, 130°52'E, under bridge, 0.1 m, Halimeda & coral rubble, coll. C. Watson, Dec 1986, (2: 1E, 25 segs, L: 2.1 mm, W: 0.74 mm); NTM W.13132, Darwin Harbour, Fannie Bay, Stn. D25A, fine sand & gravel, 4 m, coll. J.R. Hanley, July 1993, (fragment, W: 0.7 mm); NTM W.13115, Central Darwin Harbour, Stn. DW 51A, intertidal, gravel some sand, coll. J.R. Hanley, July 1993, (1NE); NTM W.13102, Stn. DW 53A, gravel & some sand, 8 m, coll. J.R. Hanley, Mar 1994, (1, 24NE, W: 0.8 mm); NTM W.25622, Stn. EA2/2, East Arm boat ramp, 12°29.5'S, 130°54'E, (fragment); NTM W.25629, Andaman Sea, Thailand, Similan Island, 8°38'N, 97°38'E, dead corals, coll. A. Nateewathana, Feb 1981, (4: 1, 30E, female with eggs, L: 3.4 mm, W: 0.6 mm; 1, 30E, male, L: 2.90 mm, W: 0.70 mm; 2 anterior ends); NTM W.25630, West Similan Island, from live Montipora corals, coll. A Nateewathana, Feb 1981, (1, 34E, ovigerous female, L: 3.4 mm, W: 1.00 mm).

Description. (based on holotype and other material where noted). Elongate, small body; prostomium with two pairs of dark maroon eyes. Golden shine to main paleae covering dorsum. Mid-body notopodia with 2-3(4) pointed lateral paleae with 6–7 ribs; 1-2 sub-unit 1 paleae (often one larger, one smaller) with 6–8 ribs. Main paleae number to 10 with 12–14 (15) ribs; up to 9 b.l. ribs, 2 often full length. Main paleae with rounded brow, distinct peaked apices often with small hoods. Apices positioned slightly away from inner margin; inner distal quarter margin with fine serration similar to that of brow. Medial-most main palea slightly narrower with less asymmetric apex. Pointed median paleae number 3 with 10–12 ribs and central, full length raised rib (Figs 1F; 5A–C, I–K). Neurochaetae of mid-body neuropodium composed of 2 superior very long falcigers with fine serration; 2 mid-

superior long falcigers (not much shorter than superior) with long serrations especially basally; about 6–8 midgroup falcigers with basal serrations; 4–6 inferior falcigers with short, slender blades (Fig. 5D–H). **Remarks.** *Paleanotus latifolia* n. sp. is characterized by main paleae with a distinctive broken-line rib pattern and robust shape of its apical point and its position on a rounded brow that has fine serration on both distal margins.

and robust shape of its apical point and its position on a rounded brow that has fine serration on both distal margins. Females have small eggs (30–40 μ m diameter, Kimberley and Thailand (Fig. 5I)) suggesting a different larval strategy to *P. aquifolia* (Fig. 4C) and the other five small *Paleanotus* species possessing large eggs described herein.

Paleanotus latifolia n. sp. is only found along the eastern Indian Ocean rim including the Arafura Sea, N Australia. Specimens from Darwin, Kimberley, Ningaloo Reef and Andaman Sea, Thailand agree in similar paleael rib numbers across all localities. One slight difference is in the shape of the main paleae: a more rounded brow is seen in material from Darwin, Ningaloo Reef, Adele Island (Figs 1F, 5B,K) and Thailand; a more sloping brow in specimens from other localities on the Kimberley coast.

A more symmetrical medial-most main palea is often seen in the paleal fan of *Paleanotus* species but is particularly obvious in *P. latifolia* n. sp. as observed in Darwin and Kimberley individuals (Fig. 5 J). Mature males and females from Kimberley and Thailand agree in body and gamete size. This species clearly has more lateral paleae: one Thai specimen had the usual 2–3 laterals mid-body with 4–5 in the posterior end. *Paleanotus latifolia* n. sp. has been found sympatrically with *P. adornatus* n. sp. and *P. inornatus* n. sp. on the west Australian coast and with *P. silus* n. sp. in Thailand.

Etymology. Species name *latifolia* is from a Latin compound noun, meaning 'broad leaf'. It refers particularly to the shape of the distal end of the main paleae.



FIGURE 5. *Paleanotus latifolia* n. sp. A–H: NTM W.23710: Kimberley, WA. A. Male, notopodium; B. Main palea detail; C. Median palea detail; D–H: Neurochaetal types; I. Ovigerous female, micropic of notopodium, NTM W.25628: Kimberley, WA; J. Micropic, detail of median and medial main paleae, NTM W.13103: Darwin, NT; K. Main paleae detail, NTM W.13103: Darwin, NT. Abbreviations: e = egg, gl = gland, la = lateral paleae, ma = main paleae, me = median paleae, mm = medial main paleae, sp = sperm, su 1 = sub-unit 1 palea. Scale bars: $A = 100 \ \mu m$, $B-H = 30 \ \mu m$.

Habitat / **Distribution**. *Paleanotus latifolia* n. sp. is found from the Arafura Sea, NT (Darwin), west to the Kimberley on the Sahul Shelf and Ningaloo Reef, WA, eastern Indian Ocean. It is also present on islands off the west coast of Thailand in the Andaman Sea. Occurs in sandy gravels, silty sediments and sedimented coral rubble in 1-18 m.

Paleanotus silus n. sp.

(Figs 1G; 6A–L)

Type material. Holotype: NTM W.9309, Eastern Indian Ocean, WA, Ashmore Reef, west side, outer reef, Stn. RH 87-22, rubble, 6 m, coll. L. Vail, Apr 1987, (1NE, mid-body section 40 segments, L: 3.5 mm, W: 0.55 mm, ovigerous female).

Other material examined. NTM W. 23731, Arafura Sea, NT, Darwin, East Point, coral head, 0.1 m, coll. C. Watson, Feb 2011, (1, 16NE, male with sperm & oil globules, W: 0.5 mm); NTM W.23711, Kimberley, Adele Island, Stn. K09/10, 33°18, 115°39, 3.5 m, coll. WAM & Woodside Kimberley Survey, Oct 2009, (1NE, mid-body section 9 segments, W: 0.4 mm); NTM W.24187, Andaman Sea, Thailand, Similan Island, dead *Acropora* corals, 5 m, coll. A. Nateewathana, Feb 1981, (2: 1, 44E, L: 3.7 mm, W: 0.4 mm; 1, 115 NE, mid-body section, L: 10 mm, W: 0.4 mm).

Description (based on holotype and other material where noted). Long, very slender body with small parapodia becoming bead-like when full of gametes; short notochaetal paleae held in tight dense fans, coloured pale gold to transparent (observed in all material examined).

Prostomium with two lateral antenae, median antenna elongate with slight club shaped tip, two pairs large red eyes, two ovoid palps. Discrete nuchal fold not seen but highly glandular area present posterior to prostomium. Segment 1 very compressed laterally with one pair of dorsal and slender ventral tentacular cirri. Notopodium of segment 2 with dorsal cirri same shape, length as tentacular cirri plus fascicle of short, slender paleae with 6–7 ribs. Neuropodium of segment 2 with spinigerous neurochaetal fascicle, ventral cirri absent. Ventral cirri present from segment 3 onwards. Mouth opening ventrally appears as small tuck; stylets slender with brown tips (Fig. 6G).

Notochaetae of mid-body notopodium composed of (2) 3–4 pointed lateral paleae with slender, fine serrate margins, with 4–6 (7 ribs); broad, symmetrical 1–2 sub-unit 1 paleae with 7–8(9) ribs (Fig. 6A). Main number up to 11, with very shallow, tiny snub-nosed apices; serrate convex margin to apex, tiny hoods may be present. Ribs number 13-15 (16); majority with full length, fine b.l. pattern (e.g., out of 16 ribs, 12 b.l.). Apices of main paleae less asymmetric (Figs 1G, 6C). Median paleae number 3, similar length to main paleae with 8, 9, 10 (11) ribs; 1 raised rib plus 1–3 b.l. Median paleae slender, almost symmetrical in shape, medial-most slimmest (Fig. 6B), others slightly broader (Fig. 6C, F). Dorsal cirri 2/3 length of main paleae.

Neurochaetae of mid-body neuropodium number about 20 with all shafts and compound articles very slender: 2 superior long falcigers plus 1 slightly shorter (Fig. 6H, I); mid-group falcigers number about 10; inferior group falcigers about 5. Ventral cirri subulate, comparatively slender (Fig. 6D, H–L). Small pygidium with two short anal cirri.

Remarks. *Paleanotus silus* n. sp. (eastern Indian Ocean), has similar body proportions in common with its sister species *P. silopsis* n. sp. (western Pacific Ocean). The two species have a relatively narrow body width compared to the length, plus the largest number of segments and potential length compared to all other *Paleanotus* species treated herein. For example, the only entire specimen of *silus* possesses 44 segments, length 3.7 mm, width 0.4 mm; another long mid-body section of 115 segments has a length of approximately 10 mm, width 0.4 mm.

Further characters shared by *P. silus* n. sp. and *P. silopsis* n. sp. include: short neuropodia tucked in under notopodia; main paleae with the majority of their ribs finely raised in the 'broken line' pattern and median paleae near symmetrical in shape in comparison to the asymmetrical median seen in other *Paleanotus* species.

Paleanotus silus n. sp., in comparison to *P. silopsis* n. sp., possesses more slender median paleae with less number of ribs (10–11vs 12–14: cf Figs 6B & 7B) and slightly fewer number of main paleae ribs (13–15 vs 14–17). *P. silus* n. sp. main paleae have a longer serration brow pattern and the shallowest, tiny snub-nosed apices of all species; *P. silopsis* n. sp. has a finer brow serration and also very small apices (Fig. 1G cf 1H). Ventral cirri of *P. silus* n. sp. appear basally slender (Fig. 6D) and broader in *P. silopsis* n. sp.



FIGURE 6. *Paleanotus silus* n. sp. A–D: NTM W.9309: Ashmore Reef, WA. A. Ovigerous female, detail of lateral paleae, subunit 1 palea; B. Micropic of median palea; C. Detail of medial main and median paleae; D. Mid-body segment (neurochaetae omitted); E. Male with sperm and oil globules, micropic of mid-body segment, NTM W.23731: Darwin, NT; F. Median paleae group, NTM W.24187: Thailand; G–L: NTM W.23731: Darwin, NT. G. Anterior end, ventral view; H–L: Neurochaetal types. Abbreviations: roman numerals I–IV = anterior segments 1–4; I.a. = lateral antenna, m.a. = median antenna, me = median paleae, mm = medial main paleae, p = palp, s = stylet, su 1 = sub-unit 1 palea. Scale bars: A, C = 30 μ m, D, F = 100 μ m, E = 250 μ m, G = 70 μ m, H–L = 10 μ m.

All specimens (except the tiny fragment from the Kimberley) are mature with females possessing large eggs (100 µm diameter) and males, large rounded sperm and oil globules. Segments full of gametes often appear beadlike (Fig. 6 D, E). Falcigerous neurochaetae are very slender with slim articles and minimal serration (Fig. 6H–L). Morphological characters in *P. silus* n. sp. material from all eastern Indian Ocean and Arafura Sea localities agrees, especially the slim median paleae eg. similarity between Ashmore Reef and Andaman Sea specimens (respectively Fig. 6B & F).

Etymology. The species name *silus* is from the Latin and refers to the very small 'pug-nosed' shape of the apex of the main paleae.

Habitat / **Distribution.** *Paleanotus silus* n. sp. is present along the eastern Indian Ocean rim (northern Australia to Andaman Sea, Thailand) and found from coral rubble in 0.1-6 m.

Paleanotus silopsis n. sp.

(Figs 1H; 7A–D)

Type material. Holotype: NTM W.24186, Western Pacific Ocean, Australia, QLD, GBR, Lizard Island, Mermaid Cove, 14°38.76'S, 145°27.216'E, CReefs, LI-10-19, coral rubble, 2 m, coll. C. Watson, Sep 2010, (1, 100NE, L: 11 mm, W: 0.64 mm). Paratype: NTM W.22923, same details as holotype, (1, 30 E, L: 3.2 mm, W: 0.8 mm).

Other material examined. NTM W.24186, High Rock, CReefs, LI-10-134C, 6 m, coral rubble, coll. C. Buxton, Sep 2010, (1 fragment, male); NTM W.23203, Day Reef, CReefs, LI-09-019, coral rubble, 10 m, coll. M. Blazewicz-Paszokowycz, Feb 2009, (1NE); AM W.46151, Lizard Island, MI QLD 2359, (1); SIO A3633, Indonesia, West Papua, Raja Ampat, Moiskon Island, coll. G. Rouse, 2012, (2: 1, male, 36E, L: 4.6 mm; W: 0.5 mm; 1, 23NE, anterior end, L: 1.5 mm; W: 0.35 mm);

NTM W.25639, Philippines, Luzon Island, Batangas Bay, Koala Point, 13°44.3'N, 120°53.4'E, rubble & yellow sponge, 10–16 m, coll. San Martin *et al.*, Dec 2010, (1, 64 NE, W: 0.45 mm); NTM W.24188, Palawan Island, El Nido, 11°41'N, 119°25'E, coral rubble with *Lithothamnion*, small red coralline algae, 3–12 m, Dec 2010, coll. C. Watson *et al.*, (1, 70 NE, ovigerous female, L: 6.5 mm, W: 0.51 mm).

P. silopsis species complex

NTM W.25637, Eastern Pacific, Moorea, Outer reef between Opunuhu Bay & Motus Islands, Stn. 487, 15–18m, coll. J. Moore, Oct 2010, (1, 92E; 1NE, mid-body fragment, male with sperm, W: 0.37 mm).

Description. (based on holotype and other material where noted). Long, slender body with small parapodia, short, notochaetal paleal fans transparent to pale golden colour. Live Philippine specimen with pale body, bright, light-gold paleae. Holotype 100 segments not entire, length 11 mm, width 0.64 mm. Anterior end same as that described for *P.silus* n. sp. with two pairs of maroon-red eyes dominating prostomium; median antenna comparatively more subulate, not with swollen tip (Fig. 7A).

Notochaetae of mid-body notopodium composed of 2–4 pointed lateral paleae with slender, fine serrate margins, 4–6 ribs; single sub-unit 1 palea with 7–9 ribs; short spine may be present (Fig. 7C). Main paleae number up to 10 with shallow apices, serrate convex margin to apex (tiny hoods may be present); 14–17 ribs, nearly all with full length b.l. pattern. Median paleae number 3–5 with (13), 14–17 ribs, including 3–4 noticeable raised ribs and up to 14 b.l. ribs; median broad, leaf-shaped with pointed tips (Fig. 7B, D).

Neurochaetae of mid-body neuropodium composed of 2 superior long falcigers; 1 slightly shorter midsuperior; 15 mid-group falciger; about 5 inferior shortest falcigers. Total number approximately 25 with all compound articles slender; ventral cirrus subulate (Fig. 7C).

Remarks. *Paleanotus silopsis* n. sp. is represented by two entire specimens from Thailand and Indonesia; other specimens are broken with no anterior or posterior ends present. One GBR individual of 100 segments, not entire, has a length of 11 mm. Diagnostic characters of *Paleanotus silopsis* n. sp. include broad, leaf shaped and pointed median paleae; broad main paleae rounded distally with a slightly more distinct apex; greater degree of serrated paleae margins and b.l. projection and ventral cirri basally more broad (Figs 1H; 7B, D).



FIGURE 7. *Paleanotus silopsis* n. sp. A. Micropic of anterior and mid-body section, dorsal view, SIO A3633: Indonesia, West Papua, Raja Ampat; B. Micropic of median paleae and medial main palea, NTM W.24186: High Rock, GBR; C. Lateral paleae group and neuropodium, SIO A3633: Indonesia, West Papua, Raja Ampat; D. Detail of median paleae group and medial main paleae, NTM W.24188: Philippines. Abbreviations: la = lateral paleae, me = median paleae, mm = medial main paleae. Scale bars: $D = 30 \mu m$.

Paleanotus silopsis n. sp. (western Pacific Ocean) is very similar to *P. silus* n. sp. (eastern Indian Ocean) but possesses median paleae of a different shape with a greater number of ribs and main paleae with a slightly greater number of ribs (detailed comparison in *P. silus* n. sp. see Remarks).

One male from Raja Ampat had sperm visible in segments 6 to 36 of an entire specimen. A Philippine ovigerous female had large eggs, similar in size to those observed in *P. silus* n. sp. Segments full of gametes may appear bead-like. A live male from Moorea had a clear body with yellow oil globules inside and white pigment on each segment, indicative of white granules; a condition seen in mature *Treptopale* species (Watson 2010).

Eastern Pacific, Moorea specimen (*P. silopsis* species complex) exhibits characters similar to the western Pacific *P. silopsis* n. sp., but agrees more with Caribbean Sea material collected by the author. These constitute a new species which will be described as part of a genetic study of the *'silus/silopsis*' complex (Watson in prep.).

Etymology. The species name *silopsis* refers to this species being very similar in appearance to *silus*. *Silus* refers to the pug-nosed shape of the main paleae and the Latin suffix '*opsis*' refers to a likeness.

Habitat / **Distribution**. *Paleanotus silopsis* n. sp. is present along the western Pacific Ocean rim at Lizard Island, GBR, Indonesia and the Philippines. Found amongst coral rubble from 1–16 m.

Paleanotus chrysos n. sp.

(Figs 1I; 8A–L; 9)

Type material. Holotype: NTM W.23203, Western Pacific Ocean, QLD, GBR, North Direction Island, 14°44.62'S, 145°30.72'E, CReefs, LI-08-019, coll. C. Glasby, Apr 2008, (23E, L: 2.5 mm, W: 0.45 mm). Paratypes: NTM W.25641, same locality as holotype, (6, including female with large eggs, 22 E, L: 2.5mm, W: 0.6 mm).

Other material examined. NTM W.23688, Yonge Reef, 14°34.40'S, 145°37.11'E, CReefs, LI-10-116, Sep 2010, (3: 1, 21E, L: 1.2 mm, W: 0.6 mm); NTM W.23673, Waining Reef, 14°27.84S, 145°19.19E, CReefs, LI-09-023, coral rubble, 2 m, coll. C. Watson, Feb 2009, (3E); NTM W.23669, Lizard Island, Coconut Beach, 14°40.88'S, 145°28.35'E, CReefs, LI-09-002, 2 m, coll. C. Watson, Feb 2009, (1, 19E, L: 1.2 mm, W: 0.6 mm); NTM W.23604, Mermaid Beach, 14°38.75'S, 145°27.21'E, CReefs, LI-08-006, fine green algae on sand, 12 m, Apr 2008, (1, 21 E); NTM W.25640, North Point, 14°38.73'S, 145°27.2'E, CReefs, LI-08-020, rubble, 2 m, coll. C. Watson & N. Bruce, Apr 2008, (1, 19E, L: 1.5 mm, W: 0.55 mm); MV F.214507, North east of Townsville, muddy sand, 26 m, (1NE); MV F.214506, Britomart Reef, 18°17'S, 146°38'E, algae & sponges, 3 m, Nov. 1982, (1, 22E, L: 2.3 mm, W: 0.7 mm); MV F 214509, same locality, encrusting algae, Nov 1982, (4, NE); MV F.125877, same locality, reef front, encrusted dead coral with fine red algae, Nov 1982, (1NE); NTM W.23190, Heron Island, CReefs, HI-09-046, Sykes Reef, rubble, 10 m, Nov 2009, (1, 17NE); NTM W.23656, CReefs, HI-10-009, Sykes Reef, rubble, 14 m, coll. M. Blazewicz-Paszokowycz, Nov 2010, (2: 1, 22NE, L: 2.2 mm, W: 0.55 mm; 1, 24E, L: 2.0 mm, W: 0.75 mm); NTM W.23658, North East Lamont Reef, 23°35.20'S, 152°3.73'E, CReefs, HI-10-013, 21 m, coll. M. Capa, Nov 2010, (1, 22E, L: 2 mm, W: 0.65 mm); SMNH 97309, Western Pacific, France, New Caledonia, Loyalty Islands, Lifou, 17 m, (1, 20E, L: 2 mm, W: 0.65 mm).

Paleanotus chrysos species complex

NTM W.13169, Philippines, Luzon, Cape Bolinao, coral rubble, red algae & sponge, 12 m, coll. B. Russell, Oct 1995, (1NE, W:0.9 mm).

Description. (based on holotype and other material where noted). Very small, elongate body with distinctive paleal notochaetae coloured deep yellow to bright gold. Paleae in neat, slightly 'prickly', raised fans over dorsum ie. not completely flattened as in other *Paleanotus* species. Neuropodia extend a little beyond notopodia.

Prostomium with 2 pairs large, dark maroon eyes often merged; median antenna slender, subulate; large, glandular nuchal fold covers posterior prostomium. Segment 2 (chaetigerous segment 1) with 2–4 slender, pointed paleae with 3 ribs (Fig. 8A, B).



FIGURE 8. *Paleanotus chrysos* n. sp. A–E: NTM W.23688: Yonge Reef, GBR. A. Anterior end, dorsal view (paleal notochaetae omitted); B. Paleae, segment 2; C. Detail lateral paleae, spine and main paleae; D. Median paleae and medial main palea; E. Micropic, median palea; F–J: Neurochaetal types, NTM W.23203: North Direction Island, GBR; K. Micropic of midbody segment, SMNH 97309: New Caledonia; L. Detail of median paleae, medial-most main palea, NTM W.23190: Heron Island, GBR. Abbreviations: ca = caruncle, la = lateral paleae, me = median paleae. Scale bars: A = 200 μ m, B–D, F–J, L= 30 μ m.

Notochaetae of mid-body notopodium composed of 2 slender, pointed laterals with 4–5 ribs; subunit 1 paleae usually absent, sometimes 1–2 small spines present (Fig. 8C). Main paleae number 6–8 with 13–15 (16) ribs. Paleae with rounded to slight sloping brow, robust margin serration; broad, curved apices. At moderate magnification superior surface of main paleae appears smooth; at high magnification ribs appear thickened, especially basally, with about 4–6 b.l. ribs. Slender dorsal cirri about 2/3 length of main paleae fan (Figs 1I; 8K; 9). Median paleae number 3; distinctive narrow shape with sloping brow. Lizard Island material median paleae slender with distinct 'upswept', broad apices, 8–11 (12) ribs (Fig. 8E, D). Heron Island, New Caledonian median paleae broader with 9–12 ribs (Fig. 8K, L). Median paleae appear smooth; under high magnification 5 b.l. ribs visible, especially basally.

Neurochaetal types of mid-body neuropodium composed of 2 superior, very slender falcigers; about 4 midsuperior falcigers; 6–8 mid-group falcigers. Latter three groups with pronounced basal serrations. Inferior group of shorter falcigers with slender blades, number 4–6. Total number about 20 (Fig. 8F–J). Ventral cirri short, subulate.

Remarks. *Paleanotus chrysos* n. sp. has the smallest maximum body segment number and length compared to all other species described in this paper; e.g., mature GBR specimen 24E, length 2.6 mm, width 0.75 mm; the New Caledonian specimen, 20E and length 3.7 mm. *Paleanotus chrysos* n. sp. is coloured deep yellow in northern GBR specimens, deep mustard yellow to gold in reefs off Townsville, and bright brassy gold in material from Heron Island, southern GBR: a depth of notochaetal pigmentation not seen in any of the other small *Paleanotus* species.

Paleanotus chrysos n. sp. is further differientated by possession of pointed lateral paleae with small number of ribs and short spine/s and the absence of sub-unit 1 paleae. The median paleae shape is unique and horizontal striae are observed more widely separated in the basal quarter of paleae becoming finer distally (Fig. 8E). Neurochaetal types are similar to those of other species but possess a greater degree of basal serration, particularly of the mid-group falcigers (Fig. 8G–I). An ovigerous female paratype specimen (starting to disintegrate), has large eggs present from chaetiger 6, measuring 200–250 μ m in diameter (Fig. 9).



FIGURE 9. *Paleanotus chrysos* n. sp. Micropic of female with large eggs (body starting to waste), mid-body notochaetael fan in part, NTM W.25641: North Direction Island, GBR.

Body size and chaetal morphology of individuals from northern and southern GBR specimens, reefs off Townsville and New Caledonia overall agrees. Lizard Island material possesses the narrowest median paleae as do *P. chrysos* n. sp. from reefs off Townsville. Heron Island specimens exhibits some broader median paleae as well as the narrower ones; the New Caledonian individual has mainly broad median paleae (cf Fig. 8D, E & K, L).

A New Caledonian specimen is cited as '*Paleanotus* LI' in Wiklund *et al.* (2009). The SMNH specimen on loan for this study is entire so another *Paleanotus* from the same collection must have been used for the DNA analysis. As there was no morphological description in the paper, a designated species name for the DNA individual is unknown. Future *Paleanotus* genetic analyses with named species may be able to reveal its identity.

A Philippine individual belonging to *Paleanotus chrysos* species complex was collected from an encrusted habitat similar to habitats of *P. chrysos* n. sp. from the GBR. Chaetal types are also very similar e.g., slender lateral paleae and spines, and the egg size is the same. However the main and median paleae have even more elevated apices; paleael sculpture is different with no b.l. ribs on main paleae and the median paleae possess a central raised rib. This specimen appears part of the *chrysos* complex and may prove to be a new species. Slender, pointed laterals, often accompanied by spines in *Paleanotus chrysos* n. sp. are also seen in the *P. silus* n. sp. species complex but the main and median paleae shape are different between the species. *P. chrysos* has been found sympatric with *Paleanotus adornatus* n. sp. in coral rubble collections from Lizard Island, GBR.

Etymology. The species name, *chrysos*, is derived from the Greek meaning 'gold' and refers to the distinctive colour of the notochaetal paleae.

Habitat / **Distribution.** Recorded from the Coral Sea: Lizard Island, reefs off Townsville and Heron Island, GBR, NE coast of Australia and New Caledonia. *Paleanotus chrysos* n. sp. appears to favour a complex habitat of encrusted coral rubble, red algae, sponges as well as fine algae on sand; depth 2–30 m.

Discussion

Morphology and habitat. All seven new small-bodied *Paleanotus* species possess a number of enlarged sensory structures: large eyes dominating the prostomium, large cushion-like nuchal folds and long interramal cilia. With the exception of *P. latifolia* n. sp., all species have large eggs and large rounded sperm. Mature *Paleanotus inornatus* n. sp., *P. adornatus* n. sp., *P. aquifolia* n. sp. and *P. latifolia* n. sp. attain up to 45 segments and length around 4.5 mm compared to *Paleanotus chrysos* n. sp. with 24 segments and up to 3.7 mm length. All species occur from 1 m to around 40 m depths. The *P. silus* species complex, so far comprising *P. silus* n. sp. and *P. silopsis* n. sp., appear a unique group possessing a large number of narrow, short segments compacted into a relatively short length e.g., 115 segments (not entire), length 10 mm. These two species occur in shallower depths to 16 m.

A number of these *Paleanotus* species may occur sympatrically within one collection of coral rubble. It is of interest that the majority of the GBR *Paleanotus* species occurred not within the Lizard Island biotope but from outlying reefs. High diversity in major coral reefal systems has been related to the availability of both hard and soft bottom habitats and the variety and complexity of suitable micro-patch habitats, within different zones in the reef landscape (Syms & Kingsford 2008). It is clear that the coral rubble habitats of outlying reefs in the northern GBR are capable of supporting a high diversity of species.

Crypticism. Coral reef habitats of northern Australia reveal no endemic chrysopetalid genera but a species rich fauna that is increasingly understood to comprise cryptic species. Within the eight chrysopetalid genera known in the GBR, six comprise cryptic species complexes i.e. morphological differences are difficult to see between species with only minor shape differences, numbers of paleal types or ribs or no observable charcters present (e.g., *Arichlidon:* Watson Russell 1998; *Treptopale:* Watson 2010; Wei *et al.* 2013).

Two taxa, *Chrysopetalum and Paleanotus*, possess species that have especially clearly identifiable notochaetal characters. The new *Paleanotus* species described in this paper, for example, are distinguished by the different shape of the main paleae. However it is now apparent that these identifiable species have themselves formed cryptic species complexes, e.g., *P. inornatus* species complex from the western Indian Ocean (Red Sea and eastern Mediterranean) has recently been described as a new species based on small differences in the paleal rib numbers (Watson & Chatzigeogiou, submitted). The same species complex also extends to Moorea in the eastern Pacific.

Biogeography. Morphological and genetic research on polychaetes of Northern Australian coral reefs is finding evidence of similar patterns of speciation between North-east and North-west coasts. Polychaetes from the North coast, Arafura Sea, have hitherto been considered a mixture of both NE and NW faunas (Watson 2010, Wei *et al.* 2013, Glasby *et al.* 2013).

Study of the chrysopetalid taxon *Treptopale* revealed new species from coral reefs of Lizard Island and Heron Island, GBR; Darwin, NT; Scott Reef and Ningaloo Reef, WA (Watson 2010). Genetic analyses of the two *Treptopale* species (Wei *et al.* 2013) revealed nine clades: one nominal species with an overall NW-NE

distribution, one nominal species and one clade with an exclusive NW range and a new species found only in the GBR. An additional five clades had CO1 confirmation of NE or NW Australia exclusive ranges. Lizard Island, GBR, in comparison with Western Australian and northern Australian reefs, possessed the highest overall clade diversity; Lizard Island and Heron Island had the highest intraspecific diversity of clades (Wei *et al.* 2013). A genetic study of three genera of nereidid polychaetes by Glasby *et al.* (2013) found each group possessing both widespread species across northern Australia and species restricted to the NE coast.

The present *Paleanotus* morphological study reveals seven new species: two species with widespread distributions (NE- NW Australia and Indo-Pacific); one species restricted to the NE coast and four species comprising two cryptic pairs with exclusively NE or NW ranges.

NE and NW distribution patterns: The two species pairs, *Paleanotus silopsis* n. sp. / *P. silus* n. sp. and *Paleanotus aquifolia* n. sp. / *P. latifolia* n. sp., share a very similar distribution pattern: *P. silopsis* n. sp. and *P. aquifolia* n. sp. are found along the western Pacific Ocean rim (north eastern Australia, Lizard Island, GBR to the Philippines) and their cryptic counterparts, *P. silus* n. sp. and *P. latifolia* n. sp., are present along the eastern Indian Ocean rim (north western Australia to west coast of Thailand). The western Pacific habitat is composed of offshore reefs and islands with clear water coral reefs and less sedimentation. The eastern Indian habitat is composed of coral reefs with a greater degree of silty sediments and gravels especially along along the Sahul Shelf of northern and north-west Australia.

N and NW distribution patterns: The most significant influence on ecosystem structure and function in northern Australia is the sea level across the region which has periodically oscillated during recent geological times. To the north east of the Arafura Sea are a series of canyons that are remnants of drowned river systems that existed in the Pleistocene era; these canyons extend from the Arafura Depression to Cape Wessel, eastern Arnhem Land. Around 20,000 yrs ago the Gulf of Carpentaria was a brackish lake and today a semi-enclosed sea bordered by Torres Straits to the east and by a sill extending from Wessel Islands in the west to Papua New Guinea in the north. Both limit the movement of water between the Gulf from the neighbouring Coral Sea in the east and Arafura Sea in the west (Marine North Bioregional Plan 2012).

There have been no chrysopetalid collections available for study from the Wessell Islands, eastern Arnhem Land. The presence in Darwin, western Arnhem land, of *Paleanotus silus* n. sp. and *P. latifolia* n. sp., with both species ranges occurring only in NW Australia, may validate the observation that the Wessell Islands are evidence of an old barrier to movement between Pacific and Indian Ocean faunas. The Wessell Islands are also identified as being the most eastern geographic locality for NW coastal marine mollusc species (R. Willan, pers. comm.)

NE distribution patterns: Paleanotus silopsis, P. aquifolia, P. adornatus and *P. inornatus* all have ranges extending north from NE Australia to the Philippines. Heads (2012) considers New Guinea and the Philippine archipelago as geological composites made up of crusts, some the result of collisions of central Pacific terranes. There is also evidence of Philippines-New Guinea-Australian clades with strong biogeographic connections for a number of animal groups (Heads 2012). Glasby *et al.* (2013) nereidid results and unpublished *Treptopale* sequences (Watson unpubl.) show strong genetic connection between GBR and Philippine clades.

The smallest species, *Paleanotus chrysos* n. sp., revealed the single restricted Coral Sea range with a GBR distribution and one record from New Caledonia. It is of interest that the higher latitude Heron Island and New Caledonian material at 23° and 19°S, share more similar median paleae types compared to the Lizard Island material at 14°S. North and south separation of clades within the GBR was found in DNA analyses of both chrysopetalid and nereidid polychaetes (Wei *et al.* 2013; Glasby *et al.* 2013).

Species with widespread Western Pacific & Eastern Indian Ocean ranges: Paleanotus inornatus n. sp. and P. adornatus n. sp. represent the two most numerous occurring species and exhibit wide geographic distributions with both species present on NW, N, and NE Australian coasts; similarly also on western Pacific (Philippines) and eastern Indian Ocean reefs (Andaman Sea, Thailand). *Paleanotus inornatus* cryptic species have been observed from the Red Sea (Eastern Mediterranean) to Moorea in the mid-eastern Pacific. It is very likely future DNA studies will reveal new species within each species group including specific NE or NW Australian taxa. Genetic study comparing northern Australian and SE Asian material may well illustrate a closer genetic relationship between NW species and South East Asia (via the Indonesian throughflow) than between NW and NE Australian species.

Summary of NE/NW chrysopetalid biogeography in northern Australia:

Watson (2010) postulated an ancestral Tethyan fauna existed for the pan-tropical chrysopetalid *Treptopale*. Previously unpublished results of *Treptopale* molecular clock analysis showed clade splits between NE/NW Australia occurring late Eocene/Oligocene, late Miocene and late Pliocene/Pleistocene (Watson unpubl.) Two scenarios were suggested leading to *Treptopale* NW/NE splits and potential speciation events: Miocene tectonic conditions including the collision of Australia with Indonesia and the more recent Pleistocene glacial cycles leading to closure of Torres Straits and greater sedimentary conditions of the Arafura Sea and Sahul Shelf (Watson 2010).

Based on molecular clock analysis Glasby *et al.* (2013) suggested the Pleistocene sea level minima had no effect on nereidid NE/NW faunal splits and that speciation within different groups occurred earlier in the mid-Miocene, a period of restricted east west dispersal. Ongoing genetic studies based on northern Australia coral reef chrysopetalid species will continue to clarify the age and nature of NE/NW faunal splits e.g., DNA study of *Paleanotus* species (Watson & Rouse, in prep.). In conjunction, South East Asian DNA study will provide further information regarding the morphological observations of Western Pacific rim chrysopetalid species connections and the new findings presented in this paper of eastern Indian Ocean rim species relationships.

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