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Revision of *Hyalopale* (Chrysopetalidae; Phyllodocida; Annelida): an amphi-Atlantic *Hyalopale bispinosa* species complex and five new species from reefs of the Caribbean Sea and Indo-Pacific Oceans

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Abstract

The formerly monotypic taxon, *Hyalopale bispinosa* Perkins 1985 (Chrysopetalinae), is comprised of a cryptic species complex from predominantly tropical embayments and island reefs of the Western Atlantic and Indo-Pacific Oceans. *Hyalopale* species are of meiofaunal size (length: 1−2.8mm), but considered non-interstitial, with the majority of species inhabiting a singular habitat of shallow littoral zones among algae and epifauna overlying sediments in rubble. *Hyalopale* adults exhibit notochaetal fans characterized by the presence of lateral and midline notochaetal spines. Species of *Hyalopale* can be distinguished by the shape of glass-like notochaetal paleae and the number of densely stacked ribs. *Hyalopale bispinosa* forms a western and eastern Atlantic species complex, comprising the type species, *Hyalopale bispinosa* s.s., a comparatively larger form with the highest number of notochaetal paleael ribs from Florida, and *Hyalopale* cf. *bispinosa,* from the western and eastern Mediterranean, a smaller form with a similar notochaetal morphology to the latter. Unfortunately, no molecular sequence data is available for *Hyalopale bispinosa* s.s. Five new species are described, with molecular sequence data provided for three: *Hyalopale leslieae* **sp. nov.**, a small form with a comparatively low number of paleal ribs, found from the Florida Keys to Belize, Caribbean Sea, *H. zerofskii* **sp. nov.** from southern California and Mexico, eastern Pacific and *H. sapphiriglancyorum* **sp. nov.**, a distinctive species with the lowest number of paleael ribs, from Raja Ampat, Indonesia and the Great Barrier Reef, Queensland, western Pacific. Two other species are described from morphology alone: *H. angeliensis* **sp. nov.** from Dampier, Western Australia and Seychelle Islands, eastern Indian Ocean and *H. furfuricula* **sp. nov.** from the Red Sea and Mozambique, western Indian Ocean, possessing a unique paleal brow shape. While well supported as a clade, support for relationships within *Hyalopale* is low. *Hyalopale* cf. *bispinosa* (Mediterranean) was recovered as sister group to the remaining *Hyalopale*, with *H. leslieae* **sp. nov.** as sister to the *Hyalopale* Pacific clade, comprising *H. zerofskii* **sp. nov.** (eastern Pacific) and *H. sapphiriglancyorum* **sp. nov.** (western Pacific). Within Chrysopetalinae, *Hyalopale* and *Paleanotus* formed a clade that was the sister group to the other paleate chrysopetalids under maximum likelihood, though *Paleanotu*s grouped with the other paleate forms under maximum parsimony. The adult morphology of *Hyalopale* species is compared with that exhibited in the larvae of *Paleanotus* species; based on these results, including possession of a shared notochaetal character, *Hyalopale* is considered to contain paedomorphic taxa.

Key words: Morphology, taxonomy, DNA, paedomorphism, cryptic species, biogeography, phylogeny

Introduction

Chrysopetalidae Ehlers, 1864 was erected to contain the paleate genera *Paleanotus* Schmarda, 1861, *Bhawania* Schmarda, 1861, *Chrysopetalum* Ehlers, 1864 and *Palmyra* Savigny in Lamarck, 1818; the latter genus since referred to Aphroditidae by Watson Russell (1989). Subsequently, a further nine paleate and spinose genera have been described (summarized in Watson Russell 2000, Rouse & Pleijel 2001, Watson & Faulwetter 2017). Furthermore, recent investigations have found that Nautiliniellidae Miura & Laubier, 1990 (inquiline in deep-sea mussels) and Calamyzidae Hartmann-Schröder, 1971 (*Calamyzas amphictenicola* Ardwisson, 1932, parasitic on ampharetids) are derived chrysopetalids and were placed within Calamyzinae by Aguado *et al.* (2013). Two other subfamilies, Chrysopetalinae including paleate taxa and Dysponetinae Aguado, Nygren & Rouse, 2013 erected for spinose taxa,

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were also recognised within Chrysopetalidae by Aguado *et al.* (2013). Dysponetinae and Chrysopetalinae were formally diagnosed by Aguado *et al.* (2015) and Watson & Faulwetter (2017) respectively. Chrysopetalidae now encompasses 27 genera and ~100 species (Watson in press 2019).

Chrysopetalids are small worms possessing distinctive metallic coloured, iridescent paleae (flattened notochaetae) or notochaetal spines held in segmental fans that imbricate down the dorsum, but in some members notochaetae are putatively absent. Chrysopetalids are found worldwide between ~65ºN–65ºS and are associated with crevicular habitats from a range of marine environments, including disrupted, anoxic habitats, intertidal to 6000m (Watson & Faulwetter 2017; Watson in press 2019). Chrysopetalinae are often found associated with fringing mainland and offshore coral reefs of the Indo-Pacific and Western Atlantic (Watson 2010). Species may possess planktonic larvae (*e.g.* Blake 1975; Watson *et al.* 2014) and are among primary colonizers in settlement studies on tropical reefs *e.g.* Great Barrier Reef, western Pacific (Hutchings & Murray 1982); eastern Indian Ocean (Peyrot-Clausade 1974); eastern Pacific (Peyrot-Clausade 1976) and the Caribbean, western Atlantic (this study). Watson (2015) recorded seven Chrysopetalinae taxa common to all Indo-Pacific and Western Atlantic coral reefs: *Chrysopetalum, Bhawania*, *Arichlidon* Watson Russell, 1998, *Paleaequor* Watson Russell, 1986, *Paleanotus*, *Treptopale* Perkins, 1985 and *Hyalopale* Perkins, 1985 with only one reefal, shallow-water, endemic genus known: *Acanthopale* San Martin, 1986, from the Caribbean (CW pers. obs.).

This paper investigates *Hyalopale,* a previously monotypic genus. *Hyalopale* has been little recorded since the description of *Hyalopale bispinosa* Perkins, 1985*,* based on mature adults from mainland Florida and smaller specimens from the Florida Keys, which Perkins (1985) considered juveniles of the former. *Hyalopale* sp. from the Red Sea was figured by Watson Russell (1987) and thought of as a juvenile form, as it had 10 segments. *Hyalopale* sp. was recorded for the first time from Australian coral reefs by Watson Russell (2000). *Hyalopale* was included within a key that determined that *Paleanotus, Treptopale* and *Hyalopale* possessed a closely related morphology (Watson 2015). *Hyalopale*, in common with these taxa, possesses a pair of stylet jaws, whose structure, allied with habitat data, is indicative of free-living carnivory and facultative symbiotic feeding modes. Stylet jaws and pharynx, including calcareous pharyngeal muscle, were figured for *Hyalopale* species from the Caribbean and Mediterranean by Watson & Faulwetter (2017).

The size, fragility and cryptic colouration of *Hyalopale* species have precluded specimens being well-represented in collections and then often only by single or broken specimens. Identification to species has been hampered by small size (length 1–2.8mm) as well as the cryptic nature of the notochaetal fan, especially the morphology of the transparent main paleae that are constructed with extremely finely-stacked internal ribs, which makes comparison among individuals difficult. This revision of *Hyalopale* includes re-description of the type species, *Hyalopale bispinosa* and involves separating the type material into two species: *Hyalopale bispinosa sensu stricto* and a new *Hyalopale* species. Specimens from the Mediterranean are referred to as *Hyalopale* cf. *bispinosa* pending gathering molecular sequence data. Four other new species are described. Diagnostic characters that differentiate species, *e.g.* shape of the convex brow, apical structure and number of internal ribs of paleal notochaetae, and gametous states, are presented. The relationship of *Hyalopale* to *Paleanotus,* its closest related taxon, is assessed, particularly in light of the similar morphology of *Hyalopale* adult and *Paleanotus* larval states. Further corroboration of this latter relationship, and intraspecific relationships, are revealed in DNA sequence data based on mitochondrial Cytochrome c oxidase subunit 1 (*CO1*), 16S rDNA (*16S*), nuclear *18S* rDNA (*18S*) and Histone H3 (*H3*).

Materials and methods

Morphology. A composite plate of main paleae belonging to seven *Hyalopale* morpho-species (six nominal) is provided in association with the key to species (Figure 1A–G). A Leica DMR compound microscope and Helicon Focus software was used to take micrographs with a Canon T6 Rebel SLR. Chaetal terminology follows that of Watson *et al.* (2014). Designations of notochaetal paleae in species of Chrysopetalinae are based on position: *i.e.* lateral group inserts below the acicula (*lp*); main group above the acicula (*ma*); the median group (*me*) overlap mid-dorsum. Within Chrysopetalinae, the main fan comprises a middle group with the broadest paleae and usually the highest number of ribs. There are also two subgroups: lateral-most main paleae (*lmm*) designating those in a position closest to the dorsal cirrus and midline-most main paleae (*mmm*) designating those in a position closest to the mid-dorsum. Among *Hyalopale* species, a short midline spine (*ms*) may additionally be present adjacent to the last paleal category (Figure 3); a specialized median paleal fascicle is absent. Primary notochaetal spines refer to chaetae present in chrysopetalid larvae, seen for instance in notopodia of the second segment in *Paleanotus* larvae and *Hyalopale* adults (Figure 10 A, B; Table 2). Roman numerals indicate segment number of the anterior end. During collecting and handling *Hyalopale* individuals are liable to fragment; the majority of studied material is broken. Abbreviations of these body states in association with measurement of segment numbers are: E, entire; NE, not entire; L, length; W, width. In the descriptions of species, for example, 1, 17NE, means one individual that is not entire and has 17 segments.

Other abbreviations used:

ac ventral acicula
a.c. anal cirri
c cilia
ci epibiont ciliates
dc11 dorsal cirri segment 2
dc111 dorsal cirri segment 3
dtc1 dorsal tentacular cirri segment 1
ep epidermis
gg green glandular material
gl gland
gu gut
la lateral antennae
lmm lateral-most main paleae
lp lateral paleae
ls lateral spine
ma main paleae
m.a. median antenna
me median paleae
mmm midline-most main paleae
mo mouth
ms midline spine
n circumoesophagical ganglion
ns11 notochaetal spines segment 2
oo oocyte
ov ovary
p palp
ph pharynx
pi paleae insertion
pr proboscis
s stalk
st stylet
vn ventral nerve

The morphology of the structure of the prostomium, pygidia, pharynges and stylets are very similar. The formulae for cirri on segments I–IV are identical across all *Hyalopale* species. Figures relative to these structures are labeled in the generic description. This information is included in individual species descriptions only if noteworthy and where live specimens are present and photographed. Notochaetal lateral and midline spines, may very infrequently number more than 1 and show small variations such as spines may be straight or more curved, with or without a serrated margin, and presence or absence of internal ribs (#1–2); these variations do not appear to be species specific.

The number of internal ribs of main paleae, which are counted from the notochaetal fan of mid-body segments, nearly always vary among individual palea in the fan; this especially noticeable in *Hyalopale* species. Therefore, counts always encompass a range with those most frequent stated and lesser or higher counts expressed in parentheses, *e.g.* (21), 26–28, (29) means most main paleae possess 26–28 ribs with an infrequent highest count of 29 ribs, and a lowest count of 21 ribs being located in the smaller lateral-most and/or midline-most main paleae. Although numbers of ribs can be confusingly similar across species, the *highest* counts in the middle group paleae are diagnostic for *Hyalopale* species, as shown in the key to species.

Most individuals newly collected for this study were fixed in seawater-formalin and then rinsed and preserved in 50% ethanol. Specimens fixed and preserved for DNA sequencing were placed in 95% ethanol. Four individuals of *H. zerofskii* **sp. nov.** were fixed overnight in 4% PFA buffered in PBS for histological sectioning. Specimens were postfixed in 1% OsO_4 for 30 min and subsequently embedded in Spurr's Resin. Semi-thin sections of 1µm were prepared using a "Diatome Histo Jumbo" diamond knife on an RMC PowerTome X ultramicrotome. Sections were stained with toluidine blue (1 % toluidine, 1 % sodium tetraborate and 20 % sucrose) and mounted on slides using Spurr's resin.

Material examined is deposited in the following institutions: Australian Museum NSW (AM); Hamburg Zoological Museum Germany (HZM); Los Angeles County Museum USA (LACM); Hellenic Centre for Marine Research (Crete) (HCMR); Museum and Art Gallery of the Northern Territory Australia (NTM); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); Scripps Institution of Oceanography Benthic Invertebrate Collection, La Jolla California, USA (SIO-BIC); University of Jerusalem Israel (HUJ); Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB).

DNA Data and Analysis. DNA was extracted from organisms using the same protocols outlined in Watson *et al.* (2016). The nuclear loci 18S rRNA (18S) and histone H3 (H3) and mitochondrial regions—16S rRNA (16S) and Cytochrome oxidase subunit 1 (COI)—were amplified and sequenced following the primers and methods also used in Watson *et al.* (2016). 18S was sequenced for all four *Hyalopale* species available for DNA extraction, but we were less successful for the other genes, especially COI. All four loci were obtained for only one *Hyalopale* species (see Table 1). We used the hesionid *Nereimyra punctata* (Müller, 1788) as the outgroup for this analysis, though rooting with other annelids, as done in Watson *et al.* (2016), gave the same topology within Chrysopetalinae and results are not shown here. DNA sequence data was aligned for 18S and 16S using MAFFT (Katoh *et al.* 2013), with the iterative refinement method Q-INS-i, and default gap open and extension values. H3 and COI were aligned using MUSCLE (Edgar, 2004). The four sequence partitions were concatenated and analyzed using RAxML v. 8.2.10 (Silvestro & Michalak 2012; Stamatakis 2014) with the data partitioned by gene and using the model GTR+G and 1000 thorough bootstrap pseudoreplicates. A maximum parsimony (MP) analysis was also conducted using PAUP* v. 4.0 v 161 (Swofford 2002), using a heuristic search with the tree-bisection-reconnection branch-swapping algorithm and 1000 random addition replicates. Support values were determined using 100 bootstrap pseudoreplicates using the same heuristic search parameters.

Taxonomy

Key to related genera and species of *Hyalopale*

1.	Main paleae mainly symmetrical in shape	*Treptopale*
-	Main paleae mainly asymmetrical in shape	2
2.	Lateral and median notochaetae in form of paleae	*Paleanotus*
-	Lateral and median notochaetae in form of spines	*Hyalopale* (3)
3.	Midline spine present	4
-	Midline spine absent	6
4.	Main paleae with less than 17 ribs	*H. sapphiriglancyorum* **sp. nov.** (W. Pacific)
-	Main paleae with more than 17 ribs	5
5.	Main paleae with 26 (29) ribs	*H. bispinosa s.s.* (W. Atlantic)
-	Main paleae with 25 (26) ribs	*H.* cf. *bispinosa* (E. Atlantic)
-	Main paleae with 21 (22) ribs	*H. leslieae* **sp. nov.** (Caribbean)
6.	Main paleae with shallow apices	*H. furfuricula* **sp. nov.** (W. Indian)
-	Main paleae with peaked apices	7
7.	Main paleae with 25 (27) ribs	*H. zerofskii* **sp. nov.** (E. Pacific)
-	Main paleae with 21 (22) ribs	*H. angeliensis* **sp. nov.** (E. Indian)

Note: Rib counts taken from middle group main paleae from mid-body chaetigers (Figure 1: A–G). Rib numbers reflect ***maximum values*** observed.

Family Chrysopetalidae Ehlers, 1864

Chrysopetalinae Ehlers, 1864

Genus *Hyalopale* Perkins, 1985

Type species. *Hyalopale bispinosa* Perkins, 1985

Diagnosis. Small bodied chrysopetalids, as adults < 3 mm in length, attaining maximally 20 segments. Dorsum covered in asymmetric-shaped, transparent main paleae with multiple stacked internal ribs; lateral spines present, midline spines present or absent. Prostomium fused with anterior segments, with two pairs of large complex eyes, median and lateral antennae, moderate-sized oval palps. Achaetous segment I with pair of dorsal and ventral cirri (= tentacular cirri); segment II with pair of dorsal cirri, notochaetae, neurochaetae, ventral cirri absent. Pharynx with pair of stylet jaws. Pygidium a shallow lobe with two small anal cirri.

Description. Small-bodied, rectangular, tapered a little at posterior end, dorsum covered with hyaline, petaloid paleae fans, long-shafted falcigerous neurochaetae extend out beyond notopodia (Fig. 7). Prostomium a shallow, broad lobe not well-defined, with 2–3 pairs of large, bright red to maroon coloured eyes, often overlapping. Finger-shaped median antenna inserts on anterior edge of prostomium, anterior to two slender lateral antennae, two ovoid palps insert ventrally (Fig. 5C, D). Muscular pharynx with small calcified pharyngeal ring, single pair of short stylet jaws with broad, inner groove, tanned distal jaw tips (Figs 4C; 5B). Segment 1 very reduced, with one pair slender, dorsal, ventral cirri; ventral pair adjacent to palps. Segment II notopodia with notochaetal spines only, dorsal cirri; neuropodia with spinigerous neurochaetae, ventral cirri absent. Segments II–III fused in part (Figs 5B; 10A, B). Mid-body notopodium with short, very slender aciculum, slender dorsal cirrus 1/2 to 2/3 length of main paleal fan; sub-acicular lateral notochaetal group composed of single spine, slightly curved with slight serrate margins, attenuated tip, inserts overlying aciculum. Main paleae notochaetal group composed of long, asymmetrical paleae with rounded or sloping brow, finely dentate convex margin, very small apices, numerous very fine internal ribs stacked close together, usually includes very shallow raised ribs. Midline spines present or absent (Figs 3; 4E; 8A).

Mid-body neuropodium with long, slender aciculum. Subacicular falcigerous neurochaetae with long shafts, comprising superior group with longest, very slender blades, minutely serrate, with minute curved distal tips; middle group with longer basal serrations to blades; inferior group short, slender bladed (Fig. 9D). Pygidia with very short to slightly longer filiform pair of anal cirri (Fig. 4B).

Remarks. *Hyalopale* is one of two chrysopetalid genera (also *Treptopale*), erected by Perkins (1985) from Florida coral reefs. *Hyalopale* and *Treptopale* are morphologically close to *Paleanotus,* with similar anterior end configurations and chaetal types (Perkins 1985; Watson 2010; Watson 2015), and similar stylet jaws (Watson & Faulwetter 2017). *Hyalopale* is distinguished primarily by its small adult size and by the presence of spines in the lateral and midline positions in the notochaetal fascicle, which in *Treptopale* and *Paleanotus* are represented by developed paleal fascicles. *Hyalopale* has an extremely small adult size (length 1–2.8 mm, segments <20) a simple body, and possesses very thin, hyaline main group paleae with a multiplicity of internal ribs finely stacked together. *Hyalopale* adult morphology is similar to larvae of other paleate chrysopetalids, which is described in more detail at the end of this paper.

Hyalopale bispinosa sensu stricto Perkins, 1985 *sensu stricto*
Figs 1A; 2

Hyalopale bispinosa Perkins, 1985: 908, Figs 28 A–F, 29 A–H

Type locality. Southern Florida, West Atlantic

Material examined. Paratype. *Hyalopale bispinosa sensu stricto*. USNM 097369, specimen designated as paratype by Perkins (1985), 1 individual in 2 pieces, 17NE (original description 20 segments entire), L: 2mm, W: 0.8mm. North Atlantic Ocean, Florida, Dade County, S Biscayne Bay, Turkey Point power plant, east of Florida Power & Light Company, *Thalassia* bed, coll. FOER personnel, 15 Feb 1978.

Additional material. *H. bispinosa s.s.* LACM –AHF 2879, Caribbean Sea, Bahamas, Great Bahama Bank, Exhuma Cays, 23° 28'N, 75° 45' W, Basil Minn's cave, marine entrance pool, bottom algae & sediment, strong hydrogen sulphide odor from black silt, coll. T. Iliffe & L. Harris, 11 Jan 2003. 1, 17NE, with gametes, L: 2.75mm, W: 1.25mm; LACM-AHF 2874, Bahamas, Great Bahama Bank, Exhuma Cays, Stocking Cay, 23° 31' 21" N, 75° 45' 21" W, Stn. 32, beneath ledge adjacent to cave entrance, 1m, coll. T. Haney & L. Harris, 9 Jan 2003, 2NE: anterior end 12 segments, anterior end 7 segments, ovigerous female with mature eggs, 2 per body segment, body starting to degenerate, neurochaetae falling out.

Diagnosis. *Hyalopale* with mid-body main paleae with sloping convex margin, 26/27 (29) ribs, raised ribs absent.

Description. (based on Florida paratype USNM 097369).

Pale body covered in glass-like notochaetal paleae with reflective shine. Segment II notopodia with four spines each. Mid-body notochaetal fan comprises: lateral spine, nine main paleae, single short midline spine. Lateral-most main paleae with 21/22 ribs, middlegroup main paleae with 26/27 (29) ribs, shorter, slightly symmetrical midline-most main palea with 19 ribs. Slender dorsal cirri just under half length of main fan. Main paleae with sloping convex margin, with very fine margin serration, inner margin with no visible serration, internal ribs densely packed with no obvious raised ribs, apices small, only slightly peaked (Fig. 1A). Mid-body neuropodia with falcigerous neurochaetae comprising: four superior long-bladed, two mid-superior long-bladed, 15–18 mid-group, 6–8 inferior falcigers; slender ventral cirri under half the length to neuropodial tip.

Remarks. Perkins (1985) figured in some detail the type material comprising mature individuals of *Hyalopale bispinosa* from the Florida mainland coast (Figs 28 A–F, 29 A–H). Perkins' generic diagnosis states main paleae with 'more than 25 internal ribs' and remarks state 'about 25 internal ribs' (1985:908). The holotype was not examined for this study, but it is clear based on Perkins' description and figures that the larger-bodied holotype and paratype material constitute *H. bispinosa s.s.* Examination of paratype material from the same locality as the holotype reveals an individual with a range of number of ribs with the middle group main paleae group numbering 26–28 (29) and lower numbers, 19–22, possessed by slender lateral and midline-most main paleae. Smaller paratypes collected from the Florida Keys, and designated as 'young specimens' by Perkins, are now described as a new species (see *H. leslieae* **sp. nov.**).

Additional material was made available of *Hyalopale bispinosa s.s.* from the Bahamas, including a live, entire individual with a yellow body and internal green pigmented patches (Fig. 2). This specimen has nine main paleae with (24) 25–26, 28 (29) ribs and another specimen has 8–10 main paleae with 27–30 ribs and slender lateral and midline main with 24/25 ribs; paleae of both specimens exhibit no obvious raised ribs. *H. bispinosa s.s.* material from mainland Florida and the Bahamas share common characters: similar length of body and number of segments, distinctive slope of brow of main paleae, absence of raised ribs as well as possession of the highest number of paleal ribs, a character which separates *H. bispinosa s.s.* from all other species. The type locality habitat was recorded as hard benthic and algal substrates (Perkins 1985). The Bahamas habitats refer to 'bottom algae and sediment' and a description of 'black silt with a strong hydrogen smell' indicating an anoxic habitat. Depths of 0–2m are recorded.

Hyalopale cf. *bispinosa*

Fig. 1B

Material examined. Mediterranean Sea, USNM 1076945, North Africa, Tunisia, Stn. 202B, coll. M.L. Jones, August 1973, 1, 10NE, L: 0.8mm, W: 0.6mm; NTM W.25601, Spain, coll. Rafael Sarda, 2: 1, 10E, L: 1.14mm, W: 0.72mm; 1, 14NE (gametes). NTM W.25602, Eastern Mediterranean, Greece, Crete, Elounda, 15m, coll. Chatzigeogiou et al, 2007, 1, 12E, L:0.6mm, W: 0.35mm; NTM W.25603, Elounda, 15m, coll. Chatzigeogiou et al, 2007, 2: 1, 9E, 1, 16E; NTM W.25600, Elounda, 20m, coll. Chatzigeogiou et al, 2008, 1 anterior end.

Diagnosis. *Hyalopale* with mid-body main paleae with sloping convex margin, 23/24 (26) ribs, 3–4 shallow raised ribs.

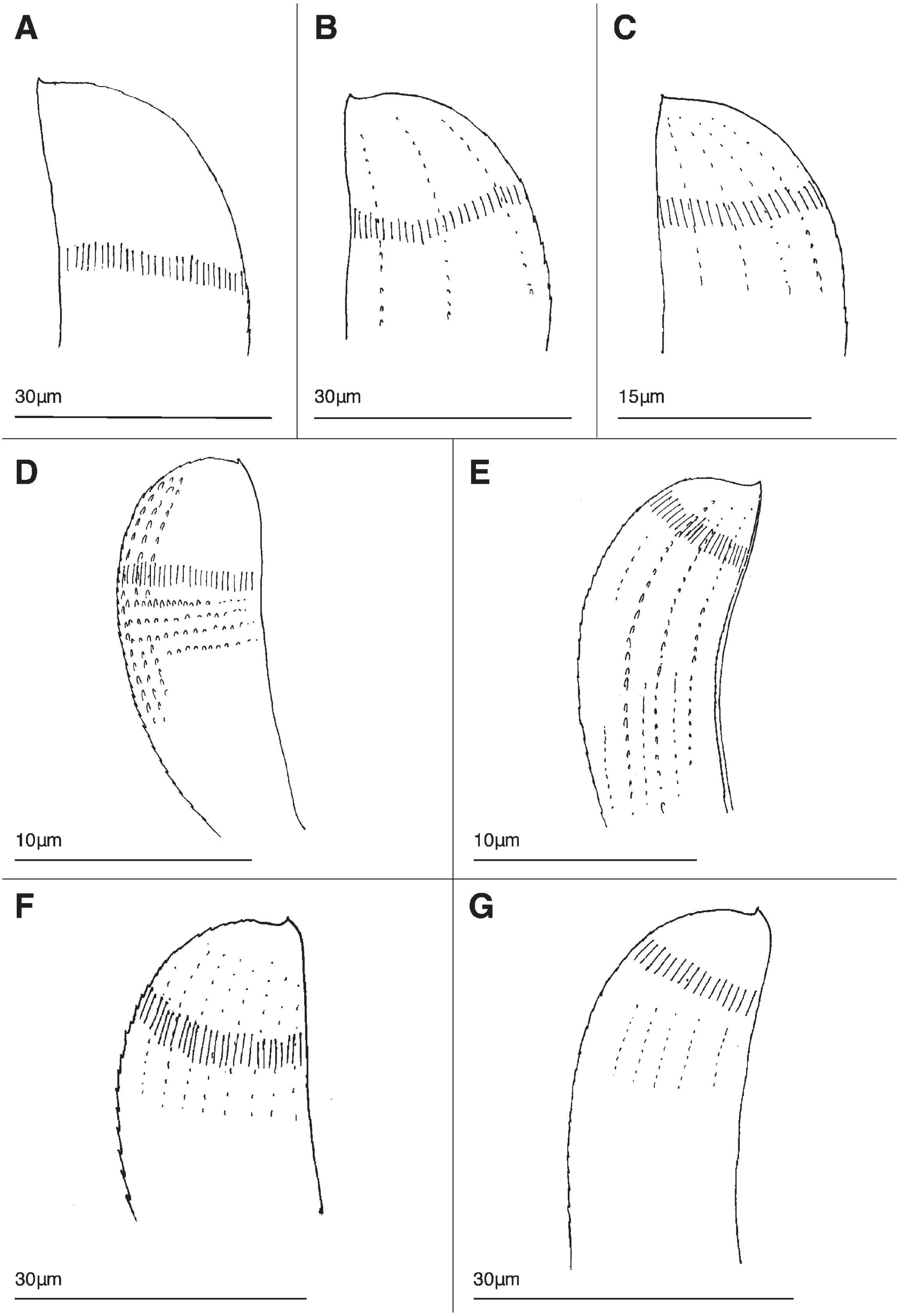

FIGURE 1. Composite plate comparing notochaetal main paleae in *Hyalopale* species. **A**. *Hyalopale bispinosa* s.s. Florida, W. Atlantic; **B**. *H.* cf. *bispinosa* Crete, Mediterranean Sea; **C**. *H. leslieae* **sp. nov.** Florida Keys, W. Atlantic; **D**. *H. furfuricula* **sp. nov.** Mozambique, W. Indian Ocean; **E**. *H. angeliensis* **sp. nov.** Western Australia, E. Indian Ocean; F. *H. zerofskii* **sp. nov.** California, E. Pacific; **G**. *H. sapphiriglancyorum* **sp. nov.** E. Indonesia, W. Pacific. Note: correct number of raised and internal ribs figured.

FIGURE 2. *Hyalopale bispinosa s.s*. Bahama Islands, LACM–AHF 2879, live, colour photo, by Leslie Harris.

Description. Older Mediterranean museum material collected from Spain light brown colour; more recent fresh collections from Crete comprise individuals coloured a dark red-brown. Notopodium of segment II with four simple spines. Mid-body notochaetal fan with single lateral spine, 6–8 (9) main paleae, 1–2 short, curved midline spines. Main paleae with 23–24 (26) ribs with ~ 3–4 very shallow raised ribs (Fig. 1B), lateral and midline-most main paleae with 19 ribs. Tunisian specimen poorly preserved. Main paleae shape similar to other Mediterranean material and possesses up to 22 ribs and four shallow raised ribs.

Remarks. In the absence of additional material from the locality the Tunisian specimen is provisionally included within *Hyalopale bispinosa* species complex. Mediterranean individuals of *Hyalopale* cf. *bispinosa* exhibit a similar shaped notochaetal fan and shape of main paleae when compared with that of *H. bispinosa s.s.*, Western Atlantic, but the main paleae of the former possess a slightly lower range of rib numbers and includes shallow raised ribs; both share similar shaped apices but the brow is a little more rounded in the Mediterranean form (cf. Fig. 1A, B; Key). Mature specimens examined in this present study from the western and eastern Mediterranean did not exceed

16 segments with a length of 1.1mm; this is in comparison with Western Atlantic material of *H. bispinosa s.s*., *e.g.* Florida, 20E, L: 2.8mm and Bahamas, 17NE, L: 2.75mm. However, the number of ribs of the main paleae in the Mediterranean specimens (up to maximum 26), is similar between *H. bispinosa* material from the Eastern and Western Atlantic Oceans. In this paper, Mediterranean material of *H.* cf. *bispinosa* is represented by a DNA sequence from the island of Crete but cannot be confirmed as *H. bispinosa s.s*. until sequences are available for comparison from the type locality in the western Atlantic.

About twelve specimens, including mature individuals, were collected from Elounda and Alykes sites in Crete, predominantly from algae on rocky substrates at 15–20m.

The Mediterranean *Hyalopale* cf. *bispinosa,* provides the only example to date of a *Hyalopale* species dwelling in deeper water. Specimens are also much darker coloured, which may indicate a degree of camouflage within a dark algal habitat. In comparison, all other *Hyalopale* species are found in shallow waters (0–2m) associated with lighter green algae and possess pale and patchy green coloured bodies. The *Hyalopale* feeding mode is hypothesized as predatory on algal-living invertebrates and is based on the buccal structure: a pair of small, pointed stylet jaws with an inner longitudinal groove and a muscular, barrel-like pharynx which includes calcified pharyngeal muscle; imaged through micro-CT for *H.* cf. *bispinosa* (as *H. bispinosa*) from Crete (Watson & Faulwetter 2017).

***Hyalopale leslieae* sp. nov.**

urn:lsid:zoobank.org:act:C2DFADE6-6DFD-436E-9F30-418940CFE070

Figs 1C; 3A; 4A–E

Material examined. Holotype. USNM 097530, original designated paratype *Hyalopale bispinosa* by Perkins (1985), now identified as *H. leslieae* **sp. nov.** Florida Keys, Monroe County, Looe Key National Marine Sanctuary, reef crest, coralline covered rubble, less than 1m, 11E, L: 1.1mm, W: 0.75mm, gametes (? sperm) present.
Paratype, USNM 1490841, same locality as holotype, 1, 10E, L: 0.75mm, W: 0.5mm,

Additional material. USNM 53171, Caribbean Sea, Bahamas, Bimini, Southern Bimini Lagoon, from plastic sponges submerged in lagoon, two anterior ends plus fragments, poor condition, coll. A. Schoener, 1970–71; LACM –AHF 2821, Caribbean Sea, British Virgin Islands, Guana Island, North Bay, 18° 28'909" N, 64° 34'485"W, dredged area inside inner reef, soft bottom of fine coralline sand & silt, with small rocks covered in turf algae & *Sargassum*, (eunicid tubes in sediment beneath rocks), 0.46m, coll. L. Harris, 12 Oct 1997, 1, 11E, L:0.85mm, W: 0.6mm, gametes; LACM –AHF 2755, Guana island, White Bay**,** 18° 28'21" N, 64° 34'26" W, fine to medium calcareous sand off low energy beach next to rocky intertidal, filamentous algae over sand, 0.5m, 16 July 2001, 2E, fragments including anterior end with 8 segments, gametes present, W: 0.7mm; LACM –AHF 2827, Guana Island, White Bay, 18° 28' 32" N, 64° 34' 39"W, off rocky shore, from low green and calcareous mats scraped from surface of coarse sand at base of large rocks, 1.5m, coll. K. Fitzhugh, 21 July 2001, 1, 13E; LACM –AHF 2834; Beef Island, 18° 26' 41" N, 64° 33' 15" W, concrete ramp, off mangrove area, in *Cladophora* clump scraped off surface of concrete wall covered in turf algae (calcareous fragments interwoven with clump of tube dwelling maldanids, *Scyphoproctus,* terebellids), 0m, Oct 1997, coll. L. Harris, 1, 12E, L:1.1mm, W:0.65mm, gametes present; LACM –AHF 2829, Beef Island, 18° 26' 41" N, 64° 33'.15 W, concrete ramp below bridge, calcareous algae on small rocks in soft bottom off mangrove, (clumps of *Halimeda, Amphiroa* scraped off dead coral sitting in soft sand/silt bottom, clumps heavily covered with tubes of tanaenids, maldanids (euclymenins and *Scyphoproctus*), 0.3–0.6m, 15Oct 1997, coll. L. Harris, 1, 11E, L:0.8mm, W:0.55mm, gametes present; LACM –AHF 2756, West Beef Island near Hans Creek, on surface of living *Pinctada* sp. bivalve attached to severed mangrove root (covered with epifauna/epiflora), 0.25m, 21 July 2000, coll. T. Haney, 1, 12E, sperm (?) present. Caribbean Sea, Belize, north tip of Carrie Bow Cay, 16.783° N, 88.067° W**,** September 2014, coll. G. Rouse, 1, 11E, specimen photographed at Scripps before being destroyed for DNA extraction and sequencing (Fig. 4A).

Diagnosis. *Hyalopale* with mid-body main paleae with sloping convex margin, (17) 18–20 (22) ribs, patchy, shallow raised ribs.

Description (based on holotype from Florida Keys). Pale body covered in glass-like notochaetal paleae with reflective shine; prostomium with two pairs of large red eyes, anterior pair melded; gametes present. Segment II notopodia with 3–4 spines each. Mid-body notochaetal fan comprises: lateral spine, 8–9 main paleae, single short midline spine. Lateral-most main paleae with 16/17 ribs, middle group paleae with (17)18–19 (20) ribs, shorter, slightly symmetrical midline-most main palea with 12/13 ribs (Fig. 3A). Main paleae with sloping convex margin, with very fine margin serration, inner margin with no visible serration, internal ribs densely packed, with 4–5 full length plus additional patchy shallow raised ribs, apices very small, blunt (Fig. 1C). Slender dorsal cirri just under half length of main fan. Mid-body neuropodia with falcigerous neurochaetae comprising: three superior long-bladed, two mid-superior long-bladed, 8–10 mid-group (some with longer basal blade serration), 6–8 inferior falcigers; slender ventral cirri under half-length to neuropodial tip. Paratype description same as holotype.

Additional description based on Belize specimen (Fig. 4A–D). Pale yellow body with shield-like white patches on anterior segments, green internal patches (Fig. 4A). Prostomium with two pairs of large eyes, notopodium of segment II with four simple spines; barrel-shaped pharynx, pair of stylets clearly visible (Fig. 4C). Mid-body notochaetal fan with single lateral spine, 8–9 main paleae, 1–2 short, curved midline spines (Fig. 4E). Main paleae with (16) 18–19 (22) ribs with ~ 3–4 shallow raised ribs and often multiple broken-line ribs; smaller lateral-most, midline-most main palea with 13–14 ribs (Fig. 4D). Pygidium with two anal cirri (Fig. 4B).

Remarks. Perkins (1985) considered the smaller material from the Florida Keys to be possible juveniles of *Hyalopale bispinosa s.s.* Re-examination of this material, including additional specimens from the Virgin Islands, showed that mature individuals were present, including ones with enlarged eyes and neurochaetae starting to denigrate. A lot of the latter material consisted of broken anterior ends, which prompted comparison of rib numbers in the main paleae of anterior ends between *H. bispinosa s.s.* and a possible new species. Comparison of these rib numbers of anterior notochaetae, and comparison where possible with those of mid-body notochaetae, showed consistent higher and lower paleal rib counts down the body between both morpho-species.

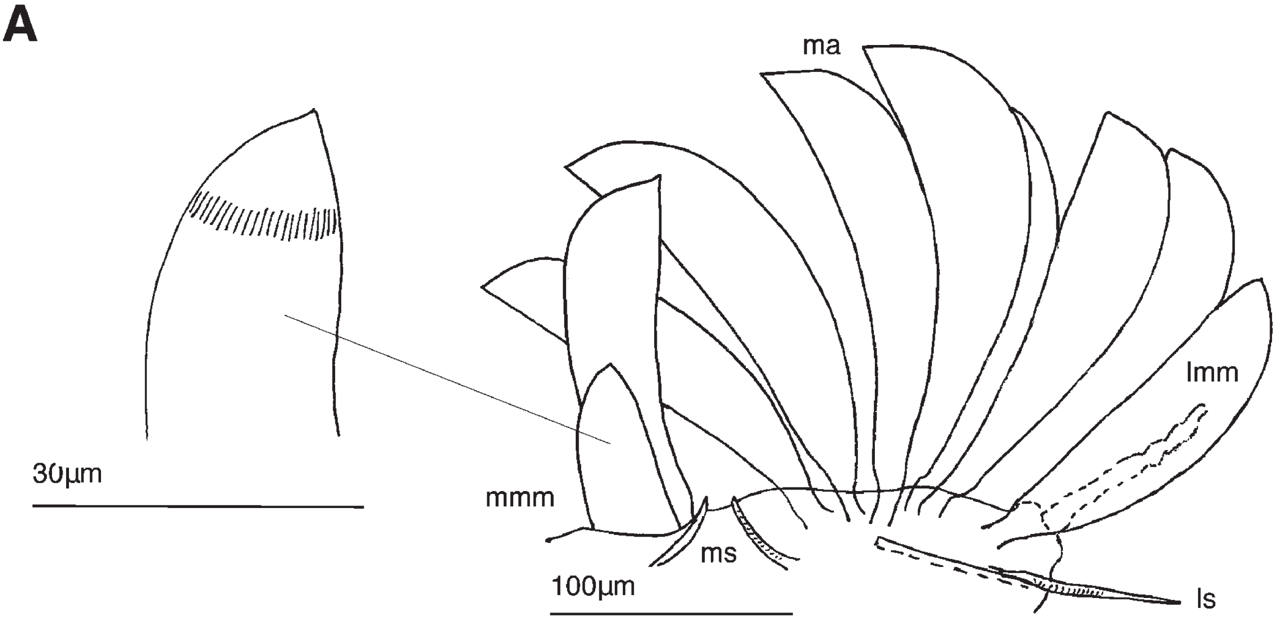

FIGURE 3. *Hyalopale leslieae* **sp. nov.** Florida Keys, Paratype USNM1490841, chaetal types of right and part left mid-body notopodia; inset: midline-most main palea.

Characters defining the Florida Keys and Caribbean new species, in comparison with *Hyalopale bispinosa s.s.* are: smaller in length and number of segments (12E, 1.1mm L *versus* 20E, 2.8mm L); main paleae with consistent lower number of ribs (18/20 *versus* 26/28) with multiple raised shallow ribs *versus* no obvious raised ribs. The presence of gametes in conjunction with morphological differences indicates the material from Florida Keys and the Caribbean Sea represents a new species, *Hyalopale leslieae* **sp. nov.** The phylogenetic analyses (Fig. 13) suggests that *H. leslieae* **sp. nov.**, occupies a closer relation to Pacific taxa rather than the Mediterranean *H.* cf. *bispinosa*, though this node is poorly supported. It is of additional interest, that distributions of *Hyalopale bispinosa s.s.* and *H. leslieae* **sp. nov.** overlap in the Bahamas.

Etymology. *Hyalopale leslieae* ***sp.*** **nov.** is named in honour of Leslie Harris from the Los Angeles County Museum (LACM). Leslie is an indefagatible identifier and photographer of polychaetes who has over the years consistently bought chrysopetalids to the attention of CW, including the large amount of material from the Caribbean Virgin Islands, which characteristically includes beautifully detailed collection data.

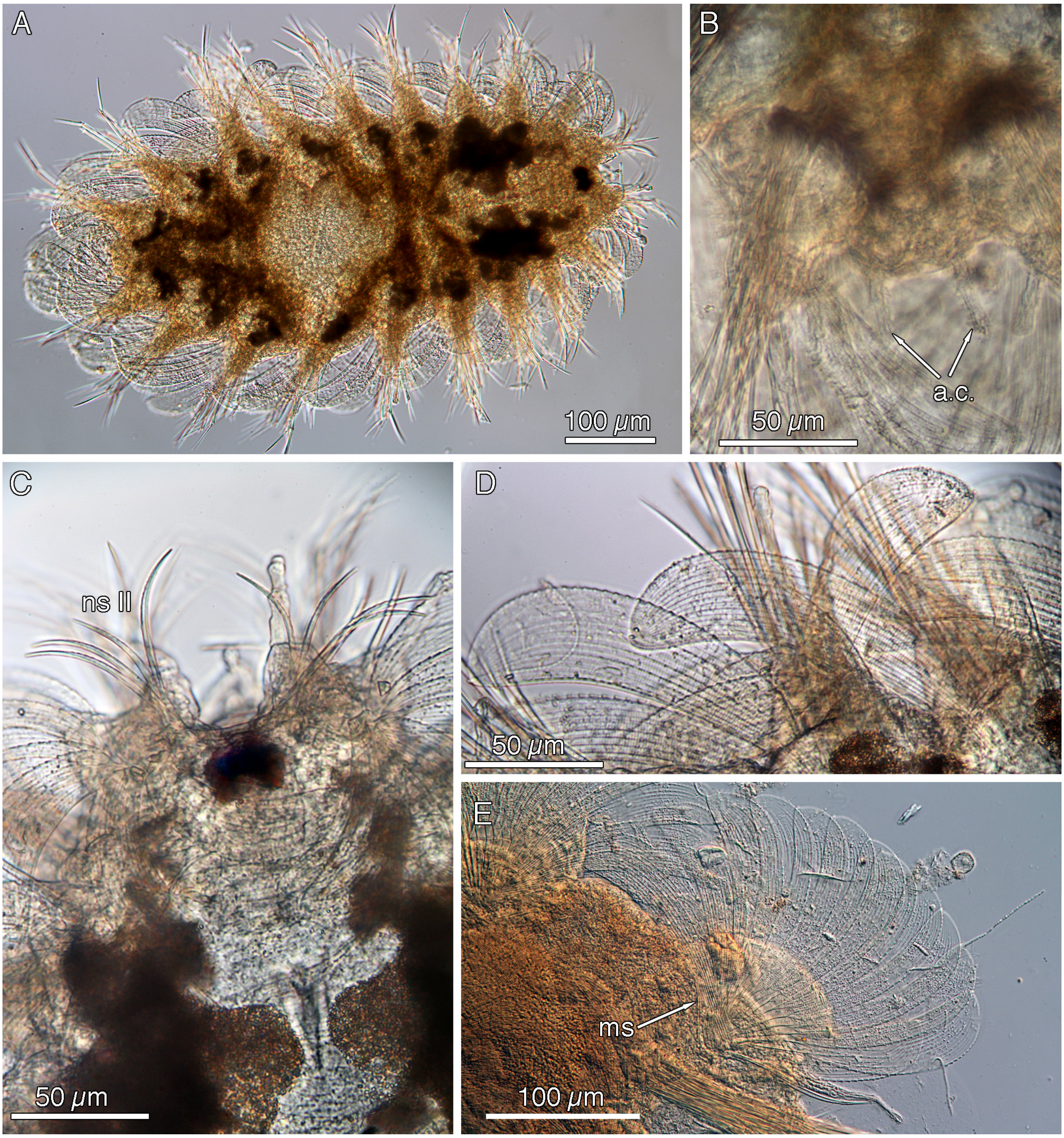

FIGURE 4. *H. leslieae* **sp. nov. A–E** Belize, micrographs, specimen photographed before sacrifice for DNA; **A**. live, dorsal view, entire body; **B**. pygidium with anal cirri; **C**. dorsal view, anterior end; **D.** lateral view, detail of main paleae & internal ribs; **E**. mid-body, notochaetal fan.

Hyalopale zerofskii **sp. nov.**

urn:lsid:zoobank.org:act:E131C388-1E2B-420C-BE89-AE479E562247
Figs 1F; 5A–F, 6A–G

Material examined. Holotype: SIO-BIC A8084, Eastern Pacific Ocean, California, San Clemente Island, 32°54'59.25"N, 118°27'50.67"W, maerl, 10 m., coll. Phil Zerofski, August 2, 2017, 1, 17E, L: 1.7mm, W: 0.9mm, ovigerous female.

Paratypes: SIO-BIC A8083 same collecting details as holotype; 3, (1, 18E, L: 1.25mm, W: 0.45mm, ovigerous female; 1, 15E, ovigerous female); SIO-BIC A8082, Eastern Pacific Ocean, California, San Clemente Island, same locality details as holotype, maerl, coll. Phil Zerofski, July 20, 2015, 1, 17E, L: 1.25mm, W: 0.45mm, ovigerous female; SIO-BIC A 10228 , ovigerous female, slide series.

Additional material. NTM W. 29628, Eastern Pacific Ocean, Estacahuite Bay, Oaxaca, Mexico, from *Padina* algae, shallow depth, coll. Christopher Cruz Gomez, 25 Aug., 2007, 1 anterior body fragment, 9NE; NTM W. 23735, Eastern Pacific, Moorea, French Polynesia, west side of fore-reef, hook inside, Stn. M531, 1m, coral rubble, November 2010, coll. J. Thomas (Moorea Biocode), 1, 15E, L: 1.1mm, W: 0.6mm, (note: 11 anterior segments used up for DNA which failed, 4 posterior segments registered).

Diagnosis. *Hyalopale* with mid-body main paleae with rounded brow, 25/26 (27) ribs, multiple shallow raised ribs.

Description (based on holotype, paratypes where noted). Live ovigerous female of 17 segments with two pairs of large cherry-red eyes, white pigmentation present dorsally in five anterior segments, green-brown internal body pigment visible; with five large eggs over segments 7–13, smaller eggs also present (Fig. 5A); smallest paratype ovigerous female of 15 segments with three large eggs plus smaller eggs. Gametous paratypes also possess light to dark green internal pigmented cells. Prostomium with slender finger-shaped median and two lateral antennae, two rounded palps ventrally, segment 1 with two pairs of slender tentacular cirri; segment 11 with six notochaetal spines; barrel shaped pharynx with pair pointed stylets situated close together with longitudinal groove facing inwards (Fig. 5B–D). Mid-body notopodium with one subacicular curved lateral spine with minute serration in part on both margins; main paleae number 11 with 25–26 (27) and two counts of 28 ribs and 12–14 very finely raised ribs (~8 more obvious, Fig. 1F); on high magnification horizontal striae are relatively widely spaced. Lateral-most and midline-most main paleae smaller with 21–23 ribs; segment 17 has two midline-most smaller main paleae, slightly symmetrical in shape, 16–18 ribs (Fig. 6E). Midline spines absent. Main paleae with slightly rounded to sloping brow, tiny upright apex, inner margin with minute serrations, convex margin with visible serration becoming minutely serrated on brow. Notopodia with slender dorsal cirrus, style extending at least half to 2/3 length of paleal fan, cilia tufts laterally and distally on dorsal cirri; rounded swollen glands visible posterior to dorsal cirrophore (Fig. 5E, F). Mid-body neuropodia with 4 (5) superior long, very slender spinigerous articles; four mid- superior very slender falcigers; mid-group number 14–18 comprise upper slender falcigers and lower slightly broader falcigers with visible blade serration; inferior group with 4–6 slender shorter blades. Ventral cirri length as long as distance to neuropodial tip.

Remarks. *Morphology.* Paleal rib counts down the body of the holotype include: anterior chaetigers, segment III, has 18 ribs, segment V with 24 ribs, mid-body chaetigers has 25, 27 (28) ribs and posterior chaetigers, segment 15 has 24–26 ribs and segment 17 possesses 2–3 midline-most smaller main with 16–20 ribs. The possible *Hyalopale zerofskii* **sp. nov.** Mexican individual from Estacahuite Bay, Oaxaca, is a smaller specimen compared to the southern Californian type material and has no sign of gametes. The original specimen was 13E; the anterior body of the examined specimen has 9 segments (L: 0.8mm, W: 0.5mm); it has a broad tapered pharynx and posterior caeca, a mouth fold with large mouth papillae and the rounded tips of the two stylets visible. Larger and slightly smaller main paleae including the smaller midline-most main, exhibit a similar shape and range of internal and raised ribs that agrees with that observed with the type material of *H. zerofskii* **sp. nov.**

The possible *Hyalopale zerofskii* **sp. nov.** specimen from Moorea (French Polynesia) possesses a mid-body notopodium comprising: lateral spine with minute serration in part on both margins; main paleae with tiny upright apices, relatively widely spaced horizontal striae, 21–26 internal ribs (lateral-most main paleae with 21 ribs), 5–6 shallow raised ribs; midline spines absent. Posterior-most notopodium, segment 15, with three main paleae: two with 18 ribs and midline-most main palea, almost symmetrical, with 15 ribs. Although *H. zerofskii* **sp. nov.** from Moorea has main paleae with apices more 'swept-up' compared to the more 'snub' apices of main paleae in the southern California and Mexican specimens, it exhibits similarity of main paleae shape and number of ribs and is therefore identified within a *Hyalopale zerofskii* **'**species complex'.

Hyalopale zerofskii **sp. nov.** lacks midline spines and has a paleal shape and degree of raised ribs quite different to that of the Western Atlantic *H. bispinosa s.s* (cf Fig. 1F with 1A, B). Morphological and molecular results indicate that *H. zerofskii* **sp. nov.** from the eastern Pacific is distinct from the Caribbean Sea species and is the sister group (though poorly supported) to *H. sapphiriglancyorum* **sp. nov.** from the western Pacific (cf Fig. 1F & G; Fig. 13).

Pigmentation & epibionts. Hyalopale zerofskii **sp. nov.** has dense white pigmented cells of the dorsal anterior-most segments in two lateral 'shield' shaped areas and internal light to dark green/brownish pigmented body cells in all live material (Fig. 5A). Both forms of pigmentation are seen in the majority of other *Hyalopale* species *e.g.* the Caribbean *H. bispinosa* s.s. (Fig. 2) and the West Pacific species *H. sapphiriglancyorum* **sp. nov.** (Fig. 7A).

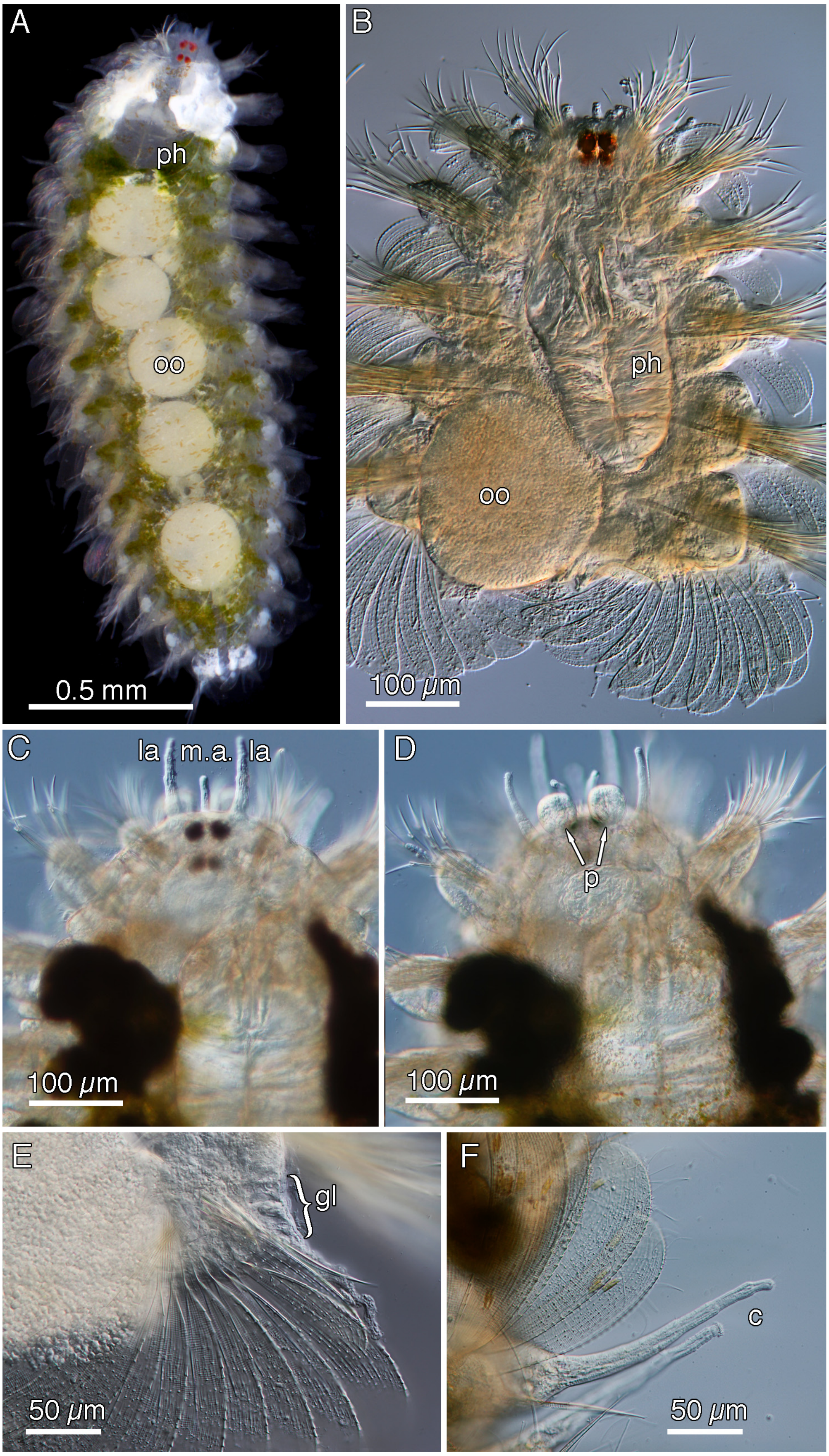

FIGURE 5. *H. zerofskii* **sp. nov.**, A–F, San Clemente Is. California, Paratypes, SIO-BIC A8083. **A**. live, colour stereo micrograph, ovigerous female; B–F. micrographs. **B**. anterior end, dorsal; **C**. anterior end, dorsal; **D**. anterior end, ventral; **E**. midbody notopodium in part with glands; **F.** detail of dorsal cirri with cilia.

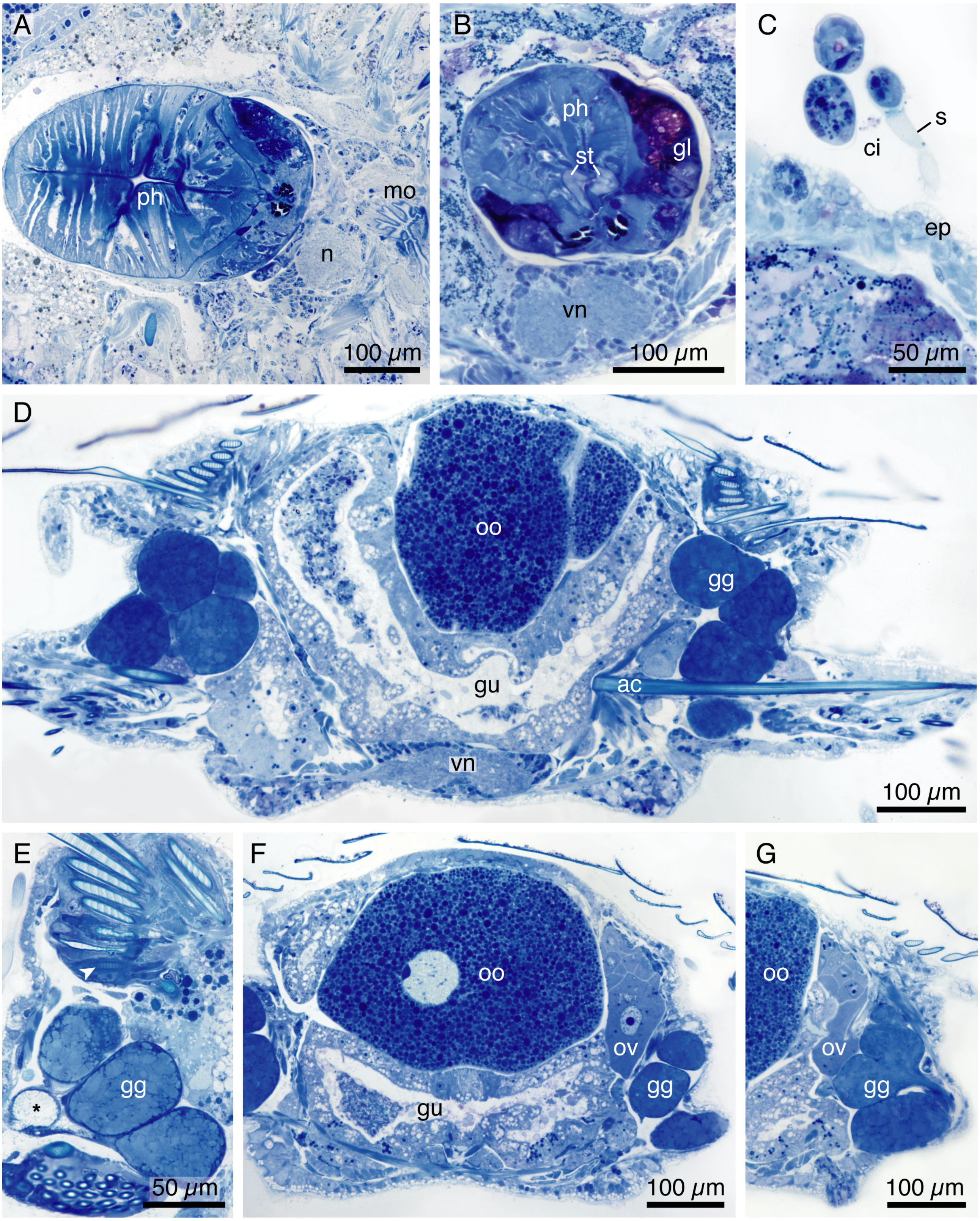

FIGURE 6. *H. zerofskii* **sp. nov.**, San Clemente Is. California, SIO-BIC A10228, **A–G**. Histology: **A**. horizontal section, **B–G.** cross sections. **A**. pharynx (ph) with circumoesophageal ganglion (n) and mouth (mo); **B**. pharynx (ph) with stylets (st) and prominent pharyngeal glands (gl); **C**. epibiont ciliates (ci) with stalk (s) attached to epidermis (ep); **D**. parapodium with ventral nerve (vn), gut (gu), oocyte (oo), green globules (gg), ventral acicula (ac); **E–G**. elaboration of **D**, including developing palea in chaetal follicle (arrow), ovary (ov), *empty vesicle.

All four of the sectioned specimens were ovigerous females. Multiple large vitellogenic oocytes (± 300–400µm in diameter) were observed dorsally in the coelomic cavity (Fig. 6D, F). Oogenesis occurs in laterally positioned ovaries, where multiple non-vitellogenic oocytes could be seen (Fig. 6F, G). The green/brown globular material visible through the live animal's body wall is likely associated with the reproductive system, due to its close proximity to oocytes (Fig. 6D–G). Though the function still remains unknown and needs further investigation, we hypothesize that these are glandular secretions. This is corroborated by their vesicular appearance, and the lack of identifiable nuclei and organelles. In certain sections, it was observed that the dark homogenous contents of these structures were emptied near the parapodia, leaving behind an empty vesicle (Fig. 6E). Developing paleae are located in the ventral rim of the paleal fan (Fig. 6E). The muscularized pharynx is equipped with large pharyngeal glands antero-ventrally (Fig. 6A, B).

Epibiont ciliates identified as loricate peritrichs are attached to the epidermis aborally by a stalk, which are then covered by the paleae (Fig. 6C). Epibiont ciliates have been recorded in a number of different taxa of the Syllidae attached to intersegmental furrows, dorsal and ventral surfaces, nuchal organs, mouth opening and anterior cirri and are known to thrive in oxygen poor waters (Campos *et al.* 2014).

Etymology. This species is named for Phil Zerofski, Experimental Aquarium Manager, Marine Technician/Collector at Scripps Oceanography. He has been a great friend of the Rouse lab and brought us many wonderful specimens over the years and we honor him with this new species.

Hyalopale sapphiriglancyorum sp. nov.

urn:lsid:zoobank.org:act:E8386468-BD79-4718-A6BC-500FA53BB5C8

Figs. 1G; 7; 8 A

Material examined. **Holotype**: MZB Poly.00409, 15E, ovigerous female, L: 1.35mm, W: 0.9mm, Western Pacific, Indonesia, Raja Ampat, slightly subtidal in front of Sorido Resort, Kri Island; rubble, algae and sand, 0.55575° S, 130.68535° E, coll. G. Rouse, Oct. 15, 2013.

Paratypes: MZB Poly.00410**,** collecting information collecting information as holotype, MZB Poly.00410, 3; SIO-BIC A 9490, 2E; Ovigerous females: 16E, L: 1.45mm, W: 0.9mm; 13E, L: 1.25mm, W: 0.75mm; 11E, L:0.8mm, W: 0.4mm; one with gametes (?sperm), 16NE, L:1.5mm, W: 0.8mm.

Additional Material. NTM W. 29627**,** Australia, Queensland, Great Barrier Reef (GBR), Low Isles, 16 °23'S, 145° 34'E, *Halimeda* washings from *Porites* Pond, coll. B.C. Russell, 23 Dec 1987, 1, 11E, male.

Diagnosis. *Hyalopale* with mid-body main paleae narrow with well-defined apices, 14–15 (17) ribs, 4–5 shallow raised ribs.

Description (based on holotype, paratypes where noted). Live holotype with pale yellow body with darker patches at base of notopodia, silvery transparent main paleae, solid white pigment present in dorsal anterior segments (to segment 6) including curving around pharynx; holotype and all paratype material with internal brownish-green pigments (Fig. 7). Prostomium partly retracted between anterior two chaetigers, with two pairs of large dark red fused eyes; slender finger shaped median antenna sits anterior to two slender lateral antennae; two rounded palps ventrally placed. Achaetous segment 1, very reduced with two pairs of slender tentacular cirri; segment II with six short, curved notochaetal spines; segment III with lateral spine, eight main paleae. Pharynx barrel shaped, extends to segment 5, very small pair of stylets visible. Mid-body notopodium with relatively narrow, long-shaped main paleae with sloping blunt brow, minute apex, inner margins with minute serrations, convex margin with visible serration leading to apex; with multiple very finely spaced internal ribs; main number 10–12, with (13) 14–15 (16) internal ribs, 4–5 shallow raised ribs; single, short midline-most spine with slight serration on distal convex margin (Fig. 8A). Lateral-most main may be slightly more symmetrical with (11) 12–14 ribs; posterior-most notopodia with midline-most main paleae, smaller, markedly more symmetrical in shape, 12–14 ribs. Notopodia with slender dorsal cirrus, style extending as long or slightly longer than main paleae fan. Neurochaetal falcigerous types with very slender blades, minutely serrate basally, with minute curved distal tips, comprising: five superior group very long-bladed; 5–6 mid superior long-bladed; 8–10 mid-group with slightly shorter-blades; 4–5 inferior group slightly shorter bladed. Ventral cirri insert relatively high on posterior margin of neuropodia; shape finger like, very slender about same length to slightly longer than length to neuropodial tip.

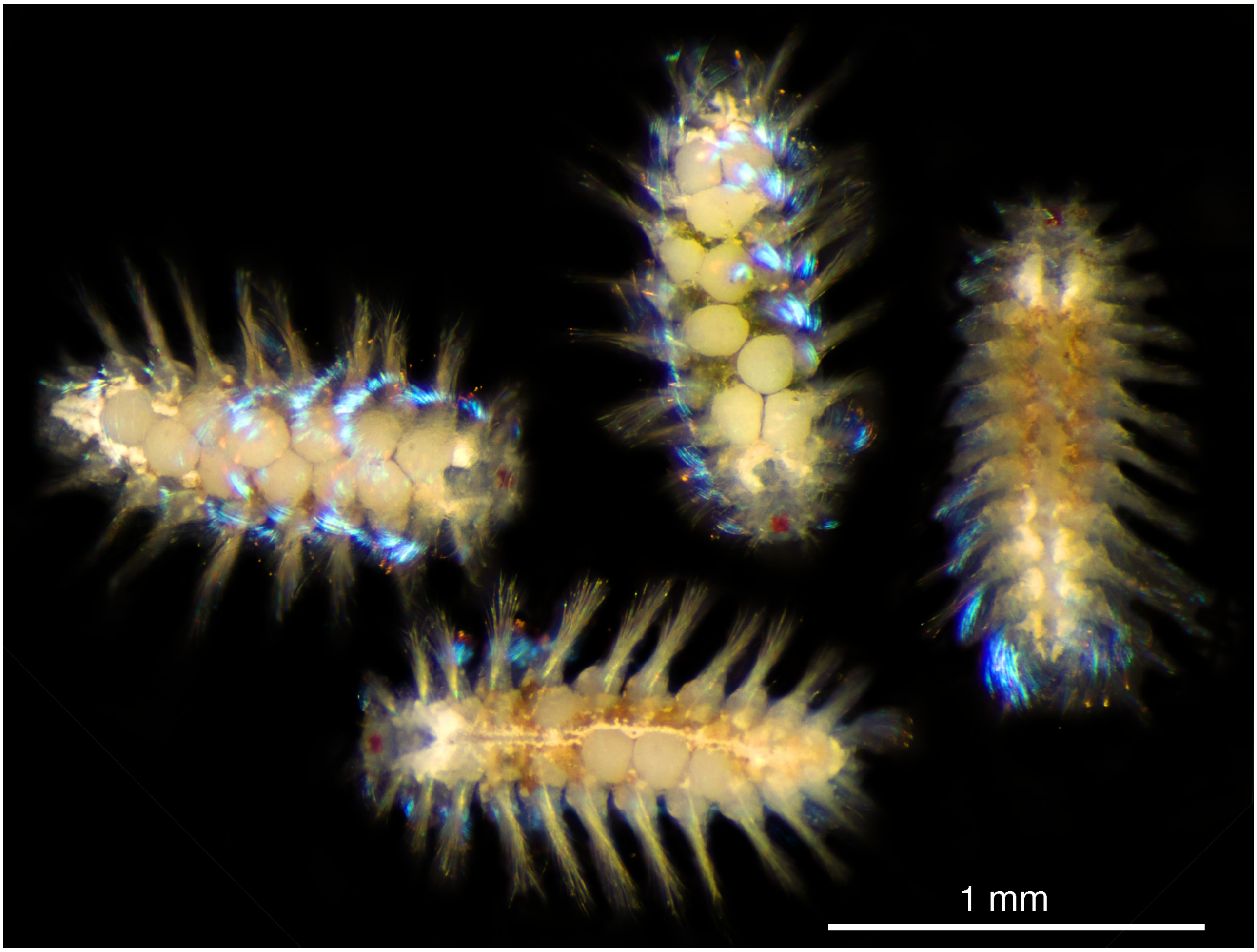

FIGURE 7. *H. sapphiriglancyorum* **sp. nov.** Raja Ampat, Indonesia, Paratypes, MZB Poly. 00410**,** live, colour stereo micrograph, gametous individuals.

Additional material. When alive, the Australian specimen had greenish-black internal pigment material in patches and very thin, transparent paleae covering the dorsum. The convex margin of main palea with very fine serration to distal tip and (14) 15, 16 (17) ribs and 5/6 shallow raised ribs; mid-body segments with a small symmetrical midline-most main, and slender, relatively long dorsal and ventral cirri. It has particularly long-bladed, superior group falcigerous neurochaetae extending out beyond notopodia, numbering five.

Remarks. *Hyalopale sapphiriglancyorum* **sp. nov.** is characterized by possession of the narrow shape of the main paleae and with the lowest number of ribs; comparatively longer dorsal cirri; neurochaetal types with particularly slender, long blades and slightly higher number of superior-most falcigers and possession of midline spines: characters sufficiently different to separate it from the other northern Australian *Hyalopale* species, *Hyalopale angeliensis* **sp. nov.**, found from the eastern Indian Ocean (see Remarks *H. angeliensis* **sp. nov.** below). *Hyalopale sapphiriglancyorum* **sp. nov.** is found in very similar shallow water, tropical coral reefal habitats from both western Pacific localities and is the sister group (though poorly supported) to the eastern Pacific temperate species *H. zerofskii* **sp. nov.** (Fig. 13).

The morphology of *Hyalopale sapphiriglancyorum* **sp. nov.** from Indonesia and north eastern Australia agree, though DNA sequences were only obtained for the Indonesia material. The specimens from the two localities share the presence of midline spines, similar length of dorsal cirri, numbers of superior neurochaetae and long, narrow main paleae with a similar range of rib number: Indonesia, 14–15 (16) *versus* Australia (14) 15–16 (17), and a similar number of raised ribs. A smaller midline-most main palea is observed in posterior chaetigers in material from Indonesia and is present in most body segments of the GBR specimen. Ovigerous females of 13 to 16 segments entire possessed 1–2 large eggs (220–230 µm) per segment and a total of 9–11 large eggs per individual, with smaller eggs also present; large eggs were absent in the 11E individual (Fig. 7A). The Indonesian and Australian material included individuals with bodies starting to disintegrate, neurochaetae falling out and eyes coalescing. Swollen horizontal to coiled glands in mature individuals are situated below the base of the dorsal cirrophore and may have a granular appearance; many individuals also possess large rounded vacuoles with a slight 'crazed' surface, situated interamally closer to the neuropodia. Similar mature glandular patterns are seen in *Paleanotus* species (*e.g.* Watson 2015, Fig. 2H, I).

Etymology. Named in honor of the Glancy family, in appreciation for the support by John and Cynthia (Cindy) Glancy for the Rouse lab and the Scripps Oceanographic Collections Endowment (this was John's gift to Cindy for their 50th wedding anniversary). Cindy and grandchildren were struck by the sapphire blue iridescence of the chaetae of the new species (Fig. 7), so we have incorporated that into the name.

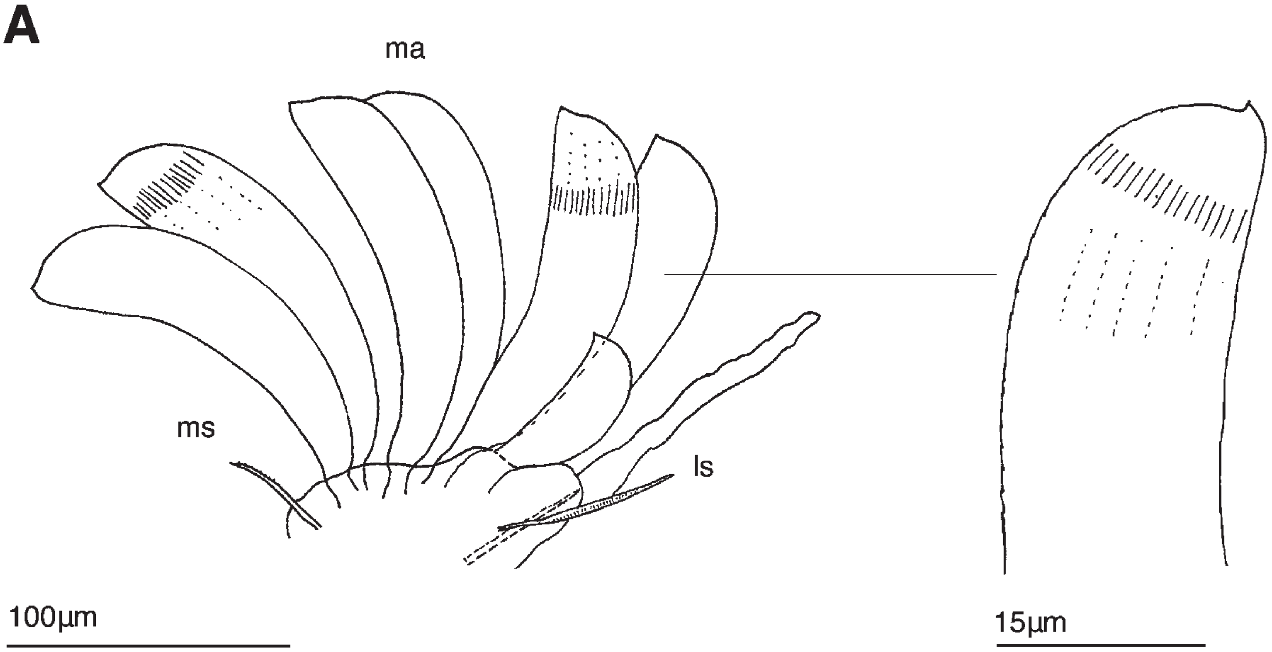

FIGURE 8. *H. sapphiriglancyorum* **sp. nov.** Raja Ampat, Indonesia, Paratype, MZB Poly. 00410**, A**. mid-body notopodium with detail of main palea.

Hyalopale angeliensis sp. nov.

urn:lsid:zoobank.org:act:9106A06A-97A8-4D5D-A208-0F9C91152008
Figs 1E; 9A–D

Material examined. Holotype. AM W.3166, Eastern Indian Ocean, Western Australia, Dampier, Angel Island, Stn. WA639, 20° 48' S, 116° 81' E, 1 Aug 2000, coll. P. A. Hutchings, L. Avery, 13E, L: 0.92mm, W: 0.4mm.

Additional material. USNM 1076948, Western Indian Ocean, Seychelles, Round Island, 19° 45' S, 57° 50'E, Sta. 14, intertidal from sponge, coll. K. Buchanan, Dec 1975, 1, 13E*,* L: 1.1mm, W:0.55mm.

Diagnosis. Mid-body main paleae narrow with well-defined apices, (16)18–22 ribs, 4–6 shallow raised ribs.

Description (based on holotype except where noted).

Slightly wasted entire individual; body pale yellow, three pairs of melded dark red eyes; cirri intact, some neurochaetal types loosening in posterior body. Segment II with 4 short, curved notochaetal spines; segment III with lateral spine, 8 main paleae. Mid-body notochaetal fan with single lateral spine, 10 main paleae with 18–22 internal ribs, 4–6 patchy shallow raised ribs; midline spines absent. Main paleae slender with sloping brow, small blunt apices, inner margin may be slightly folded with minute serrations, convex margin with widely spaced serrations mid-way, becoming finer on brow leading to apex (Fig. 9A, Western Australia; Fig. 9B, Seychelles). Narrower, lateral-most main with 16–17 ribs and 2–3 smaller, more symmetrical-shaped, midline-most main with lower number of ribs (Fig. 9C, see 16–11 ribs). Neurochaetae mid-body comprise: four superior group very long-bladed; three mid superior group long-bladed; 8 mid-group with slightly shorter-blades, basal serration; 4–5 inferior group slightly shorter bladed. Mid-body neuropodia with broader mid-group falcigers (Fig. 9D, Seychelles).

Remarks. The two specimens of *Hyalopale angeliensis* **sp. nov.** are found at localities occurring on a similar parallel at ~ 20° S in the Eastern and mid-Indian Ocean. *Hyalopale angeliensis* **sp. nov.** is a small species, possessing a relatively low number of paleal ribs; material examined from north-western Western Australia and the Seychelles Islands exhibit very similar, relatively narrow main paleae shape (respectively Fig. 9A,B) with slightly upswept apices, 18–22 ribs and 4–6 shallow raised ribs. Both individuals also consistently possess 2–3 smaller, midline-most main paleae (Fig. 9C); other *Hyalopale* species may only have 1–2 (rarely 3) smaller, midline-most main paleae. *Hyalopale angeliensis* **sp. nov.**, and *H. sapphiriglancyorum* **sp. nov.** have a general similarity in the narrow- shaped main paleae (cf Fig. 1 E, G), but the former has more distinct 'upswept' apices, a slightly higher range of rib numbers and absence of midline spines, compared to the latter. The absence of midline spines seen in *Hyalopale angeliensis* **sp. nov.** (Eastern Indian Ocean) is also observed in *H. furfuricula* **sp. nov.** (Western Indian Ocean) but both species possess very different main paleae shape and raised rib patterns (cf Fig. 1 E, D). Unfortunately, no DNA sequences could be acquired for this new species.

Etymology. The species name is named after the remote Angel Island off Dampier on the northwestern Australian coast.

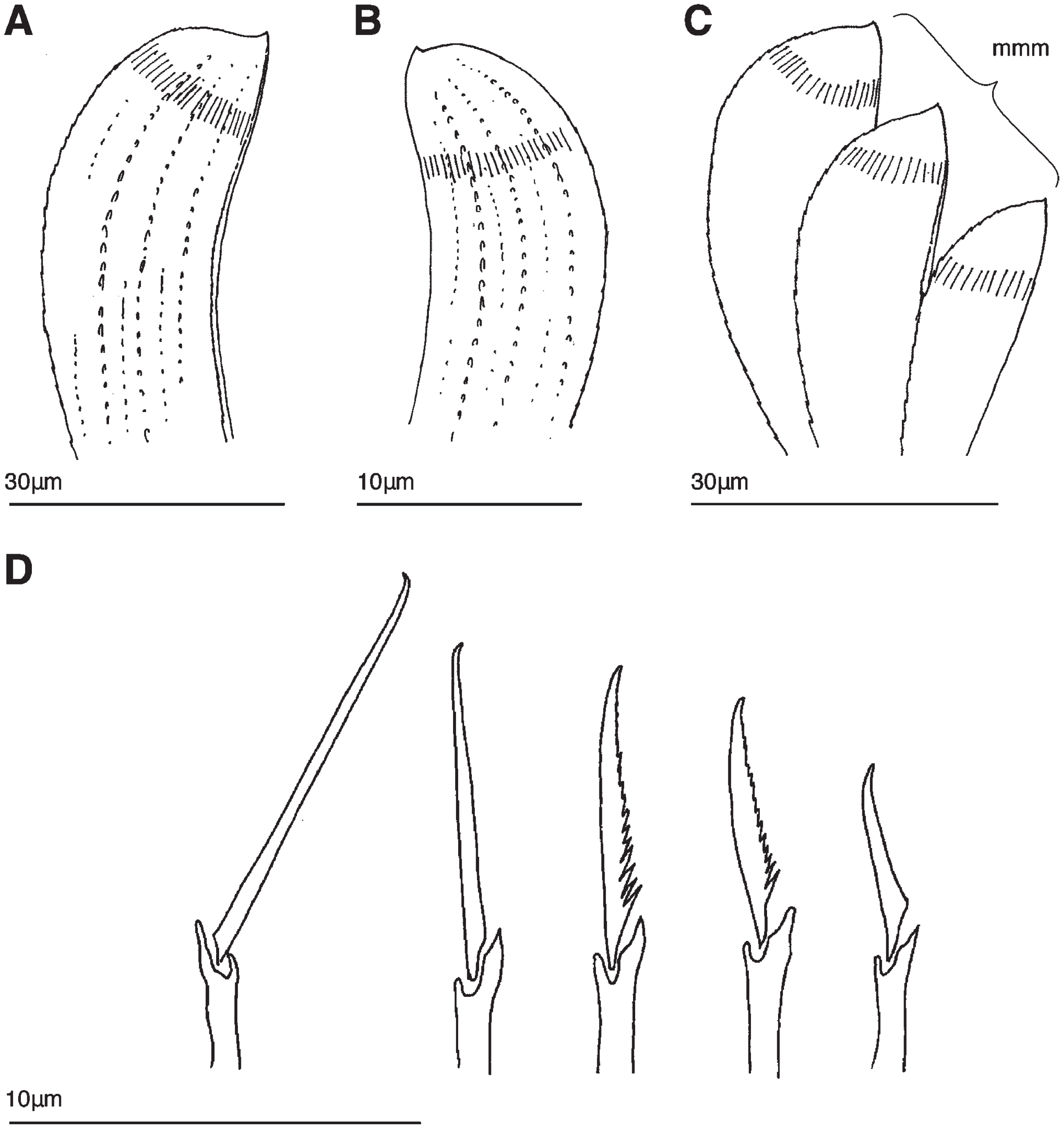

FIGURE 9. *H. angeliensis* **sp. nov. A,C.** Dampier, Western Australia, Holotype, AM W.36166 **A**. detail middle group palea, **C**. detail of midline-most main paleae; **B,D**. Seychelles, USNM 1076948. **B**. detail middle group palea, **D**. neurochaetal falcigerous types from mid-body segment, left to right: superior very long bladed, mid-superior long bladed, mid-group broader bladed with larger serrations, inferior group short bladed.

Hyalopale furfuricula sp. nov.

urn:lsid:zoobank.org:act:2338A919-41EE-4C0F-AF55-B118ADC145B4
Figs 1D; 10A–B; 11 A–C

Paleanotus chrysolepis Hartmann-Schröder, 1960: 71
Paleanotus cf. *chrysolepis* Ben- Eliahu, 1976: 159
Hyalopale sp. Watson Russell, 1987: 668, fig. 27.4

Material examined. Holotype. NTM W.25602, Red Sea, Egypt, Al Ghurdaqah, Stn. B27, littoral, coll. V. Storch, donated 1986, 1: 16NE, L: 1.1mm, W: 0.4mm, gametes.

Paratype. HZM P. 277743, Al Ghurdaqah, intertidal, near sub-fossil coral reef, bushy algae, coll. Remane, March, 1956, 1: 9E, L:0.6mm, W:0.38mm.

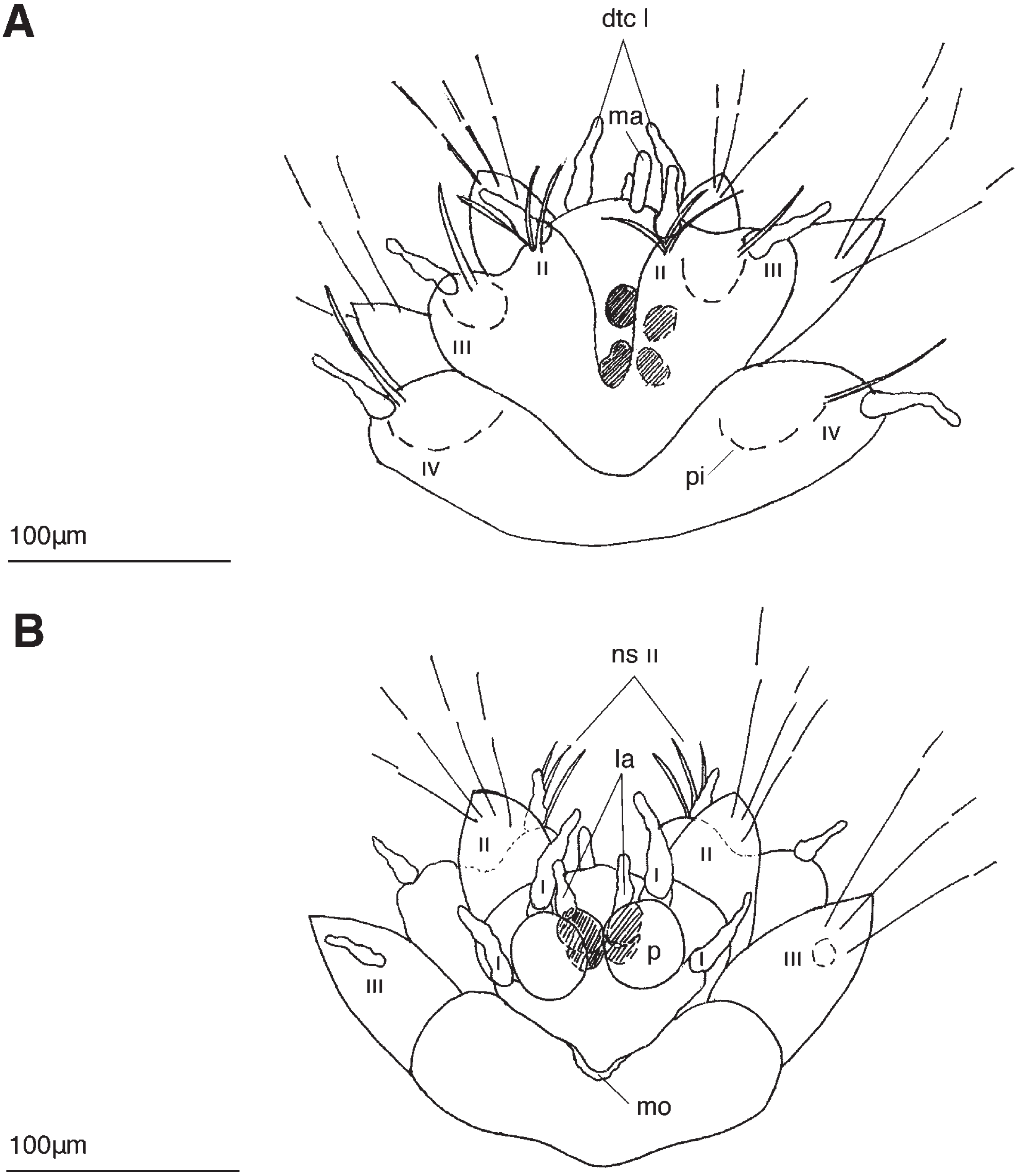

FIGURE 10. *H. furfuricula* **sp. nov.** Red Sea, Holotype, NTM W.25602. **A**. anterior end, dorsal view; **B**. ventral view.

Additional material. HUJ AN.1.53, Red Sea, Israel, Gulf of Elat, Wadi Kabila, *Dendropoma* infauna, intertidal, 2: 1E, 16 segments, L: 1.1mm, W: 0.38mm; HZM P.14052, Western Indian Ocean, Mozambique, Inhambane, 23 47'S, 35° 31'E, 25 Sept 1967, coll. Hartmann-Schröder, algal scrapings, 1, 14NE in 3 sets of fragments, W:0.6mm.

Diagnosis. Mid-body main paleae with rounded brow, minute apices, (20) 22–24 ribs, multiple shallow raised ribs with minute denticles.

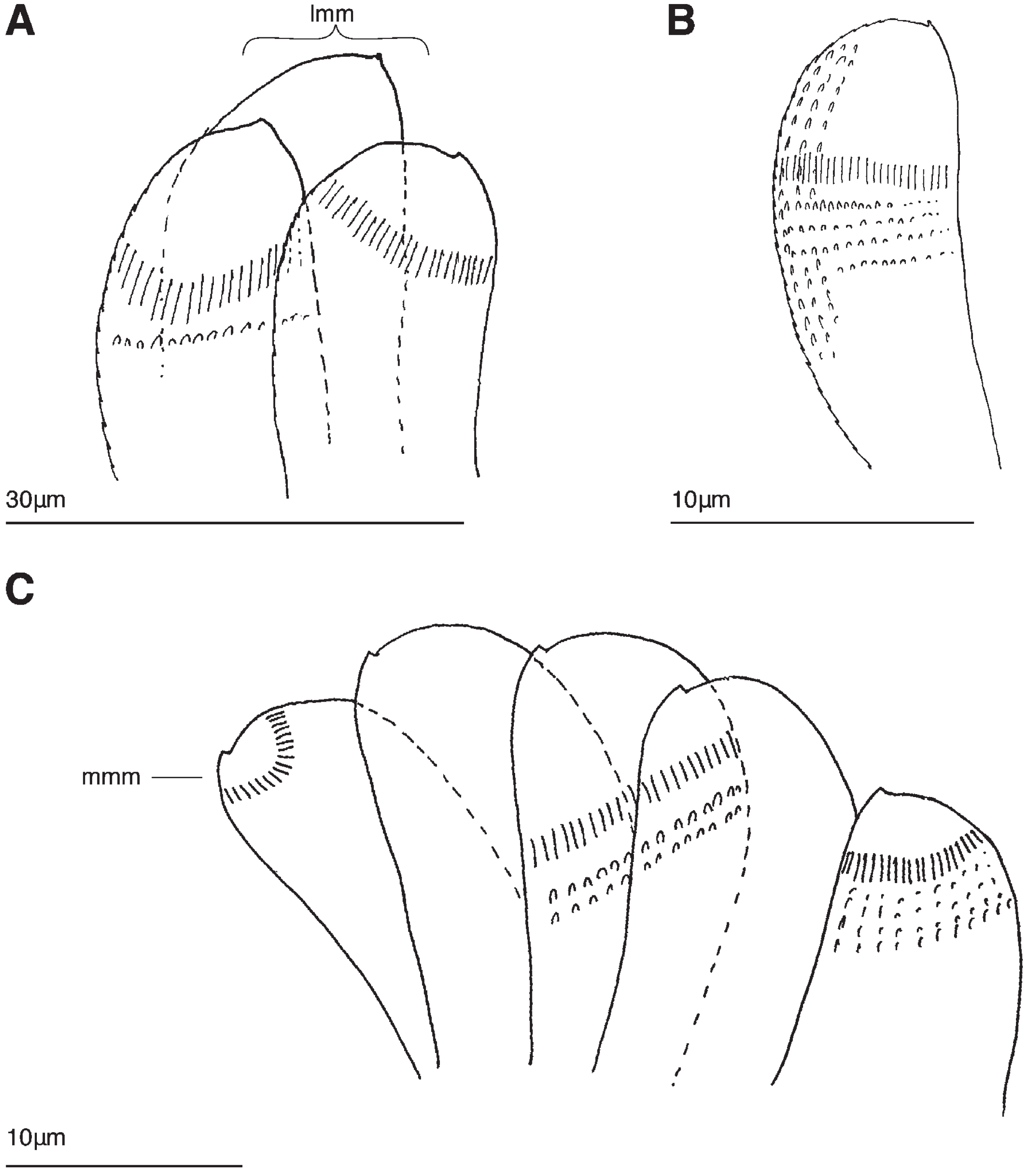

FIGURE 11. *H. furfuricula* **sp. nov.** A–B. Inhambane, Mozambique, HZM P.14052. **A**. detail of 3 lateral-most main paleae, **B**. detail of middle group palea; **C**. Red Sea, Holotype, NTM W.25602, detail of midline-most main and middle group paleae.

Description (based on holotype unless indicated otherwise). Prostomium retracted within segments II and III, more visible in ventral view, with two pairs melded red eyes; notopodia of segment II with six spines (Fig. 10 A, B). Barrel-like pharynx with two stylets, posterior caeca present. Mid-body notopodium with lateral spine; main paleae number nine, with (20) 22–24 (25) ribs and 9–10 (12) shallow raised ribs supporting small denticles that loosely line up in rows (Fig. 11 A, Red Sea; Fig. 11B, Mozambique); midline spines absent. Lateral and midline-most main paleae slightly more symmetrical, often with slightly involute shallow apices and 18–22 ribs (Fig. 11C). Main paleae relatively broad, with rounded brow, tiny, rounded apices, inner margin with minute serrations, convex margin with better-formed serration leading to apex. Notopodia with slender dorsal cirri, style extending just over half length of main paleae fan. Mid-body neurochaetae comprise: four long-bladed superior group; five mid superior; ~10 midgroup falcigers with slightly shorter, broader-blades with longer serrations; ~5 inferior group with shorter, slender blades. Total approximately 25/26. Ventral cirri finger- like, length to neuropodial tip.

Remarks. Watson Russell (1987) figured a small individual of *Hyalopale* sp. from the Red Sea, possessing three pairs of eyes and typical lateral spines (Watson Russell 1987: 668, Fig. 27.4). Hartmann-Schröder (1960) identified material from Ghardaga as *Paleanotus chrysolepis* and Ben-Eliahu (1976) recorded *Paleanotus* cf. *chrysolepis* from intertidal sabellariid and vermetid reefs in the Gulf of Elat, with lateral 'acicular notosetae' (= lateral spines) and noted green material in the body. Re-examination of these specimens in addition to that from HZM museum collections identified as *Paleanotus chrysolepis* by Hartmann-Schröder from Mozambique, proved to be *Hyalopale furfuricula* **sp. nov.** The morphology of *Hyalopale furfuricula* **sp. nov.** main paleae from individuals of the Red Sea and Mozambique closely agrees especially in the characteristic main paleal shape with a distinctive rounded brow with tiny, almost involute apices plus the numbers of internal ribs and raised ribs with small denticles. These notochaetal characters distinguish *Hyalopale furfuricula* **sp. nov.** from all other conspecifics, including those in adjoining regions: *H.* cf. *bispinosa*, Mediterranean Sea, to the north (cf Figs 1D, B) and *H. angeliensis* **sp. nov.** to the east (cf Figs 1 D, E). The mid-body neurochaetae of *Hyalopale furfuricula* **sp. nov.** are shorter, with broader more robust blades, and distinct curved distal tips that are less attenuate, when compared to those of *H. angeliensis* **sp. nov.** and *H. sapphiriglancyorum* **sp. nov.** Unfortunately, no DNA sequences could be acquired for this new species.

Etymology. The species name, *furfuricula,* is a diminutive form of *furfur* from the Latin and refers to the many tiny raised denticles or flakes on the dorsal surface of the main paleae, which forms a type of 'scurf'.

Phylogenetic Results

The phylogenetic results (Fig. 13) are essentially the same as reported in Watson *et al.* (2016) with the addition of data here from four species of *Hyalopale*. In the ML analysis, *Hyalopale* formed a well-supported clade that was sister group to *Paleanotus* and this in turn was the sister to the remaining paleate chrysopetalids, forming Chrysopetalinae. In the MP analysis *Hyalopale* also formed a well-supported clade but did not group with *Paleanotus*. Instead it was the sister group to all other Chrysopetalinae, though that clade was poorly supported. Within *Hyalopale*, *H*. cf. *bispinosa* was the sister group to the remaining three species in both the ML and MP analyses (Fig. 13). *Hyalopale leslieae* **sp. nov.** from the Caribbean, was then sister group to the two Indo-Pacific species, though neither of these nodes was consistently well supported.

Discussion

Morphology. Among the *Hyalopale* taxa there are four morphological characters that either alone or in combination with other characters identify the *Hyalopale* species and offer degree of relationship: 1. presence/absence of midline spines; 2. shape of main paleae; 3. number of main paleae ribs; 4. presence and numbers of small midline-most main paleae.

The presence of midline spines is confirmed in the Atlantic/Caribbean clades and interestingly in the west Pacific species, *Hyalopale sapphiriglancyorum* **sp. nov.** They are absent in the eastern Pacific and Indian Ocean taxa. The phylogenetic significance of presence/absence of a midline spine in *Hyalopale* species is not fully understood and a more complete phylogeny is needed. *Hyalopale* 'larvae' have not yet been found to verify whether a midline spine is present in the larval form of all species. It should be noted, however, that midline spines *per se* are not necessarily considered a novel adult character in *Hyalopale* as such short spines are found in the notochaetal fan of other paleate taxa (Watson, unpublished), but their presence in the midline position combined with absence of median paleae is novel. The shape of main paleae and their number of ribs proves the single most reliable character that is used to identify and separate individual and groups of species *e.g.* Atlantic species (Fig. 1A, C) and northern

Australian species (Fig. 1E, G). These two characters are basic to species identification in all other Chrysopetalinae paleate species (Watson pers. obs.). The majority of *Hyalopale* species possess smaller paleae with a lower number of ribs that are more symmetric in shape, in the midline- most position of the notopodial fan. These may number only one *e.g. H. leslieae* **sp. nov.** (Fig.3A, detail) or two to three, as seen in the Indian Ocean *H. angeliensis* **sp. nov.** (Fig. 9C). These smaller paleae insert at a similar angle as the main fan (Fig. 3A) and do not appear homologous to the specialized median paleae fascicle that inserts at an opposite angle to the fan, as seen in *Paleanotus* larvae and adults (Fig. 12 cf B, C).

Molecular results and biogeography. The molecular phylogeny suggests that the Mediterranean terminal, *Hyalopale* cf. *bispinosa* is the sister group to other *Hyalopale* (Fig. 13). The Caribbean *H. leslieae* **sp. nov.** is more closely related to the *Hyalopale* Pacific clade, *H. zerofskii* **sp. nov.** (Eastern Pacific) and *H. sapphiriglancyorum* **sp. nov.** (Western Pacific). However, the support values are low (Fig. 13) and the lack of additional genes for three of the *Hyalopale* species included here (Table 1) precludes any strong conclusions.

TABLE 1. Sequenced specimens and GenBank (GB) accession numbers. New sequences in **bold**.
MB=Museu Nacional de História Natural, Lisboa (Museu Bocage); NTM= Museum and Art Gallery of the Northern Territory Australia; SIO = Scripps Institution of Oceanography Benthic Invertebrate Collection; USNM= National Museum of Natural History; Smithsonian Institution

Terminal	Voucher	18S	16S	COI	H3
CHRYSOPETALIDAE					
Calamyzinae					
Iheyomytilidicola lauensis	SIO A2267	JX078942	JX078952	JF304502	JX078966
Laubierus alvini	SIO A2282	JX078940	JX078950	JF304494	JX078964
Natsushima bifurcata	MB29-000186	JX078943	JX078953	JF304492	JX078960
Natsushima sashai	SIO A1619	JX078944	JX078954	JF304496	JX078961
Shinkai fontefridae	SIO A2204		JX078948	JF304499	JX078962
Shinkai longipedata	SIO A2283	JX078945		JF304500	
Calamyzinae sp.	SIO A3410		JX078951	JX078957	JX078963
Calamyzas amphictenicola	SIO A5852	JX078939	JX093563	JX078956	JX078967
Boudemos ardabilia	GB	EU555042	EU555051	EU555052	JX078959
Boudemos flokati	GB	EU555043	EU555034	EU555065	
Micospina auribohnorum	SIO A3640	JX078941.1	KU057930	KU057937	KU057934
Vigtorniella zaikai (benthic)	SIO A5639-40	KU057929	KU057932	KU057939	KU057936
Chrysopetalinae					
Arichlidon reyssi	GB	EU555036	EU555045	EU555054	
Chrysopetalum debile	GB	EU555037	EU555046	AF221567	
Chrysopetalidae sp.	GB	AY176284			
Paleanotus sp.	GB	EU555041	EU555050	EU555056	
Paleaquor heterosetosa	GB	EU555035	EU555044	EU555053	
Hyalopale* cf. *bispinosa	**NTM W.25602**	**MN175296**			
***Hyalopale leslieae* sp. nov.**	**USNM 097530**	**MN175298**	**MN175300**		
***Hyalopale sapphiriglancyorum* sp. nov.**	**SIO A9490**	**MN175299**	**MN175302**		**MN259122**
***Hyalopale zerofskii* sp. nov.**	**SIO A8082**	**MN175297**	**MN175301**	**MN258705**	**MN259121**
Dysponetinae					
Dysponetus sp.	GB	EU555038	EU555048	EU555055	
Dysponetus caecus	GB	AY839568	EU555047	AF221568	
Dysponetus caecus 2	GB		GQ426603		
Dysponetus bulbosus	SIO A4696	JX078946	DQ442570	JQ623501	
Dysponetus populonectens	SIO A2583	JX078955	JX078955	JQ623495	
OUTGROUP Hesionidae					
Nereimyra punctata	GB	DQ779661	DQ442577	DQ779746	AY644796

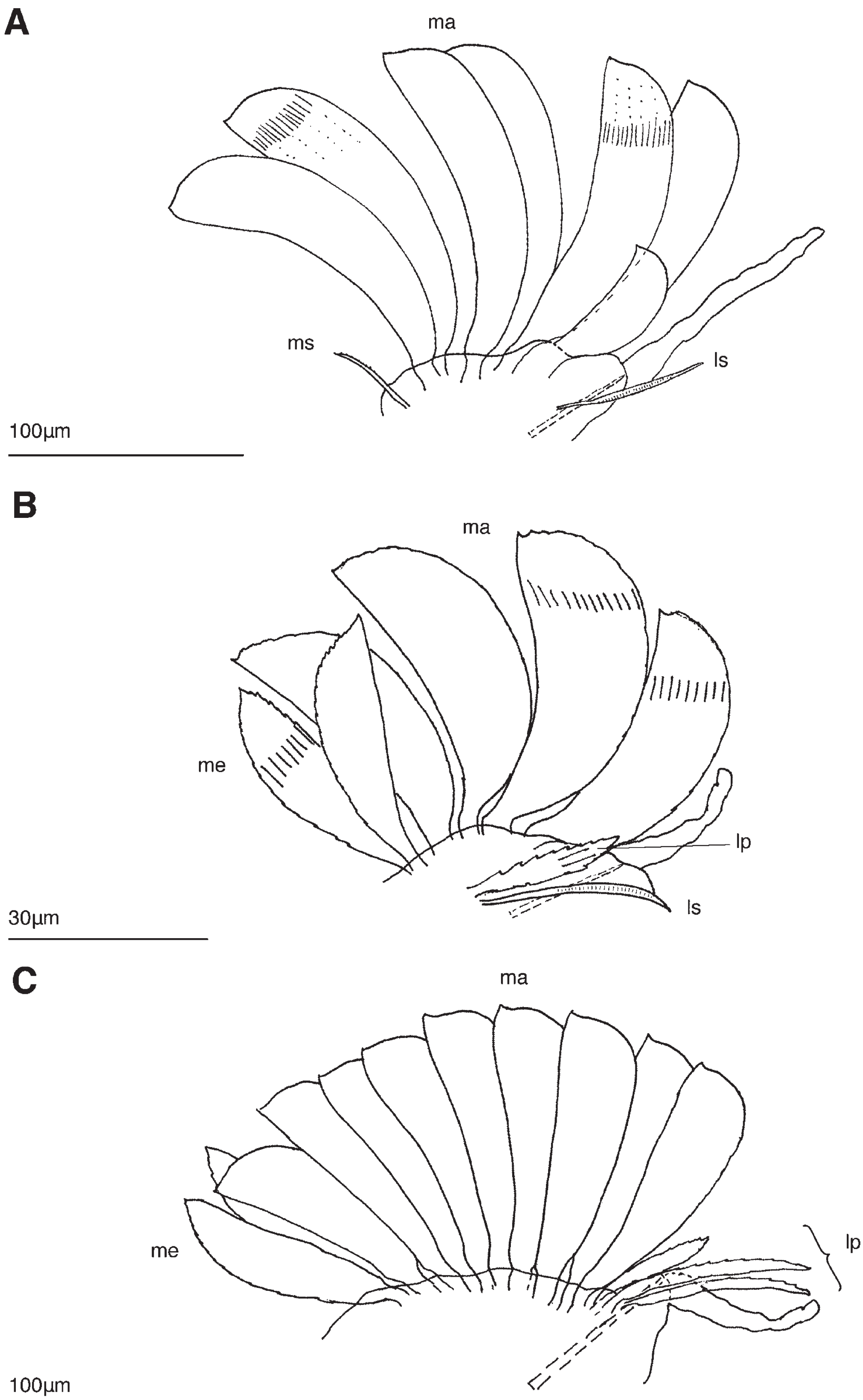

FIGURE 12. Comparison of mid-body notopodial fans of *Hyalopale* adult with *Paleanotus* larva and adult. A. *Hyalopale sapphiriglancyorum* **sp. nov.** paratype SIO-BIC A9490, adult, mid-body notopodium with fully developed notochaetal types; B. *Paleanotus* cf. *bellis* planktonic nectochaete larva, NTM. W. 29629, notopodium segment V with larval lateral spine, adult developing lateral palea, main paleael fan, developing median paleal fan; C. *Paleanotus bellis*, adult, LACM–AHF POLY 4402, mid-body notopodium with fully developed lateral paleae, main paleae, median paleae.

East /West Atlantic. *Hyalopale* cf. *bispinosa* (Mediterranean), is a deeper water, temperate dwelling species. The morphologically similar *Hyalopale bispinosa s.s*., is found from coastal southern Florida, at the transition zone between tropical and subtropical environments. The similarity of main paleae shape, higher-end number of ribs and presence of midline spines, links *H*. cf. *bispinosa* Mediterranean with that of the Florida type locality in the western Atlantic. Other molecular studies indicate presence of cohesive species throughout a distribution range across the Atlantic for both meiofaunal annelids (*e.g.* Westheide *et al*. 2003) and larger-bodied annelids (*e.g.* Ahrens *et al*. 2013). However, it is also possible that *Hyalopale* cf. *bispinosa* (Mediterranean) represents a new cryptic species with its comparatively smaller size at maturity, degree of paleal ornamentation versus no ornamentation and its different biotope and depth range.

West Atlantic/**Caribbean.** It is of interest that recent collections reveal both *H. bispinosa s.s*. and *H. leslieae* **sp. nov.** co-occur in the Bahamas. The most northern location of *Hyalopale leslieae* **sp. nov.** is in the Florida Keys and it also occurs from the Bahamas, Virgin Islands and west to Belize. *Hyalopale bispinosa s.s.* and *H. leslieae* **sp. nov.**, possess midline spines and some similarity of main paleal shape (Fig. 1 A, C) indicating a close relationship, though this needs to be corroborated with DNA of *H. bispinosa s.s*.

Caribbean/Pacific. Figure 13 indicates *Hyalopale leslieae* **sp. nov.** (Belize, Caribbean) as the sister group to the clade made up of *H. zerofskii* **sp. nov.** (Eastern Pacific) and *H. sapphiriglancyorum* **sp. nov.** (Western Pacific). Similar results have been seen with the meiofaunal annelid taxon *Saccocirrus 'papillocercus'* group (Saccocirridae) from the Caribbean and the western Pacific (Di Domenico *et al*. 2014); and the cryptic coral reef *Palola* (Eunicidae)*,* species groups A and B, with clade group A present in the Caribbean and tropical eastern and western Pacific and clade group B occurring both in the Caribbean and tropical Western Pacific (Schulze 2006; 2015).

Pacific/Indian Ocean. *Hyalopale zerofskii* **sp. nov.** is recorded from southern California, southern Mexico and possibly Moorea (Eastern Pacific). Cryptic species complexes ranging from Moorea to the Red Sea are seen in a number of coral reef paleate chrysopetalid taxa (Watson & Rouse in prep.). However, *Hyalopale zerofskii* **sp. nov.** and *H. sapphiriglancyorum* **sp. nov.** (Western Pacific) are clearly separate morphological species with molecular support (Fig. 13). *Hyalopale sapphiriglancyorum* **sp. nov.** is found in Indonesian and north eastern Australian waters of the Great Barrier Reef; specimens from both localities agree in distinctive species characters. Such a range has been reflected in studies of coral-dwelling, cryptic annelids, particularly on northern GBR reefs, that have revealed new species extending from Lizard Island, GBR, north to islands of Indonesia and Philippines *e.g.*, morphological study of small-bodied *Paleanotus* species (Watson 2015) and molecular studies on nereidid annelids (Glasby *et al*. 2013).

The shape of the main paleae, especially the slope of the brow, and a degree of finely raised ribs, is seen to have some similarities between *Hyalopale sapphiriglancyorum* **sp. nov.** GBR, and *H. angeliensis* **sp. nov.** NW Western Australia (Fig. 1 G, E), particularly when compared with those of other species. While there are differences in the numbers of ribs and presence/absence of a midline spine, the similarities indicate these may be sister species. This northern Australia sibling species divide has been documented in a number of related chrysopetalid taxa *e.g., Paleanotus* (Watson 2015) and *Treptopale* (Watson 2010; Wei *et al.* 2013).

Hyalopale angeliensis **sp. nov.** is found at localities occurring on a similar parallel at ~ 20° S in the eastern and mid- Indian Ocean. *Hyalopale angeliensis* **sp. nov.** is not distinguished by any particular unique characters, but rather a combination of characters not seen in other *Hyalopale* spp. These characters, especially the shape of the main paleae and number of ribs, are very similar between individuals from localities of north-western Western Australia and the Seychelles (respectively Fig. 9A, B). Although few DNA analyses of Indian Ocean polychaetes exists, sequences revealed a distinctly separate species from the Seychelles, in comparison with populations from the Mediterranean and Atlantic, during a study of a cosmopolitan syllid cryptic species complex (Westheide & Haß-Cordes 2001).

The main paleae of *Hyalopale angeliensis* **sp. nov.** (eastern and mid-Indian Ocean) is morphologically distinct to those observed in *H. furfuricula* **sp. nov.** (Red Sea, western Indian Ocean) (Fig. 1 cf E, D). The habitat of *Hyalopale furfuricula* **sp. nov.** is the same as that of other tropical-dwelling *Hyalopale* species, but individuals possess a main paleae shape and raised rib pattern that is unique and not seen in any other *Hyalopale* species.

Hyalopale **compared with** ***Paleanotus*** **and** ***Treptopale.*** The phylogeny shown in Figure 13 shows that *Hyalopale* is the sister group to *Paleanotus* with high support in the ML analysis. This relationship was not found in the MP analysis, with *Paleanotus* grouping with the other Chrysopetalinae, though with low support. A close relationship for *Hyalopale* and *Paleanotus,* and also *Treptopale* has been previously proposed on morphological grounds based on their similar anterior end configurations and chaetal types (Perkins 1985; Watson 2010; Watson 2015; Watson & Faulwetter 2017); a molecular study also corroborated a very close relationship between *Treptopale* and *Paleanotus* (Wei *et al.* 2013). Buccal structures, internal pigmentation and gamete characters are considered in more detail here.

Hyalopale, Paleanotus and *Treptopale* share buccal characters in terms of the possession of a similarly shaped pair of pointed grooved stylet jaws and the presence of a calcareous pharyngeal band circling the stylets (Watson & Faulwetter 2017; Fig 23 G–I). The feeding function, as hypothesized for all paleate chrysopetalids with this type of jaw, is one of interlocking stylets that achieve traction and pierce prey tissue with pointed jaws and in concert with the muscular movements of the pharynx suck out prey fluids down the stylet groove. These buccal structures indicate a predatory and facultative symbiotic lifestyle (Watson & Faulwetter 2017).

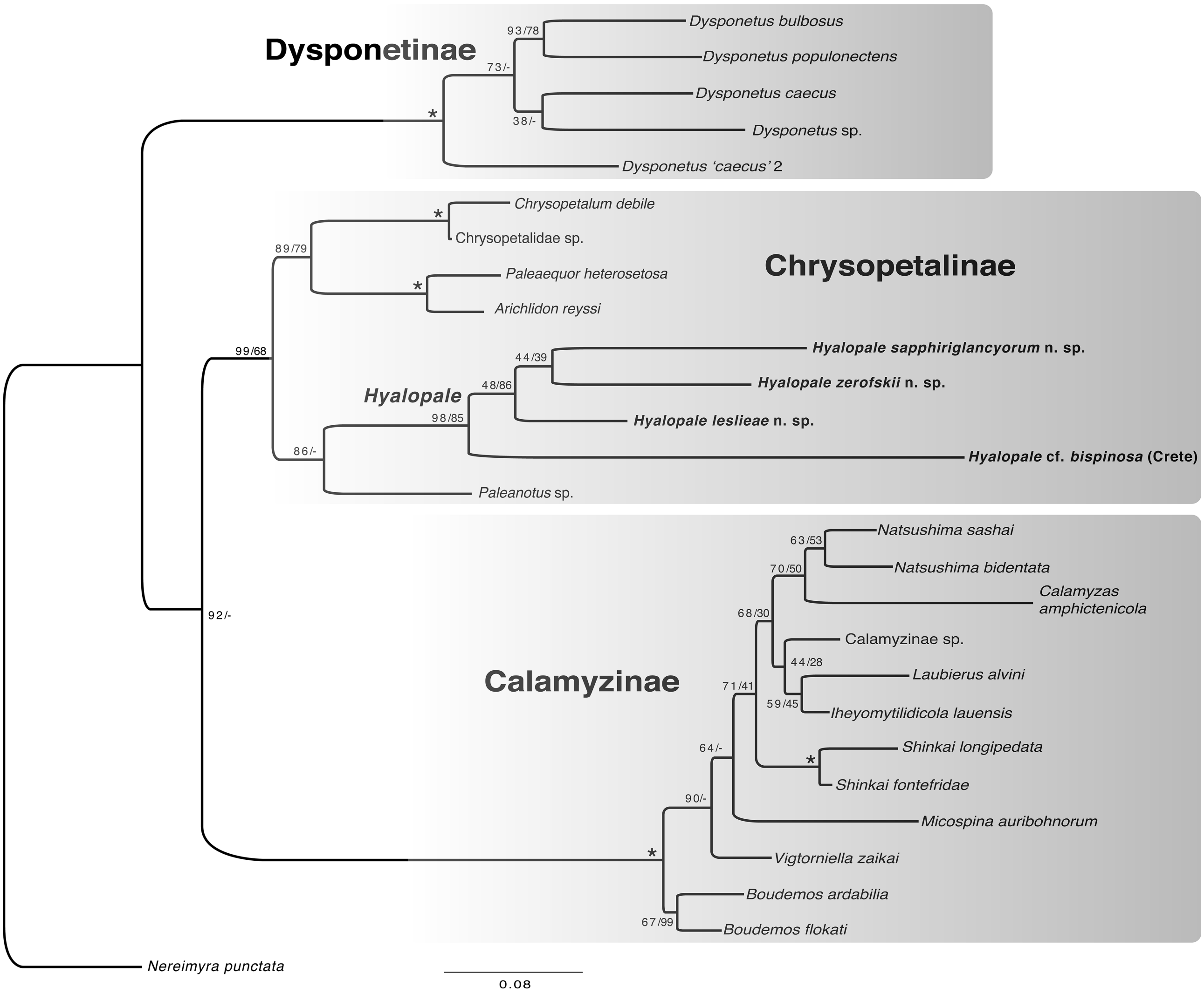

FIGURE 13. Maximum likelihood tree obtained with the molecular combined data (COI, 16S, 18S and H3) and with the hesionid *Nereimyra punctata* as outgroup. Values at nodes are shown as ML bootstrap then MP jackknife values. * = >90% values for ML bootstrap and MP jackknife values. The single MP tree was identical except that it recovered *Paleanotus* as the sistergroup to the remaining Chrysopetalinae, rather than to *Hyalopale*, though with only 53% jackknife support.

The internal body green pigmentation evident in all shallow-dwelling *Hyalopale* species is also observed in small-bodied species of *Paleanotus* (Watson 2015) and in larger *Treptopale* species (Watson 2010). The properties and function of these pigments is not yet understood (see discussion under *Hyalopale zerofskii* **sp. nov.**). *Hyalopale, Paleanotus* and *Treptopale* individuals share similar morphological gametous developmental characters: interramal cilia, parapodial lacunae (Perkins 1985; Watson & Faulwetter 2017), and enlarged horizontal or flower-shaped, interramal glands posterior to the dorsal cirri *e.g. Hyalopale*, Fig. 5E; *Paleanotus* (Watson 2015; Fig. 2I) and *Treptopale* (Watson 2010). White pigmentation patches in anterior segments and parapodial, oil globules, and 'white granules', associated with sperm in mature males, have also been described in *Treptopale* (Watson 2010) and *Paleanotus* (Watson 2015). *Hyalopale* possesses white pigmentation in anterior-most segments *e.g.* Fig. 5A, and oil globules. Large oocytes numbering one to two and filling an entire segment were observed in *Hyalopale* species, *e.g. Hyalopale zerofskii* **sp. nov.** 17E, L.1.7mm, eggs 300–400µm in diameter (Fig. 5A, B); large oocytes are also is seen in one of the smallest-bodied *Paleanotus* species, *e.g. Paleanotus chrysos* 22E, L. 2.5mm, (Watson 2015 fig. 9: 230–270 µm). Spherical-headed sperm have also been observed in *Treptopale* and *Paleanotus* (Watson 2010; Watson 2015). Individuals of *Hyalopale* species appear to consist largely of females; sperm has not yet been precisely identified.

Paleanotus and *Treptopale* adults have been found swimming in the plankton (Watson 2015) and *Paleanotus* possesses planktonic larvae (see next section). No *Hyalopale* larvae have been found, but *Hyalopale leslieae* **sp. nov.** has been collected from a number of artificial settlement substrates (this paper). *Hyalopale* mature specimens show enlarged eyes with all three pairs melded into one block, loosened neurochaetae and body tissue starting to degenerate, indicative of possible movement into the water column and rupture of gametes through the body wall.

Morphology of adult *Hyalopale* and *Paleanotus* larvae. Of particular interest is the similarity of morphological states observed between *Hyalopale* adults and *Paleanotus* larvae. Table 2 sets out a comparison of body and prostomial morphologies and notochaetal types between *Hyalopale* adults and *Paleanotus* nectochaete larvae and adults. Figure 12 illustrates a mid-body *Hyalopale* adult notochaetal fan with that of *Paleanotus* larval and adult notochaetal fans. Knowledge of the morphology of *Paleanotus* larvae has been based on a single paper by Blake (1975) (specimens subsequently lost, Blake pers. comm.). *Paleanotus* characters, based on examination of *Paleanotus bellis* planktonic and recently settled nectochaete larvae and developing juvenile and benthic adults, has been undertaken as part of ongoing research into comparative larval states of Chrysopetalinae taxa (Watson in prep.). *Paleanotus* is one of only two paleate taxa (Chrysopetalinae) whose notochaetal morphology is clearly identifiable to species; the taxon comprises small species (<5mm) and larger species (~15mm) (Watson & Faulwetter 2017).

TABLE 2. Comparison of features between *Hyalopale* and *Paleanotus*

Characters	*Hyalopale* adults	*Paleanotus* larvae	*Paleanotus* adults
Length; # segments	1–2.8 mm; <20	0.48 mm; 6	15 mm; up to100
Prostomium shape	large broad lobe	large broad lobe	small lobe
Prostomial & parapodial cirri	slender finger-shaped	slender finger-shaped	more developed
Notopodial chaetae segment 11	primary spines	primary spines & few short paleae	few short paleae
Notopodial form of lateral chaetae down body	single spine	segments III–IV single spine; V–VI spine plus paleae	developed lateral paleal fascicle
Notopodial form of median chaetae down body	discreet fascicle absent; single short spine present or absent	spines absent; small paleal fascicle present from segment IV	developed median paleal fascicle
Dorsal cirri	pseudo-articulations marked with hairs; cirri tips with pits & hairs	pseudo-articulations marked with hairs; cirri tips with pits & hairs	slightly pseudo-articulated; hairs or pits absent
Nuchal fold: present/absent	absent	absent	present
Global range	35N–35S	Not known	52N–52S
Habitat/depth	rubble, sediment, algae, infaunal 0–2m (1 species ~ 15m)	nectochaete larvae in plankton	rubble, algae, crevices, infaunal 2–40m

Comparison of characters illustrate that adults of *Hyalopale* species share a similar morphology with *Paleanotus* larvae: the prostomium retains a typical larval episphere shape (Fig. 10A); prostomial and parapodial cirri retain typical larval simple morphology including terminal cilia (Blake 1975: Fig. 6A; this paper, Fig. 5F); retention of notochaetal primary spines in segment II (Fig. 10A, B) and the lateral notochaetal spine (Figs 4E; 5F) and an absent nuchal fold (Figs 5B, C; 10A). *Paleanotus* planktonic larvae exhibit larval chaetal types (*e.g.* lateral spines) and adult notochaetal paleal types (*e.g.* lateral and median paleael fascicles), co-existing in mid-body notopodia

(Fig. 12B). During metamorphosis, initiated by benthic settlement, *Paleanotus* post-larvae (7–8 segments) exhibit: shrinkage of the prostomial episphere; development of prostomial and body cirri; loss of segment II notochaetal spines and replacement by short paleae; loss of sub-acicular lateral spines and replacement by lateral paleae and continuing development of the median paleal fascicle which progresses in the adult to develop at a discreet angle to the main paleae fan (Fig. 12C). Importantly, a nuchal fold forms and in conjunction with retractile properties of the anterior segments may cover the prostomium in part. Midline spines are not evident in *Paleanotus* nectochaete larvae and adults (Watson 2015; CW larval studies in prep.).

Paedomorphosis. Paedomorphic annelid taxa have generally been regarded as meiofaunal (Westheide 1987; Struck 2005; Worsaae & Kristensen 2005). Such species exhibit above all small body dimensions, often lack parapodia and chaetae and possess a mixture of juvenile (*e.g.* retention of larval ciliary patterns) and new adult characters which may include adaptive specializations that allow colonization of the interstitial space *e.g.* adhesive organs and copulatory organs (Westheide 1987). Other paedomorphic annelids include the dwarf males of *Osedax* (Siboglinidae) described in detail by Worsaae and Rouse (2010), who inferred progenesis as the mechanism for the paedomorphosis based on the retention of many larval features.

Hyalopale arguably exhibit a form of paedomorphosis that results in a simple body plan reminiscent of chrysopetalid larval body plans, sexual maturation at a small segment stage, and body miniaturization that falls within the meiofaunal size range. However, there are no discernible novel adult characters or specific reproductive adaptive characters evident in *Hyalopale* species that have been commonly described for other paedomorphic interstitial annelid species, for instance, male copulatory organs found in the dysponetid, *Dysponetus bipapillatus* (Dahlgren 1996). Paedomorphosis in *Hyalopale* can be further inferred based on degree of relationship with its sister group *Paleanotus* (Fig. 13). The morphology of adult *Hyalopale* and larvae/juveniles of *Paleanotus* are very similar. Furthermore, these taxa share the same asymmetric, broad notochaetal main paleae, which constitutes an apomorphic character: a character not seen in any other paleate chrysopetalid taxon.

The morphology of species of *Hyalopale* appears to preclude an interstitial life style between sand grains. The body form is light and fragile and comparatively broad with greater width conferred by slender neuropodia and neurochaetae with long slender falcigerous articles, that extend out beyond the notopodia; structures that allows purchase among substrates, as well as possibly enabling floating with the movement of tides in shallow waters. The notochaetal paleae that cover and protect the dorsum of *Hyalopale* species are thin and transparent allowing the internal body green pigments to create a patchy camouflage effect in light-filled, shallow water benthic habitats where individuals potentially traverse open sedimented areas in between sheltering in algae or dense coralline substrates such as maerl. Detailed collecting data indicates *Hyalopale* species are also found in association with shallow-water epifaunal aggregations, *e.g. H. leslieae* **sp. nov.** among tubicolous invertebrate aggregations of maldanid and taenaid colonies in shallow reefs of the Virgin Islands and *H. furfuricula* **sp. nov.** among intertidal sabellariid and vermetid reefs in the Gulf of Elat. This infaunal association is observed in its closest congener, *Paleanotus,* species of which are commonly found dwelling within carapaces and gills of other invertebrates (Watson & Faulwetter 2017). Metabolic scaling puts intense selective pressure on small individuals, such as *Hyalopale* species, to avoid ingestion of diluents and to process lipid-rich organic matter (Jumars *et al*. 2015). Based on stylet jaw structure and habitat association it is possible that *Hyalopale* species may possess a similar facultative symbiotic lifestyle within tubes, carapaces and gills of other shallow water invertebrates.

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