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Transformative notochaetae: larval development and metamorphosis in *Chrysopetalum* spp. (Chrysopetalinae: Chrysopetalidae: Annelida)

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Abstract

The morphology of an early nectochaete larva belonging to *Chrysopetalum* sp. is aligned with that of a planktotrophic larva at a crucial stage of benthic settlement: an entire provisional spinose notochaetal scleritome, large episphere with prostomial nascent sensory structures and larval podia and cirri of the anterior two segments in transition. Morphological sequences of post-larvae and juveniles, common to a number of *Chrysopetalum* species, indicate that long, slender, provisional, camerate notochaetal spines are replaced during metamorphosis and growth with an entire adult, camerate notochaetal scleritome consisting of broad paleae with internal, longitudinal ribs. The *Chrysopetalum* sp. six segment larva supports achaetous notopodia I and chaetous notopodia II, each with a pair of dorsal cirri, ie. 4 cirri in total; segment II has acirrose neuropodia. Individuals of post-larvae and juvenile *Chrysopetalum* species, 8–15 segments, possess a total of 6 cirri on segments I and II: segment I with a pair of tentacular dorsal cirri and the formation of a pair of tentacular ventral cirri, and segment II comprising a pair of dorsal cirri, spinous notochaetae and acirrose neuropodia. During metamorphosis the acirrous neuropodia of segment II are reabsorbed and replaced in stages with a pair of ventral tentacular cirri until the adult state is achieved: achaetous segment 1 with two pairs of tentacular cirri and segment II similar, ie. total of 8 cirri. The cirri arrangement of segments I and II before final metamorphosis in post-larval stages of *Chrysopetalum* species is, interestingly, that described for adults in the majority of other Chrysopetalinae taxa. Ontogenetic developmental processes of formation and loss of acirrose neuropodia and replacement of spinose larval notochaetae with adult paleae observed in *Chrysopetalum* species are compared with species of other taxa of the Chrysopetalinae.

Key words: larval morphology, adult morphology, transformative notochaetae, Chrysopetalinae

Introduction

The taxonomy of *Chrysopetalum* has been sparse: Ehlers,1864 described *Chrysopetalum* as the type genus for the family Chrysopetalidae and the type species of the genus, *Chrysopetalum fragile* (= *C. debile*), from the Mediterranean. *Chrysopetalum occidentale* Johnson, 1897 was described from California and *Chrysopetalum ehlersi* Gravier, 1901 from the Red Sea. More recently Hartman-Schröder (1981) described a single species from Australia; Perkins (1985) three *Chrysopetalum* species from the Caribbean; and Aguado *et al.* (2003) two species from the East Pacific. *Chrysopetalum* is the most speciose genus of all Chrysopetalinae taxa and there are at the moment at least 25 undescribed species which have been designated by species numbers (Watson Russell, 2000a, Watson *in press*, 2020). The majority of these undescribed *Chrysopetalum* species are from the tropics, some of which are referenced in post-larval and juvenile material examined in this paper.

There are two larval developmental studies in the literature describing planktonic trochophore to late nectochaete stages in paleate chrysopetalid taxa (Chrysopetalinae): *Chrysopetalum debile* (Grube, 1855) from the NE Atlantic Arcachon Basin by Cazaux (1968) and *Paleanotus bellis* (Johnson, 1897) from the northern Californian coast by Blake (1975). Watson Russell (in Bhaud & Cazaux, 1987) figured and simply described various developmental stages, on the basis of single specimens, for *Hyalopale* sp., *Chrysopetalum* sp., *Paleanotus sp., Strepternos* sp., and n. genus 1 (=*Arichlidon*) (Chrysopetalinae), as well as *Dysponetus* sp. (Dysponetinae).

In a study of Chrysopetalidae from NE Atlantic seamounts, Watson *et al.* (2014) included descriptions of

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planktonic larvae belonging to *Arichlidon reyssi* (Katzmann *et al.* 1974) and *A. gathofi* Watson Russell, 2000b. Examination of the former larvae, made available through Cazaux from Arcachon, proved that *A. reyssi* larvae were formerly misidentified by Cazaux (1968) as *Chrysopetalum debile.* Effectively this means there is no record of early larval developmental stages of *Chrysopetalum* species in the literature.

This study provides the first description in the literature of a the morphology of an early nectochaete larva of *Chrysopetalum* sp. The singular find of this six segment larva has been a key to recognizing the unique morphology of the planktonic larval state, prior to the critical settling phase, in *Chrysopetalum* species. Description and integration of the morphology of this larva with those known of post-larval stages in *Chrysopetalum* species (Watson Russell, 1987; Watson, unpubs.) has enabled a series of ontogenetic states to be connected in nectochaete, post-larval, and juvenile stages in *Chrysopetalum* species.

Here the morphology of this larva is described and integrated with that of postlarval stages in *Chrysopetalum* species, based on *Chrysopetalum debile* and *Chrysopetalum* spp. 5, 8 and 22 (formal descriptions pending). Diagnosis of the subfamily Chrysopetalinae includes particular emphasis on the two different cirral formulae of the anterior two segments observed in adults in two groups of Chrysopetalinae. A formal diagnosis of the genus *Chrysopetalum* is provided. The systematic context is instrumental in understanding broader evolutionary developmental relationships between *Chrysopetalum* and larval states observed in species of other taxa in the Chrysopetalinae.

METHODS

Morphology

Larval chaetal terminology follows that of Watson *et al.* (2014), with provisional notochaetal spines describing the first notochaetae evident, and primary notochaetal paleae referring to the first paleal types initiated in the developing larvae. Adult chaetal terminology follows that of Watson *et al*. (2019). Designations of notochaetal paleae in species of Chrysopetalinae are based on position. The lateral group inserts below the acicula (la); the main group above the acicula (ma); and the median group (me) overlaps the mid-dorsum. Within Chrysopetalinae, the main fan comprises a middle group (mm) with the broadest paleae and 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 (Fig. 2A). Roman numerals indicate segment number from the anterior end (e.g. Fig. 1A–D). Abbreviations of body states in association with measurement of segment numbers are: E, entire; L, length; W, width.

Other abbreviations used include *c*, caruncle; *dc I*, dorsal cirri segment 1; *dc II*, dorsal cirri segment 2; *la,* lateral paleae; *l.a.,* lateral antennae; *lmm,* lateral-most main paleae*; l.n. II,* larval neuropodium segment 2*; m.a*., median antenna; *m.c*., mouth cover; *me,* median paleae; *mm,* mid main paleae; *mmm,* midline-most main paleae; *n.f.,* nuchal fold; *n.g.,* neuropodial glands; *p,* palp; *p.i.,* paleae insertion; *p.n.,* provisional notochaetae; *pyg,* pygidium; *s,* stylet; *sp,* spines; *tp,* terminal papillae; and *v.c. III,* ventral cirrus segment 3.

Specimens observed by scanning electron microscopy (SEM) were fixed in 98% ethanol followed by dry ethanol at room temperature two times for 20 minutes each. Dehydrated samples were critical point dried (Baltec CPD 030) and mounted on stubs prior to sputter coating with 20 nm thick gold (Baltec SCD 050). Observation was carried out using a JEOL JSM-6390LV SEM at 15 kV operating voltage.

Material examined is deposited in the following institutions: Museum and Art Gallery of the Northern Territory, Darwin (note registrations prefaced NTM at MAGNT); Western Australian Museum, Perth (WAM); Australian Museum, Sydney (AM); Hamburg Zoological Museum (HZM); Hellenistic Centre for Marine Research (Crete) (HCMR).

RESULTS

Systematics

Family Chrysopetalidae Ehlers, 1864

Chrysopetalinae Ehlers, 1864

Diagnosis. Small to large bodied; segments short and close together; flattened to slightly convex dorsum covered in imbricating notochaetal paleal fans, paleae coloured silver to gold. Flat ventrum and segmental ventral pads present. Prostomium free or fused with anterior segments, with complex eyes, median antenna, lateral antennae and palps. Nuchal organs (caruncle or nuchal fold) present. Pharynx with terminal papillae, pair of well-developed stylet jaws, ventral mouth cover. Ventral cirri absent on segment II in Group 1 taxa; dorsal and ventral cirri on each segment in Group 2 taxa. Camerate simple paleael notochaetae and camerated shafts of compound neurochaetae; simple spines may be present in notopodia and neuropodia. Body with segmental ciliation, lateral organs; complex nervous system and complex body wall musculature. Pygidium quadrate or conical with two anal cirri.

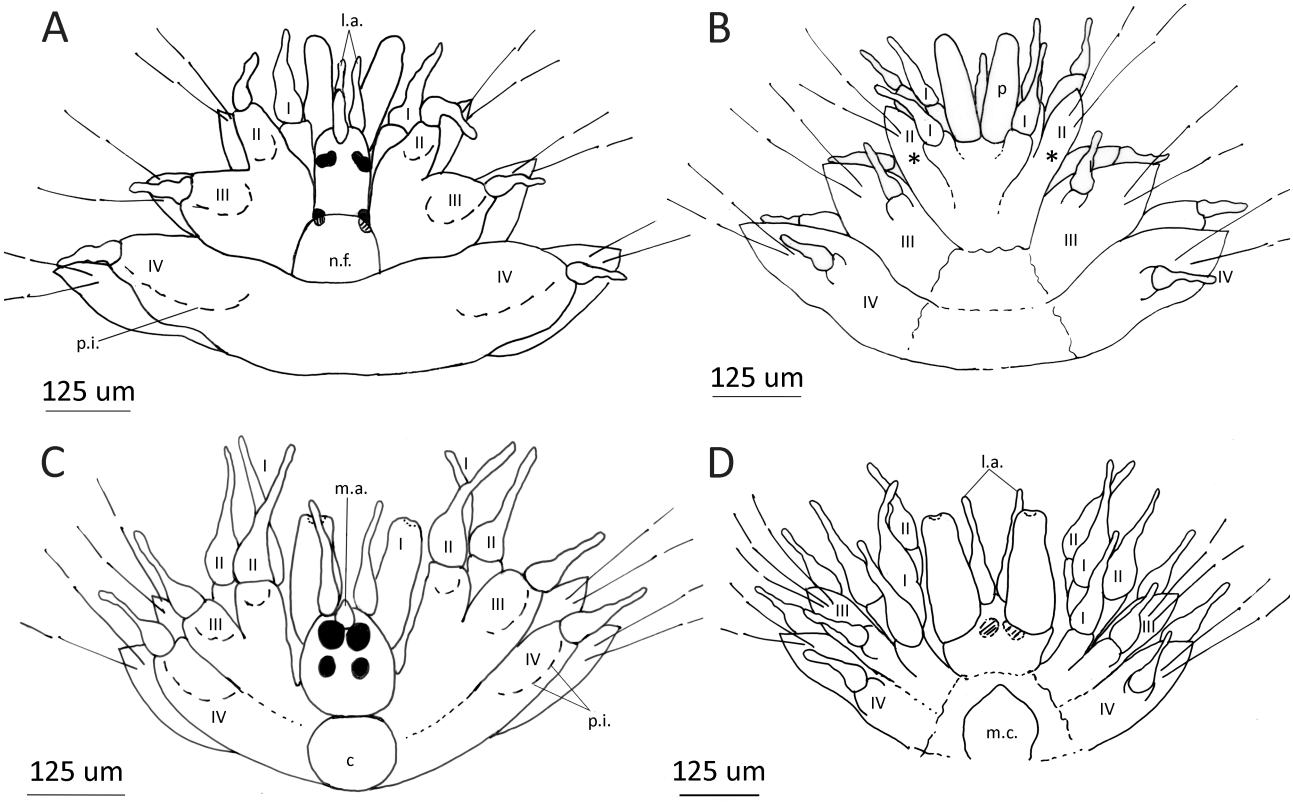

FIGURE 1. Comparison of anterior segments I–III in adult Chrysopetalinae taxa. Group 1. A, dorsal, B, ventral, based on *Paleaequor setula* Watson Russell, 1986, NTM W.1674; Group 2. C, dorsal, D, ventral, *Chrysopetalum debile* NTM W. 25614, this paper. The asterisk (*****) indicates the acirrose neuropodia of segment II, Fig. 1B.

Adult Morphology

Anterior segmental arrangement in Chrysopetalinae taxa. The pattern of fusion between prostomium and anterior segments I–III, and the number of cirri of segments I and II, exhibit two different patterns in adults of taxa within the Chrysopetalinae.

Group 1. Fig. 1A, B, based on *Paleaequor setula* Watson Russell, 1986. A majority of Chrysopetalinae shallow-water taxa and one deep-sea taxon possess similar formulae of cirri on segments I and II: segment I achaetous with pair of dorsal and ventral tentacular cirri, segment II biramous, notopodia with a pair of dorsal cirri and notochaetae, neuropodia with chaetae, ventral cirri absent (i.e. six cirri in total present on segments I and II). Segment III is biramous with a dorsal and ventral cirri pair and notochaetae and neurochaetae. Group 1 taxa further share a distinct combination of characters: prostomium fused with anterior segments and a flexible nuchal fold present posterior to the prostomium; a median antenna originates on the anterior

edge of prostomium well anterior to the anterior pair of eyes. Segment 1 has the cirri pair in a more ventral position; segments II and III are fused dorsally. References: *Paleaequor setula* Watson Russell, 1986 (Figs. 2, 3); *Strepternos didymopyton,* Watson Russell, 1991 (Fig. 2A–C); *Arichlidon hanneloreae* Watson Russell, 1998 (Figs. 2A, B); *Tretopale paramolos* Watson Russell, 2010 (Fig. 6A, B); *Paleanotus silus* Watson, 2016 (Fig. 6G); *Hyalopale furfuricola* Watson *et al.* 2019 (Fig. 10A, B); Watson & Faulwetter, 2017 (Table 2).

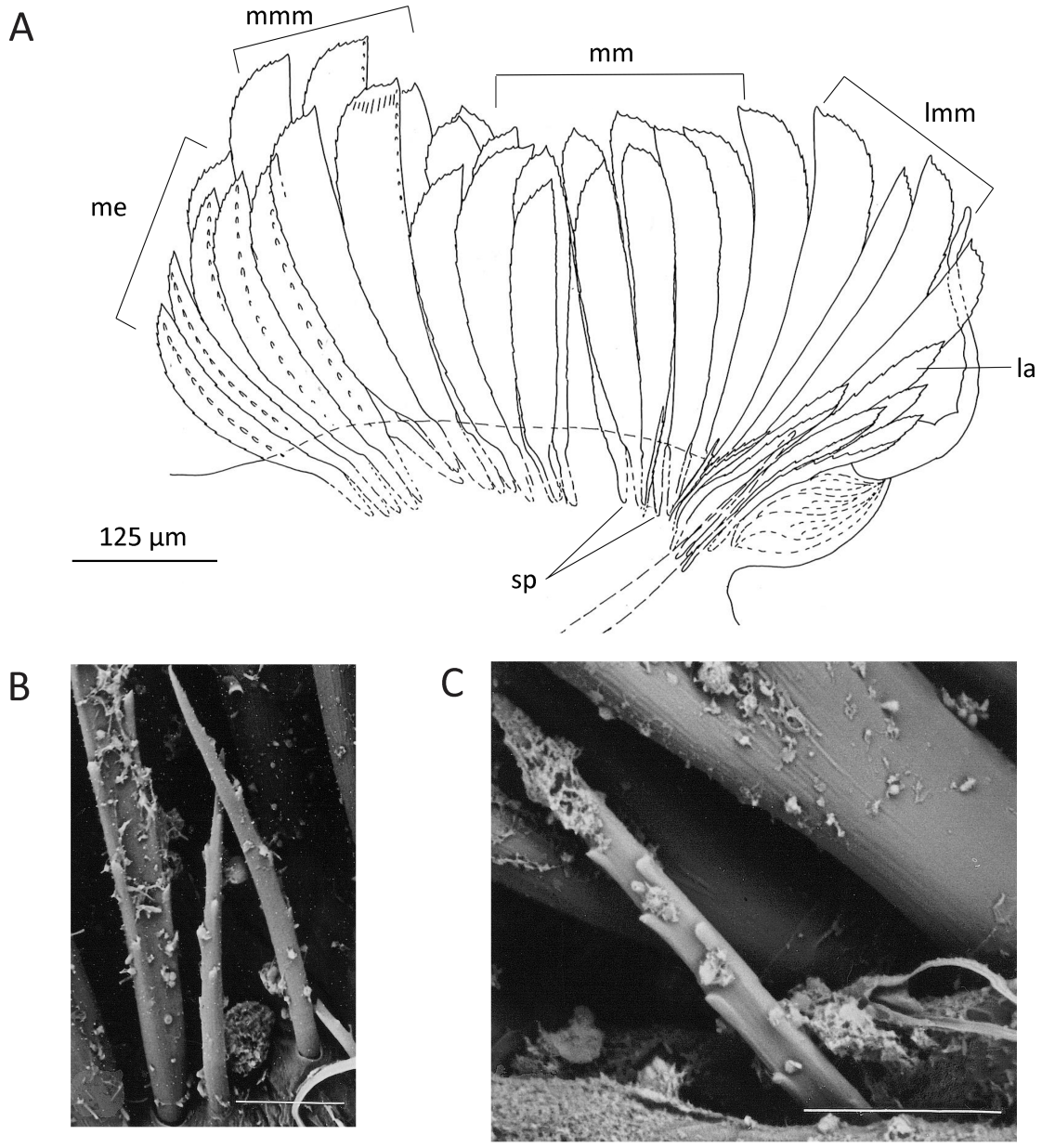

FIGURE 2. *Chrysopetalum debile*, Mediterranean, NTM W. 25614, adult, A–C. A. mid-body notopodium with major chaetal types, including small spines anterior to fan; B–C, SEM, details of small spines anterior to main paleal fan. B. larger, flattened spine and short rounded spines, C. short, slightly flattened spine.

Group 2. Fig. 1C, D, based on *Chrysopetalum debile* (Grube 1855). A minority of shallow and deep-water Chrysopetalinae taxa possess similar formulae of cirri on segments I and II: segment 1 achaetous with pair of dorsal and ventral tentacular cirri, segment II with pair of dorsal and ventral cirri (i.e. eight cirri present in total present on segments I and II). Segment II notopodia may exhibit aciculae and in some species short notochaetae. Segment III, and subsequent segments, biramous with notopodial and neuropodial chaetae and a pair of dorsal and ventral cirri. Group 2 taxa further share a distinct combination of characters: prostomium free, not fused with anterior segments with a discreet non-retractile caruncle present posterior to the prostomium;

a short median antenna originates just anterior to the anterior pair of eyes. References: *Chrysopetalum debile* (this paper, Fig. 1C, D); *Thrausmatos dieteri* Watson, 2001 (Fig. 4A, B); *Acanthopale perkinsii* San Martin, 1986; CW personal examination of material; Watson & Faulwetter, 2017 (Table 2).

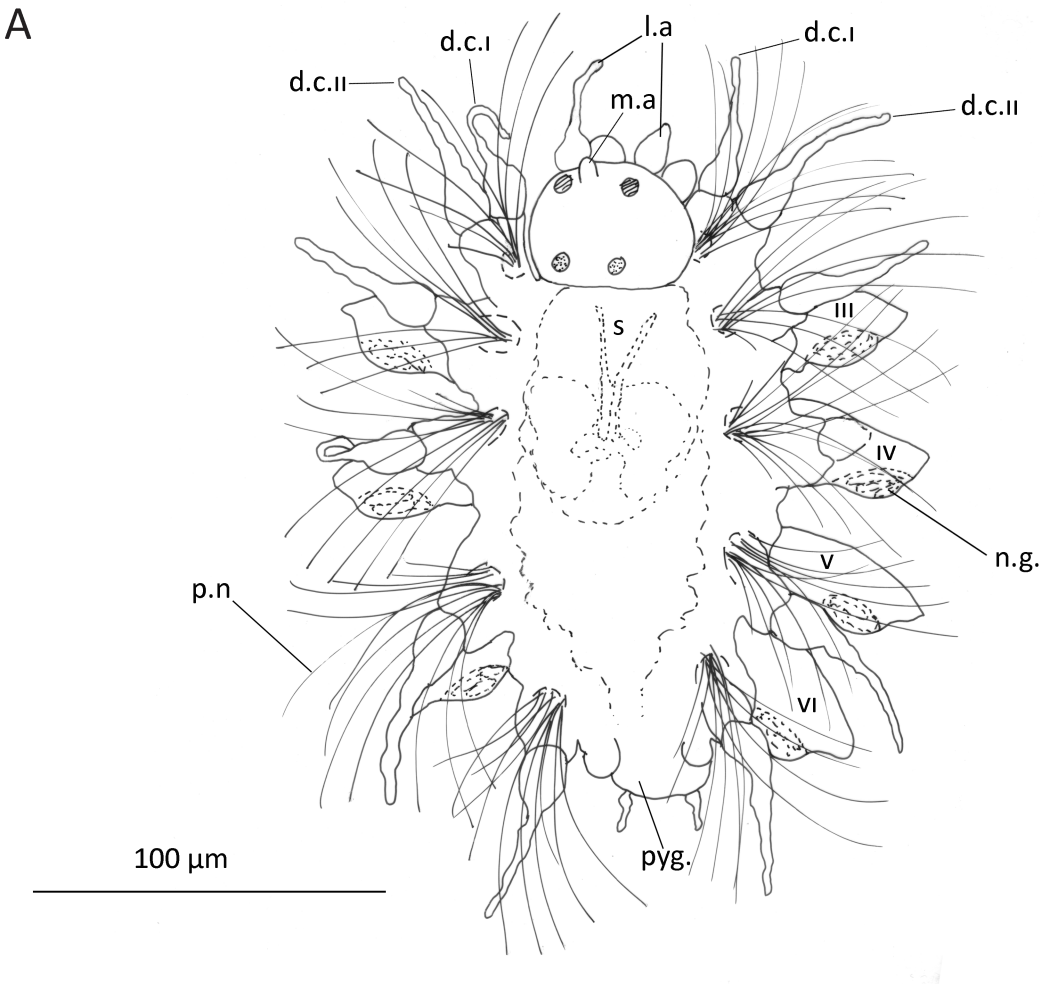

FIGURE 3. *Chrysopetalum* sp. Western Australia, WAM 8674, early nectochaete, 6E, dorsal view.

Genus *Chrysopetalum* Ehlers, 1864

Type species *Chrysopetalum debile* (Grube, 1855)

Diagnosis. Elongate body with up to 70 segments. Prostomium and cirral arrangement of anterior segments described in Group 2. Mid-body notopodia with slender dorsal cirri; lateral paleae subacicular, main paleae arise from multiple centres, median paleael fascicle inserts at dorsal mid-line; short, simple notochaetal spines present anterior to main fan (Fig. 2A). Main paleae sabre-shaped to broad, symmetrical, spatulate shaped; dorsal paleae surface with tubercules. Median paleae with central raised rib. Short, simple notochaetal spines present anterior to main fan (Fig. 2A–C). Mid-body neuropodia with slender ventral cirri; falcigerous neurochaetae grade in size from longer blades in superior position to shorter blades in inferior position.

Remarks. The structure of the prostomium, prostomial cirri and formulae of segments I–III is very conservative across all *Chrysopetalum* species (Watson, pers. obs.). Adults of *Chrysopetalum* species exhibit a degree of fusion between the anterior five segments; subsequently segmental delineation is often difficult to discern. Uniramous achaetous segment I is much reduced and often only clearly visible in ventral view. It possesses two pairs of long dorsal and ventral cirri; the ventral pair are more clearly discernible originating adjacent to the palps (Fig. 1D). Uniramous segment II has two pairs of long dorsal and ventral cirri, dorsal aciculae, and in some species (e.g. *Chrysopetalum debile*), a small fascicle of notochaetae.

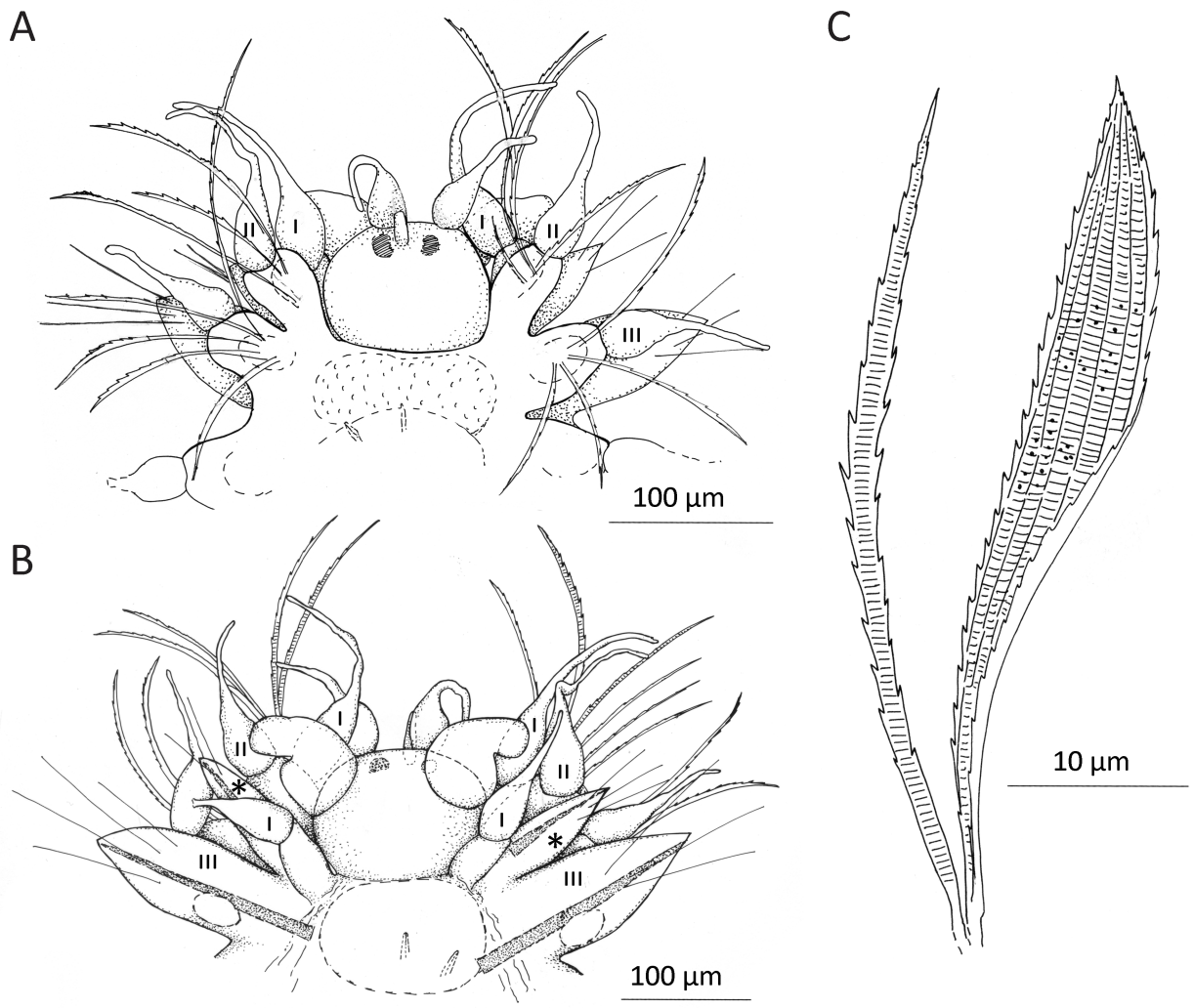

FIGURE 4. *Chrysopetalum* sp. 8. Victoria, HZM P. 17010, post-larva, 9E, anterior end with provisional notochaetal spines in segments I–III. A–C. A. anterior 3 segments, dorsal view; B. anterior 3 segments ventral view. C. notochaetal details of provisional spine and primary palea, segment 6. The asterisk (*****) indicates the acirrose neuropodia of segment II, Fig. 4B. Note: Fig. 4B after Watson Russell, 1987 Fig. 27. 2.

Biramous segment III possesses dorsal cirri, (comparatively shorter than those of segments I and II), notochaetae, neurochaetae and ventral cirri. The segmental line between segment III and IV may be faint. The first clear external segmental line occurs between segment IV and V, along the boundary of the dorsal caruncle and the ventral mouth cover; the latter when relaxed forms a triangular shape, when contracted a puckered horizontal lip (Fig. 1 C, D). Mature notochaetal types occurs from segment V onwards.

Mid-body notochaetal paleal fan comprises a fan of three types of paleae and anterior short spines (Fig. 2A). The short, simple spines anterior to the main paleal fan range from a rounded shape with small serrations (Fig. 2B) to flattened spines with serrated margins with denticles offset (Fig. 2C). Some of the larger flattened spines may have one internal rib (spine extreme left, Fig. 2B). These short spines in the adult notochaetal fans are considered remnant spines from larval stages (see following text). Without knowledge of larval notochaetal developmental patterns for different *Chrysopetalum* species it is not certain whether remnant spine patterns in adults constitute a species specific character, as suggested by Perkins (1985: 865).

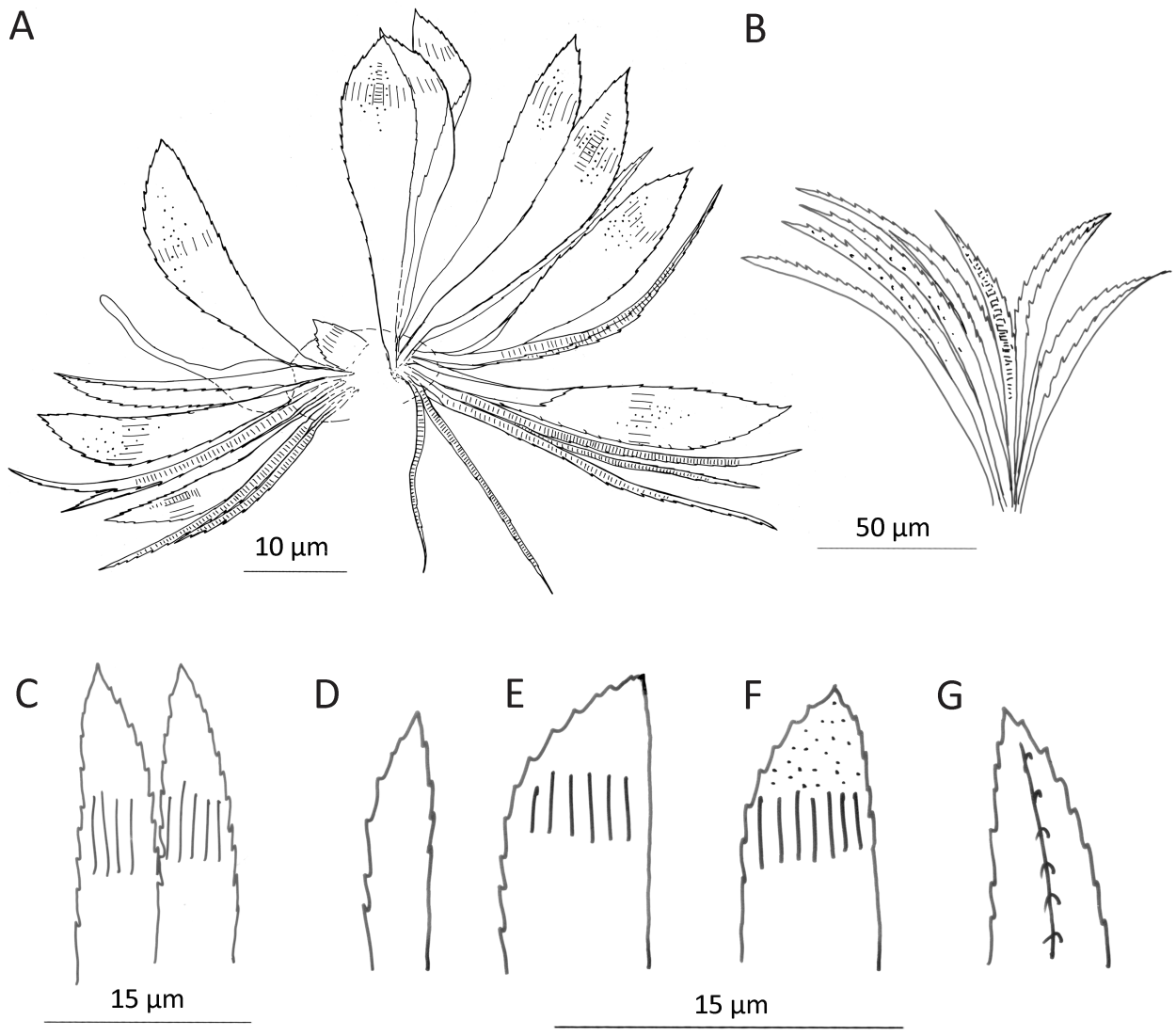

FIGURE 5. *Chrysopetalum* sp. 8. Victoria, HZM P. 17010, post-larva, 9E, A. notochaetal fan with provisional notochaetal spines and primary paleae from segment 6; *Chrysopetalum debile*, Mediterranean, NTM W. 25560, juvenile, 12E, B–G. B. provisional notochaetal spines and primary paleae of segment III; C. detail of primary palea from B; D–G, segment 5, primary notochaetal adult types present for the first time: D. lateral, E, F. main, G. median. Note: Fig. 5A after Watson Russell, 1987, Fig 27. 3.

Larval and Juvenile Morphology-Group 2

***Early nectochaete, 6 segments, benthic settling phase*, Figs. 3, 6A**

Material examined: *Chrysopetalum* sp., 5 chaetigers, 6E, L: 0.7mm, W: 0.65mm, WAM 8674, SW Western Australia, benthic, possibly floating above substratum, coll. G. Rouse.

Description. Body squarish in shape with extended notochaetae and neurochaetae approximately same length. Large rounded larval episphere, separate from anterior segments, with: two pairs small red eyes, anterior pair with apparent lenses, posterior pair with pigment flecks; median antenna a small cone-like protruberance; two lateral antennae (one fully formed); and palps comprising two pads visible on anterior edge of prostomium, rounded distally (Fig. 3). Well-developed pair of grooved stylets, proboscis with terminal papillae, and rounded pharynx partly obscured by internal contents (Figs. 3, 6A).

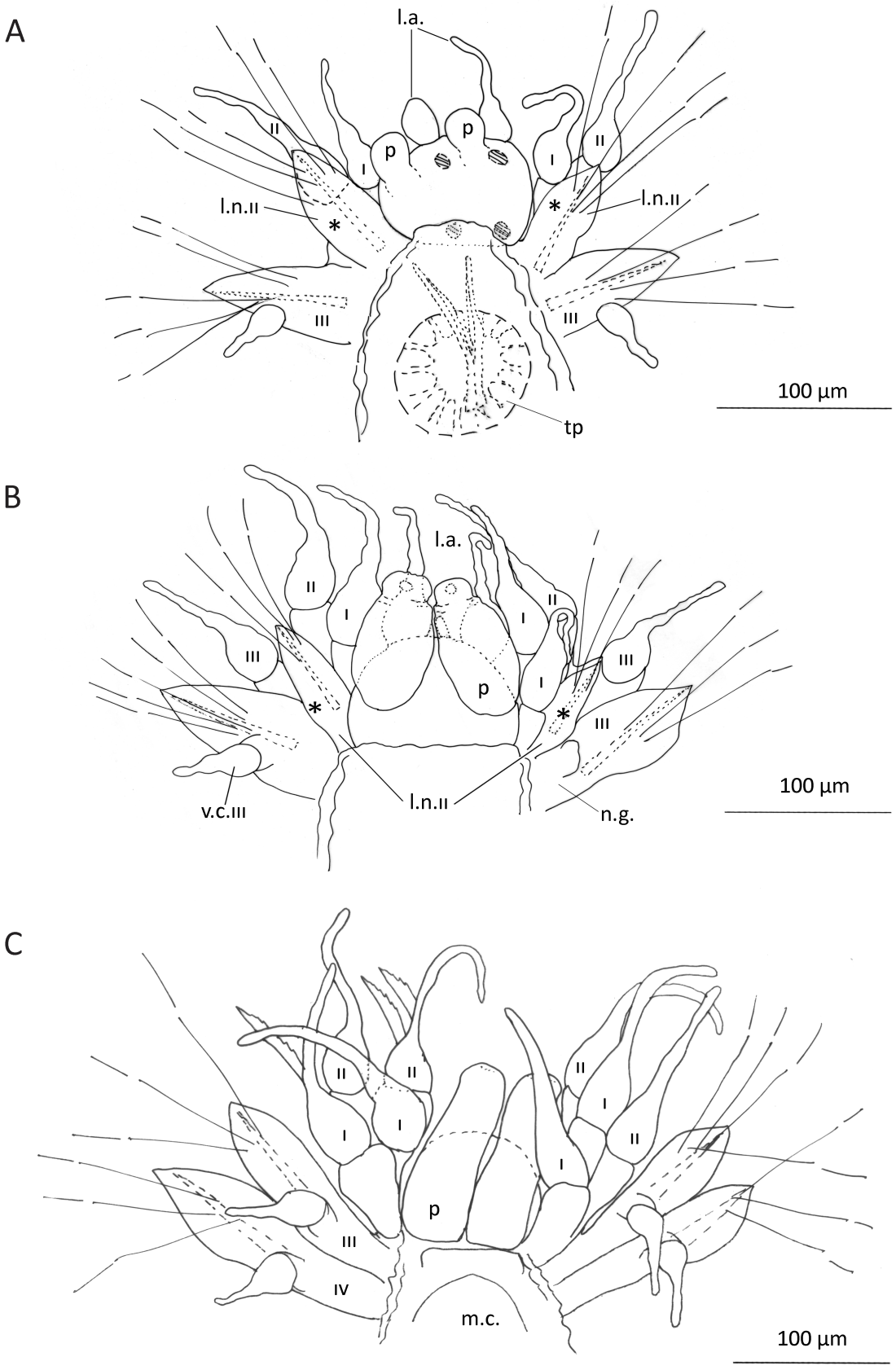

FIGURE 6. Comparative developmental stages of segments I–III, ventral view, *Chrysopetalum* species. A–C. A. *Chrysopetalum* sp., 6E, nectochaete, WAM 8674; B. *Chrysopetalum debile*, 12E, post-larva, NTM W. 25560; C. *Chrysopetalum* sp. 22, 17E, young adult, NTM W. 23086. The asterisk (*****) indicates the acirrose neuropodia of segment II, Figs A, B.

Achaetous segment I posseses one pair of dorsal tentacular cirri that insert closest to prostomium, adjacent to or a little ventrally to the dorsal cirri pair of segment II. Segment II with a pair of dorsal cirri and provisional, spinous notochaetal fascicles (Fig. 3). In ventral view segment II possess small *acirrose* neuropodia with fascicles of compound spinigerous-type neurochaetae; neuropodia positioned immediately latero-posterior to prostomium (Fig. 6A).

Segment III is the first true biramous segment, similar to segments IV–V. Notopodia with slender, relatively long dorsal cirri, provisional notochaetal fascicles insert in a tight spiral, originating close to the base of dorsal cirrophore, comprise longer and medium length simple pointed spines; majority with a distinctive single serrate margin, some with a major and lesser serrate margin, internal ribs absent, internally camerate (Fig. 3). Neuropodia with compound neurochaetae comprising long, slender, camerate shafts with very slender blades appearing spingerous but with very small curved tip (i.e. falcigerous); ventral cirri insert midway on neuropodia. Distinct protruding glandular pockets on posterior margin of all neuropodia. Small dorsal lobes, sites of developing notopodia, visible between notopodia V1 and pygidium. Pygidium rounded with two small anal cirri (Fig. 3).

Remarks. Based on the state of the well preserved six segment larva it is estimated it corresponds to an early nectochaete stage prior to full metamorphosis while settling out from the plankton to the benthos. Identification to *Chrysopetalum* (Group 2) is based on the distinct shape of the rounded prostomium which is free from segments I and II, the position of the median antenna just anterior to the anterior pair of eyes, the shape of pointed stylets, and the rounded pygidium with two short anal cirri. These characters are characteristic of the adult state and observed in all species of the genus *Chrysopetalum* (Watson & Faulwetter, 2017). The presence of a large pair of stylets, proportionally larger in comparison to body size, indicates the importance of these jaws, and may indicate that the larva is capable of feeding in the plankton.

The most obvious differences in this larva compared to an adult of *Chrysopetalum* are that notopodial segments II–VI bear fascicles of long provisional notochaetal spines, the caruncle and mouth cover are not yet formed, segment 1 and II each possess one pair of dorsal cirri only, and segment II has acirrose neuropodia.

Primary notochaetal paleae are not yet formed which makes identification to species impossible. Other planktonic Chrysopetalinae larvae at this same nectochaete stage possess primary paleal adult types in the posterior segments which makes identification to species possible (e.g. *Arichlidon* spp., Watson *et al.* (2014)).

***Late nectochaete, 9 segments*, Figs 4A–C, 5A**

Material examined. *Chrysopetalum* sp. 8, 8 chaetigers, 9E, HZM P.17010, Victoria, Warrnambool, Pr. 69–75, coralline algaes from rock pool, coll. G. Hartmann-Schröder, Dec 1975; *Chrysopetalum debile,* 8 chaetigers 9E, NTM W.25560, Mediterranean, Crete, Elounda, algaes, 15m, coll. G. Chatzigeogiou, June 2008.

Description. Larval episphere smaller but not yet adult size; filiform median antenna, developed lateral antennae, two palps with distinct anterior constriction and rounded distal ends, situated ventrally mid-way on prostomium (Fig. 4A). Caruncle and mouth cover not fully formed. Ventral tentacular cirri pair, segment I, iniatiated on cirrophores next to prostomium (Fig. 4B). Small acirrose neuropodia II now positioned latero-posterior to ventral tentacular cirri I; neuropodia II smaller in size compared to neuropodia III (Fig. 4A, B, asterisk). Part fusion of notopodia segments II and III apparent in dorsal view (Fig. 4A). Provisional notochaetal spines solely present notopodia II–V (Fig. 4A); provisional notochaetal spines and primary paleae types present from segment VI to end of body (Figs. 4C, 5A).

***Juveniles, 11–15 segments*, Figs 5B–G, 6B**

Material examined. *Chrysopetalum debile,* NTM. W.25560, Mediterranean, Crete, Elounda, rubble and algae, 15m, coll. G. Chatzigeogiou, June 2008, 10 chaetigers, 11E, L: 1.3mm, W: 0.5mm; 11 chaetigers, 12E, L: 1.4mm W: 0.8mm; *Chrysopetalum sp. 5,* NTM W. 23813, Indonesia, Flores, Maumere, black sand, rubble and algaes, 3m, coll. C. Watson, 1987, 14 chaetigers, 15E, L: 1.25mm, W: 0.6mm.

Description. Body more rectangular in shape. Prostomium smaller, closer to adult size; larger palps with distal depressions, situated lower on prostomium. Segment I with pair of dorsal cirri; ventral cirri present

right side, not formed on left (Fig. 6B). Acirrose neuropodia II, right side, smaller than that on left. Cirrose neuropodia on segment III with developing falcigerous neurochaetal types; glandular pockets present on posterior margin of neuropodia down body. Notopodia of segment II possess long and short provisional chaetal spines. Notopodia of segment III with fascicles of provisional spinous chaetae and first evidence of short primary paleae types (Fig. 5B), latter with internal longitudinal ribs (Fig. 5 C, detail). Lateral (Fig. 5D), main (Fig. 5E, F) and median (Fig. 5G) paleae types, diagnostic for adult *Chrysopetalum debile,* evident from segment V to end of body.

***Young adult, 17 segments*, Fig.6C**

Material examined. *Chrysopetalum sp. 22,* 16 chaetigers 17E, L: 1.35mm, W: 0.65mm, NTM W. 23086, Queensland, Townsville, Rib Reef, deep lagoon with *Callianassa* mounds, coll. AIMS, July 1985.

Description. Body rectangular. Prostomium adult size and surrounded by notopodia of segments I and II; long, cylindrical palps positioned at ventral edge of prostomium (Fig. 6C). Fully formed caruncle and mouth cover present. Segments I and II with Group 2 adult configuration (Fig. 6C). Notopodia mid-body with adult paleal types, remnant short spines present anterior to main fan. Neuropodia with adult falcigerous types; glandular pockets on neuropodial margin absent.

Remarks on developmental stages *of Chrysopetalum* species

The adult morphological state, exemplified in the young adult of 17 segments, illustrates that final metamorphosis has been accomplished. This is seen particularly in the anterior three segments, where the loss of acirrose neuropodia of segment II has allowed iniation of the ventral tentacular cirri pair of segment II which are positioned on cirrophores dorsal to ventral tentacular cirri of segment I. Ventral cirri of segment II may appear shorter compared to the length of the other tentacular cirri, which may be due to their later development (CW pers.obs.). The initiation of the latter is accompanied by final fusion of segments I and II, now evident in ventral view. Anterior segments I–III in the young adult reflect the adult state: segment I with a pair of tentacular cirri; segment II with a pair of tentacular cirri; segment III with a pair of dorsal and ventral cirri and chaetigerous notopodia and neuropodia (compare similarity of anterior segments I–III, Fig. 6C, with that of mature adult, Fig. 1D).

Primary notochaetal paleae are initiated at about the nine segment stage from posterior segments: a mix of spines and paleae are present on segments IX–VI and provisional spines only on segments V–II. Primary paleae types are completely replaced by adult paleae types at about the 17 segment stage, concurrent with the timing of full metamorphosis of the anterior segments taking place. During this notochaetal changeover very small numbers of larval short spines are retained into adulthood in species of *Chrysopetalum* e.g. Fig. 2A–C.

Two notoaciculae are present in the cirrophores of the dorsal tentacular cirri of segment II in adults of *Chrysopetalum* species (Dahlgren & Pleijel, 1995**;** Tilic *et al.* 2018). Notoaciculae appear singular in notopodia down the body of the *Chrysopetalum* nectochaete larva studied in this paper. In this study, individuals of *Chrysopetalum* species from the developmental stage of 17 segments exhibit a very slender second notoaciculae parallel to the larger one, which appears concurrent with resolution of the full complement of adult paleal types.

Larval and Juvenile Morphology-Group 1

Within the sub-family Chrysopetalinae anterior segmental change and notochaetal replacement during metamorphosis has been described in studies of planktonic larvae of *Arichlidon reyssi* (Cazaux 1968, Watson *et al.,* 2014) and *Paleanotus bellis* (Blake 1975, Watson unpub.), and the late nectochaete settlement phase in the deepwater genus *Strepternos didymopyton* Watson Russell, 1991.

Segment I & II development. Description of planktonic six segment nectochaetes of *A. reyssi* in Watson *et al.*, 2014, illustrates larval segment I with two pairs of long dorsal and ventral tentacular cirri. Dorsal to

these cirri are large dorsal lobes that support large fascicles of long, simple, provisional spinous notochaetae. Situated immediately between the prostomium and larval segment I are ciliate 'buds'that represent nascent adult segment I. Segment II is biramous with notopodia supporting primary paleae fans, dorsal cirri and acirrose neuropodia with composite chaetae. Segment III is biramous, and possesses ventral cirri (Watson *et al.*, 2014, Fig. 5A–D).

A late nectochaete benthic larva of 10 segments belonging to the deep-sea taxon *S. didymopyton* (Watson Russell, 1997) displays larval segment I with two pairs of long, slender dorsal and ventral tentacular cirri. Immediately between the prostomium and larval segment I are two ciliate 'buds'; the most dorsal bud represents nascent adult notopodia I and the second, notopodia of segment II. In ventral view, segment II has acirrose neuropodia with composite chaetae. A 12 segment individual displays loss of larval tentacular cirri and formation of adult segment I with short, broad dorsal and ventral tentacular cirri. Segment II is similarly developed to that of segment I, with notopodia further developed with dorsal aciculae and notochaetae (Watson Russell, 1997, Figs. 3A–E, 4 A–C).

Chaetal change. Long, camerate provisional spines are observed in larval segment I of the planktonic trochophore stage in *A. reyssi* (Cazaux 1968, Fig. XVIII (1)) and *P. bellis* (Blake, 1975, Fig. 4–C). Early metatrochophore larvae of *P. bellis* also possess simple notochaetal spines in segments II and III (Blake, 1975, Fig. 5). In both taxa initiation of folded primary paleal notopodial fans occurs at the 4–5 segment stage which then open across the dorsum at around 6–7 segment nectochaetae stage prior to metamorphosis. Provisional notochaetal spines of anterior segments are beginning to be lost and primary paleae replaced by adult paleae, sequentially from posterior segments, at benthic settlement (Cazaux 1968, Figs XVIII (4), XIX (1)); Blake, 1975, Fig. 6A, B; Watson *et al*. 2014, Figs. 5A–F, 6A).

Adults of *Arichlidon* species retain a single, very short larval spine both in the notopodia and neuropodia (e.g. *A. hanneloreae*: Watson Russell, 1998, Figs 1A, 3A). Short larval notochaetal spines are retained in segment II and segmental notopodia in recently settled benthic juveniles of *Paleanotus* species and lost with maturity (Watson, pers. obs.); in juvenile *Treptopale paramolos* (Watson, 2010, Fig. 9C); and in all species of the paedomorphic taxon *Hyalopale* which retain simple spines in the lateral and medial positions of the adult notochaetal fan e.g. *H. leslieae* (Watson *et al*, 2019, Fig. 3A).

Recently settled late nectochaete larvae of *S. didymopyton* exhibit rounded primary paleae in all notopodia which are entirely replaced by very different-shaped, narrow adult paleae over the 8–30 segmental growth phase. Adult paleae are initiated from posterior segments and from the lateral position in the main fan (Watson Russell, 1997, Figs. 6 A–E, 7A). Short larval spines are present in segment II notopodia in juveniles, as is a single neuropodial larval spine present in neuropodia down the body. These larval spines are lost with growth (Watson Russell, 1997, Figs. 5B, 7B).

DISCUSSION

It has been the contention of some authors, e.g. Perkins (1985), that presence of acirrose neuropodia of segment II in Group 1 taxa is due to loss of ventral cirri of segment II during ontogeny. Studies of planktonic larvae of Group 1 taxa (e.g. *Arichlidon reyssi* and *A. gathofi*: Watson *et al*. 2014) and *Strepternos didymopyton* (Watson Russell 1997) have established acirrose neuropodia of segment II are present from the early ontological stages and are retained throughout metamorphosis and settlement into adult life.

This morphology observed in Group 1 taxa is also present in larvae of species of *Chrysopetalum* (Group 2). The ontogeny of *Chrysopetalum* sp. (Group 2) larvae indicates the acirrose neuropodia of segment II undergo metamorphic change after benthic settlement with loss of the neuropodia concurrent with development of ventral cirri on segment II. In adults of *Chrysopetalum* species the first pair of cirrose neuropodia visible is that seen in segment III. The process of late and disjunct development of two pairs of adult tentacular cirri on segments I and II with the loss of larval neuropodia of segment II, means that *Chrysopetalum* species display a degree of fusion of the first three segments that is peculiar: dorsally notopodia of segments II and III appear partly fused, but ventrally segments I and II appear fused.

'Transformative notochaetae' is a term used to describe a developmental process wherein the loss of larval, long, slender notochaetal spines are completely replaced by adult, broad, paleate notochaetae with internal

ribs. This process is effected by genetic programming of notochaetae in each notopodium, iniatiated from posterior segments.

Species of larvae of Group 1 taxa, *Arichlidon* and *Paleanotus,* possess long, provisional spines in segments 1–111. Acquisition of notochaetal paleae begins with primary paleae types formed at the 4–5 segment stage in the plankton; formation of adult paleae types is initiated prior to settlement. *Chrysopetalum* (Group 2 taxa) exhibits provisional notochaetal spines in every notopodial body segment of planktonic larvae. Development of primary paleae types in *Chrysopetalum* larvae occurs after benthic settlement. Development of adult paleae types occurs at a late juvenile growth phase and comparatively over a much longer developmental period compared to taxa of Group 1.

Very small numbers of larval short spines may be retained into adulthood in notopodia and neuropodia in species of taxa belonging to both Group 1 and 2. The remnant short spines in adults of *Chrysopetalum* species represent developing states of transformative spine morphology: rounded with offset denticles to more flattened with marginal denticles to flattened with 1–2 internal longitudinal ribs, which may hypothetically reflect a template of evolutionary notochaetal development.

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