

Chrysopetalidae (Annelida: Phyllodocida) from the Senghor Seamount, north-east Atlantic: taxa with deep-sea affinities and morphological adaptations

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Abstract

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Senghor Seamount is located in the north-east (NE) Atlantic Ocean, 550 km west of Senegal, Africa, in the Cape Verde Archipelago. Macrofaunal sampling was undertaken from the summit (~100 m depth) to the base of the seamount (~3300 m depth) during the RV *Meteor* cruise (November 2009). The Chrysopetalidae fauna represents the first record for the family from a tall seamount habitat and is composed of East Atlantic continental margin and deep-sea species. *Dysponetus* sp. 1 is present at the summit and *Dysponetus caecus* at base depths. *Thrausmatos* is recorded for the first time in the Atlantic Ocean, as *Thrausmatos senghorensis* sp. nov., and is found at mid-slope depths only. The taxon with the largest number of individuals, *Arichlidon reyssei*, is most evident at the summit, with one record mid-slope. All Senghor species belong to the only three chrysopetalid genera that possess epitokous, swimming neurochaetae. Adults of *A. reyssei* from the Senghor Seamount and planktonic metatrochophore larvae from the NE Atlantic coast are compared and described in detail. The West Atlantic benthic nectochaete larvae of *Arichlidon gathofi* are also described in the interest of recognising and separating the two cryptic Atlantic *Arichlidon* species.

Keywords

North-east Atlantic, polychaete, Chrysopetalidae, swimming neurochaeta, depth distribution, chrysopetalid larva

Introduction

Seamounts are undersea mountains with heights above 1000 m and usually of volcanic origin. They are highly abundant in the Pacific Ocean but occur also in the Atlantic and Indian Oceans (Consalvey et al., 2010). Less than 0.3% of seamounts have been biologically sampled in any detail, and infaunal studies including quantitative sampling methodologies have been scarce (Schlacher et al., 2010; Ramirez-Llodra et al., 2010).

Recent mid NE Atlantic seamount studies include descriptions of the structure and function of seamount ecosystems in the Cape Verde region (Christiansen et al., 2010) and quantitative research into polychaete diversity of the Senghor Seamount (Chivers et al., 2013). Polychaetes are the most common infaunal organisms on NE Atlantic seamounts, with the majority represented by Onuphidae, Syllidae, Eunicidae and Amphinomididae collected by

large-aperture-mesh trawl and dredge (Surugiu et al., 2008). Dominant taxa present among the Senghor Seamount fauna are Syllidae, Spionidae, Cirratulidae and Chrysopetalidae collected by quantitative cores (Chivers et al., 2013).

Chrysopetalidae have been recorded from all oceans and are one of the most common polychaetes living in crevicular habitats in tropical, shallow coral reefs of the Indo-Pacific and Atlantic (Watson, 2010). Chrysopetalids are small, often fragmentable polychaetes with golden or silver notochaetal palaeal or spinous fans that cover the dorsum. Separate sexes have been described, and they possess an eversible proboscis with a pair of grooved stylets and an omnivorous, scavenging lifestyle. Over the past 20 years new chrysopetalid taxa have been collected from continental shelves and abyssal oceanic depths associated with wood and whale falls, nodule fields, hydrothermal vents and cold seeps (e.g. Watson, 2001; Dahlgren, 2004).

Specialised swimming neurochaetae have been recorded in species of three chrysopetalid taxa—*Arichlidon*, *Dysponetus* and *Thrausmatos* (Aguirrezabalaga et al., 1999; Watson Russell, 1998, 2000; Watson, 2001). These three genera constitute the only taxa collected at Senghor Seamount, and swimming neurochaetae are described for the first time in *Dysponetus caecus* (Langerhans, 1880).

Dysponetus caecus and *Arichlidon reysyi* (Katzmann et al., 1974) have been reported over a wide range of depths in the western Atlantic (Watson Russell, 1998; Böggemann, 2009) and *A. reysyi* in this study from Senghor Seamount. Whether these taxa are able to move between different depths, or whether each taxon comprises a number of cryptic species living at different depths, is discussed.

Differences in larval dispersal mode have been considered one of the main factors related to species genetic connectivity between seamounts, and between seamounts, their adjacent islands and continental margins (e.g. Samadi et al., 2006; Cho and Shank, 2010). Planktonic larvae are typically present in a number of chrysopetalid taxa (Cazaux, 1968; Watson Russell, 1987) and also comprise a major part of the first polychaete fauna settling on artificial reefs, in both temperate and tropical studies (Hutchings and Murray, 1982; Cole et al., 2007).

Planktonic larvae of *Arichlidon reysyi* from the NE Atlantic are described in detail, as are larvae of *Arichlidon gathofi* Watson Russell, 2000 from the West Atlantic, in order to morphologically distinguish the larvae of these two cryptic species. Six- to seven-segmented larvae can be identified to species by examination of palaeal chaetal types of the posterior-most setigers. Clarification is provided of the morphological changes of the first three anterior segments in planktonic metatrochophore larvae and late nectochaetae larvae during metamorphosis and benthic settlement.

Materials and methods

Sampling region. The Senghor Seamount is situated in a meso- to oligotrophic region of the NE Atlantic Ocean and forms an isolated topographical feature located in the Cape Verde Archipelago, ~550 km from the West African mainland at 17.17°N 21.92°W (fig. 1a). The seamount is almost symmetrical in shape, with a summit plateau in ~100 m water depth and a northern base located at a depth of ~3300 m (fig. 1b).

The Senghor summit and upper slopes are composed of craggy areas of bare volcanic rock alternating with patches of coarse sand consisting of coral and bryozoan fragments, sponge spicules, shell gravel from molluscs and barnacles, and some detrital matter. Mid-slope sediments are finer sand covered with shell fragments, and deep-sea stations at the base of the seamount comprise fine, clay-like deposits. Seafloor video footage shows very diverse habitats and faunal communities, especially at the summit, where the seafloor is covered in sediment showing ripple marks (indicating strong currents). Rocks protruding through sediment are overgrown with soft corals, gorgonians and sponges. Deeper stations, at ~800 m depth, have more sparsely populated soft-bottom habitats, but also rocky areas with soft corals and diverse fish communities (Christiansen et al., 2010).

Sampling methods. Chrysopetalid data presented in this study were derived from Senghor Seamount samples collected from a northern transect with four stations (fig. 1B) and an eastern transect with four stations, at depths of ~100–3300 m. No chrysopetalids were found on the southern or western transects (where only two stations were sampled) or at a reference station situated 110 km north of Senghor.

The macrofauna was sampled using a German Multicorer (MUC) with a core diameter of 94 mm, equivalent to 69.4 cm² surface area per core. Three deployments were made at each station, with a minimum of three cores taken from each deployment (i.e. a total of nine cores per station). The upper 5 cm of sediment was sliced for faunal analysis, and each sediment sample was placed into a 4% formaldehyde solution for a minimum of two days to fix the tissues prior to sediment washing (to reduce damage to the individuals). The samples were then gently washed on a 250- μ m-mesh sieve with filtered seawater (20- μ m mesh size) and further rinsed in fresh water before being transferred to 70% ethanol with 2% glycol added.

The macrofauna was initially sorted into major taxonomic groups and counted. The polychaete fauna was then pooled, a wet weight biomass value was obtained, and then sorting (nominally to putative species level) was carried out. The Scottish Association for Marine Science (SAMS) and the German Centre for Marine Biodiversity Research (DZMB) undertook collections at Senghor Seamount, and the chrysopetalid material is housed at the National Museums of Scotland, Edinburgh (NMS), Senckenberg Museum, Frankfurt (SMF) and the Museum and Art Gallery of the Northern Territory, Darwin (NTM). *Arichlidon gathofi* specimens are in the National Museum of Natural History, Washington DC (USNM).

Chaetal terminology follows that of Watson Russell (1991) with designations of notochaetal paleae based on position: i.e. lateral group inserts below the acicula; main group above the acicula; median group at the mid-dorsal line. Abbreviations used: prefix *l* denotes larval; *a* = adult; *p* = primary; *s* = segment. Chaetae: *tc* = transitory chaetae; *la* = lateral paleae; *ma* = main paleae; *me* = median paleae; *en* = epitokous neurochaetae; *sn* = superior group neurochaetae; *if* = inferior group neurochaetae. Anterior end: Roman numerals (I–III) indicate segment number; *dc* = dorsal cirrus; *vc* = ventral cirrus; *dtc* = dorsal tentacular cirrus; *vtc* = ventral tentacular cirrus.

Systematics

Family **Chrysopetalidae** Ehlers, 1864

Thrausmatos Watson, 2001

Thrausmatos dieteri Watson, 2001: 57–66, Figs 1–5 [type species]

Thrausmatos senghorensis sp. nov. Watson, 2014

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Figures 2A–D.

Material examined. Holotype: NE Atlantic, Cape Verde Archipelago, Senghor Seamount, East transect, 17°09.66'N 21°53.12'W, some dead coral, 1656.5 m, Core #01, coll. DZMB, Oct 2009, SMF 22963.

Paratypes: same details as holotype, Core 517 #08, coll. SAMS, 1, NMS.Z.2013.160.01; 1, NTM W25388.

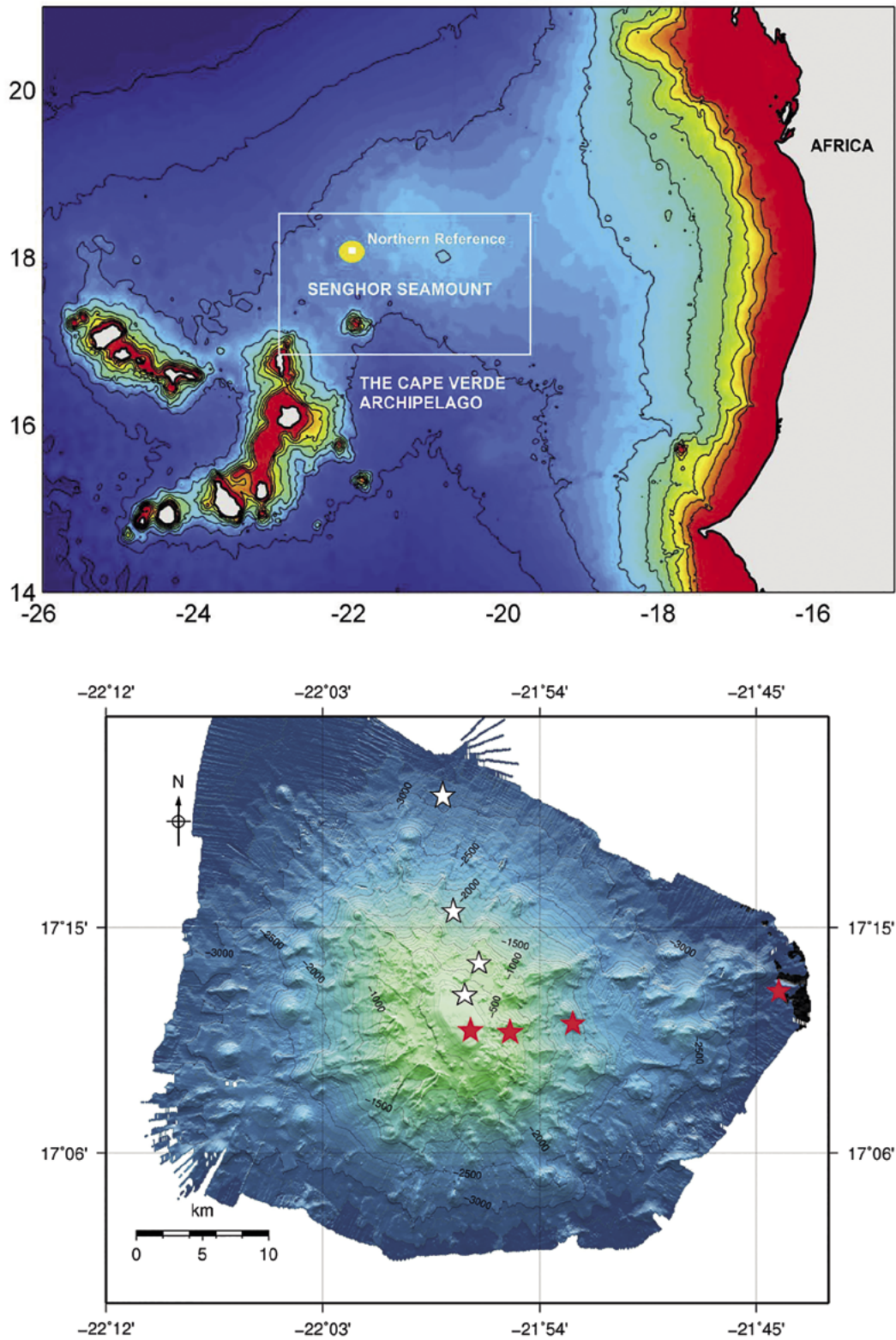


Figure 1. A, Map of Senghor Seamount, located in the Cape Verde Archipelago, NE Atlantic. Data extracted from Smith and Sandwell (1997); dataset created by A. Dale (SAMS). B, Senghor Seamount with the location of transects. Data and map created by Thor Hansteen and Alexander Schmidt, GEOMAR. (A, B, reproduced from Chivers et al., 2013.)

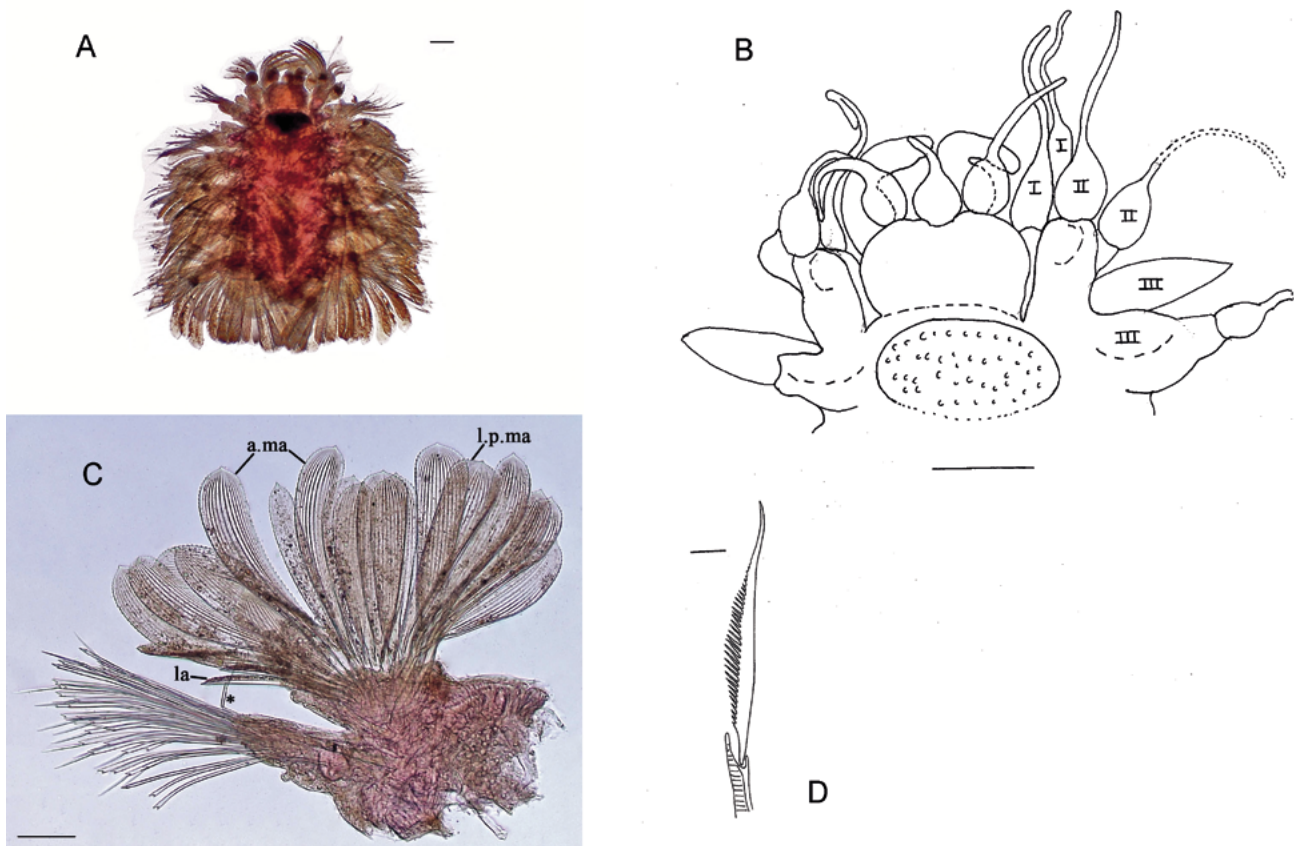


Figure 2. A–D: *Thrausmatos senghorensis* sp. nov., Senghor Seamount, SMF 22963. A, Anterior end, dorsal view, slide preparation; B, anterior end, dorsal view; C, mid-body parapodium, slide preparation; D, detail of superior-most neurochaeta (asterisked in fig. 2C). Scalebars: A–C, 100 μm ; D, 10 μm .

Description. Based on holotype, an anterior end of 15 segments, length 2.5 mm, width 1.35 mm. Prostomium with subulate median and two lateral antennae; two palps with ovoid bases, subulate distal halves with broad, rounded tips; ovoid caruncle; eye pigment absent. Segment I achaetose with 2 pairs of long cirri; segment II with 2 pairs of long cirri, notochaetal fascicle; segment III biramous with dorsal and ventral cirri, noto- and neurochaetae. Prostomium, caruncle, all ceratophores darker coloured, appear glandular; body epidermis dense with small, rounded structures, probably bacteria. Elongate pharynx with pharyngeal papillae and posterior muscular bulb, extends to segments 8–9 (figs. 2A, B).

Pale golden palaeal notochaetae insert in fans that cover the dorsum. Mid-body notochaetal fascicle with 2–3 short, pointed lateral palae with 5–6 ribs. Main palaea number 10–12 with 16–17 ribs and a couple of lightly raised ribs; medial main a little shorter with same number of ribs; widely spaced horizontal striae. Larval-type main palaea distally with broad ‘shoulders’; adult-type main palaea more slender with rounded ‘shoulders’; apices prominent (fig. 2C). Very thin, short dorsal acicula; slender dorsal cirri shorter or same length as fan. Neurochaetae number about 30; with long blades and bifid tips. Specialised superiormost fascicle with 2 short falcigers

with large basal serrations, inserts supra to overlying long, robust ventral acicula (see asterisk indicating position, fig. 2C; detail, fig. 2D). Mid-superior, middle and inferior neurochaetal groups with very finely serrate falcigerous blades with tiny bifid tips; long, slender ventral cirri (fig. 2C).

Remarks. Elaboration of body shape and posterior end is not possible as all type material is fragmented. The two paratype specimens are both composed of anterior ends of seven segments and display no deviations in chaetal morphology from the holotype.

Thrausmatos species are deep-sea dwellers found only at depths >1000 m. *Thrausmatos dieteri* Watson, 2001 was originally described from hydrothermal vents and seeps from Fiji and New Guinea, SW Pacific. *Thrausmatos* is a new record for the Atlantic and *T. senghorensis* sp. nov. is the first record from a nominal non-chemosynthetic habitat.

Thrausmatos senghorensis individuals are smaller bodied than those of *T. dieteri* and differ in: the more rounded shape of the main palaea and their lack of numerous heavy raised ribs; lesser number of lateral palaea (3 vs. 5–6); shorter dorsal cirri; short falcigers rather than long spinigers of the specialised neurochaetal superior fascicle (fig. 2D); and

absence of pronounced ventral pads. It is very difficult to discern gametes with the opacity of the thick epidermis, which is covered in multiple rounded structures resembling bacteria (fig. 2C). This was also observed in *T. dieteri* (Watson, 2001).

Thrausmatos senghorensis is found at the Senghor Seamount in depths of between 1000 and 3000 m, where ferromanganese crusts are formed at the interface of waters of the oxygen minimum zone and deeper waters (Wang et al., 2011). Although there is no indication of vents or seeps in the area (Chivers, unpublished data), a megacore sample from mid-slope depths on the East transect revealed numerous barnacle plates, suggesting a former vent community that had collapsed (Christiansen et al., 2010). It is possible that the presence of *T. senghorensis* at Senghor Seamount indicates past or as yet undetected hydrothermal activity.

The specialised neurochaetal fascicle appears to be a permanent structure in both small and large individuals of *Thrausmatos* species. These compound chaetae insert in a superior position overlying the ventral acicula of the neurochaetal fascicle. They are much shorter than the transient, long fascicle observed in gametogenic swimming individuals of *Arichlidon* and *Dysponetus*. Larval stages of *Thrausmatos* species are not yet documented.

Distribution and habitat. *Thrausmatos senghorensis* is found at Senghor Seamount, NE Atlantic, at ~1600 m, among bare volcanic rock and patches of predominantly fine sand and shell fragments.

Etymology. The species name, *senghorensis*, is named after Senghor Seamount.

Dysponetus Levinsen, 1879

Dysponetus pygmaeus Levinsen, 1879: 9, Pl. 1, Figs 1–6 [type species]

Dysponetus caecus (Langerhans, 1880)

Figures 3A, B.

Chrysopetalum caecum Langerhans, 1880: 278–279, NE Atlantic, Madeira Island.—Laubier, 1964: 125–138, Mediterranean, 32 m.

Dysponetus caecus Dahlgren and Pleijel, 1995: 159–173, NE Atlantic, Mediterranean, intertidal to 85 m.—Böggemann, 2009: 283–296, East Atlantic, Angola Basin, to 5494 m.

Material examined. *Dysponetus caecus* NE Atlantic, Cape Verde Archipelago, Senghor Seamount, 17°21.82'N 21°57.93'W, North transect, Core 1511 #11, 3241 m, coll. SAMS, Oct 2009, SMF 22964.

Description. Anterior fragment with 13 segments, 3.4 mm long, 1.6 mm wide. Streamlined body, with tapered anterior end. Transparent to silvery notochaetal spines in long fascicles covering dorsum; neurochaetae extend out beyond notochaetae. Prostomium rounded to quadrate, with glandular, ovoid, unpigmented patches on the prostomium, lateral antennae broken, medial papillae (median antenna?) present; 2 ventrolateral palps with broad bases, subulate tips, moderate length. Elongate, single lobe present on posterior margin of mouth; elongate pharynx to segment 7–9 with pair of slender, red-brown stylets (fig. 3A).

Anterior segment I very contracted, with 2 pairs of cirri, dorsal tentacular cirri broken, ventral tentacular cirri present. Segment II biramous with notochaetae and dorsal cirri, neurochaetae, no ventral cirri; notopodia of segment III with notochaetae and dorsal cirri, neuropodia with subulate ventral cirri.

Notochaetal spines long, especially mid-body; with 2 rows of long spinelets. Notopodia with elongate dorsal ceratophores; cirrostyles mostly broken. Shorter dorsal cirri on anterior segments become longer after segment 5. Compound neurochaetae with slender shafts with bifid tip at joint and long, slender, finely serrate blades, minute blade tips unidentate to bifid. Very long-shafted, specialised swimming neurochaetae, numbering 4–6 insert in superior-most position (fig. 3B).

Remarks. In the absence of extant type material of *Chrysopetalum caecum* (Langerhans, 1880) from Madeira Island, NE Atlantic, Dahlgren and Pleijel (1995) designated a neotype from southern France, Mediterranean. The authors redescribed the species and placed it within the genus *Dysponetus*. More recently Böggemann (2009) described *Dysponetus caecus* from abyssal depths off Angola, West Africa, South-east (SE) Atlantic.

Dysponetus caecus Senghor Seamount and Madeira Island specimens of Langerhans (1880: Fig. 9C) have moderate length palps. Palps are lost in Böggemann's specimens of abyssal material from Angola (2009: Figs 20A, B). All Mediterranean material described by Laubier (1964: Fig. 1A) and Dahlgren and Pleijel (1995: Fig. 3A) have longer palps. The arrangement of segments of the anterior end, based primarily on Mediterranean material, and agreed on by Laubier (1964) and Dahlgren and Pleijel (1995), are as follows: segment 1 with 2 pairs of cirri; segment 2 uniramous with notochaetae and dorsal and ventral cirri; segment 3 biramous with dorsal and ventral cirri and chaetigerous lobes. Segment 1 of Senghor material agrees with the above but segment 2 is biramous with chaetigerous lobes and dorsal cirri but no ventral cirri. There appears no sign that ventral cirri were broken off from neuropodia 2, although cirri are fragile and easily lost in dysponetids. More entire material would be needed for confirmation.

A marked increase in notochaetal length has not been observed before in *Dysponetus* (CW, pers. obs.). These longer notochaetae appear in *D. caecus* from Senghor Seamount in segments 9–13, the same segments that possess epitokous neurochaetae (fig. 3A). Slender, non-epitokous neurochaetal blades of *D. caecus* appear spinigerous under the light microscope. Only on highest magnification do the tips of neurochaetae appear unidentate or bifid within the same individual (also observed by Dahlgren and Pleijel (1995)). Neuropodia are very slender with a compressed, dense neurochaetal fascicle. Simple neurochaetae, described in *D. caecus* (Dahlgren and Pleijel, 1995), were not discerned.

Epitokous swimming neurochaetae, similar to those described in planktonic adults of *Arichlidon* species (Watson Russell, 1998, 2000), have been observed in *Dysponetus gracilis* Hartman, 1965 from deep waters of the NE Atlantic by Aguirrezabalaga et al. (1999) and in gametogenic

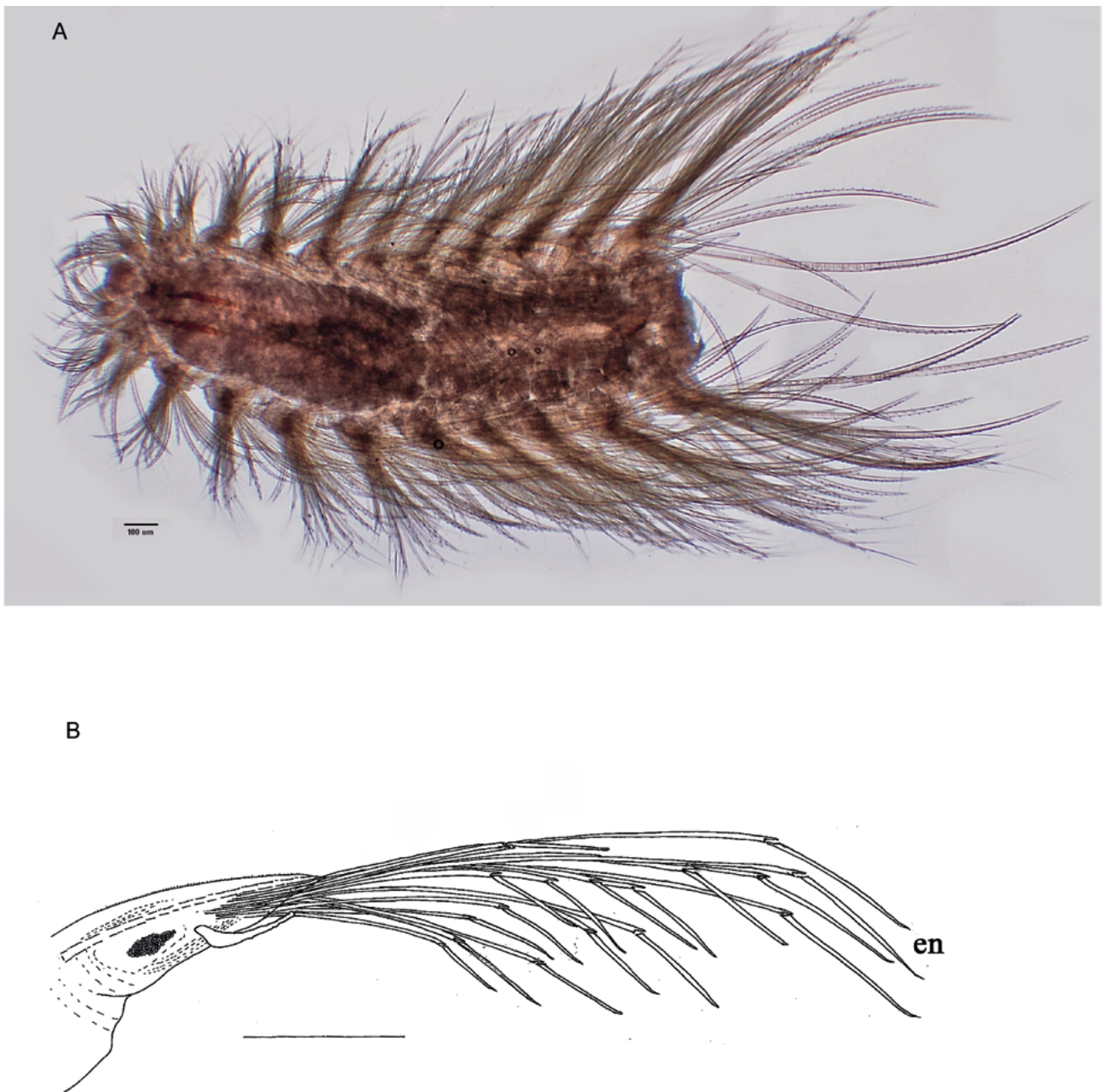


Figure 3. A–B: *Dysponetus caecus*, Senghor Seamount, SMF 22964. A, Anterior end, dorsal view, slide preparation; B, neuropodium XII with superior swimming neurochaetae. Scalebars: A–B, 100µm.

undescribed species of *Dysponetus* and *Pseudodysponetus* (Böggemann, 2009) from southern Australia (CW, unpubl. obs.). These extended, very long-shafted and bladed, compound chaetae insert in a superior position within the neurochaetal fascicle and are recorded for the first time in the male *D. caecus* from Senghor Seamount (fig. 3B).

Very little is known of the larval stages of *Dysponetus* species. The only two instances recorded are of benthic larvae

of *Dysponetus pygmaeus* (Watson Russell, 1987) and planktonic larvae of *Dysponetus* cf. *pygmaeus* (Yokouchi, Fig. *in litt.*).

Dysponetus caecus can be separated from its congeners based on a few combinations of characters. However, it is clear that within *D. caecus* there are a number of morphological and ecological disparities between Mediterranean and NE Atlantic forms, e.g. palp length and anterior segment formulae; and large depth differences reported between regions e.g. intertidal

in Mediterranean to ~5000 m off Angola. Morphological revision and genetic analysis of fresh material would help to resolve whether NE Atlantic and Mediterranean *Dysponetus caecus*, as presently understood, is a single species or a complex of cryptic species.

Habitat and distribution. At Senghor Seamount *Dysponetus caecus* occurs among the least-biomass and fine clay-like sediments recorded at the base in ~3000 m depths (Chivers et al., 2013). The nominal distribution of *D. caecus* is currently from 52°N to 19°S in the East Atlantic, including the Mediterranean. *Dysponetus caecus* has been collected from hard and soft substrates, from 1 m to depths of over 5000 m (Dahlgren and Pleijel, 1995; Böggermann, 2009).

Dysponetus sp. 1

Material examined. Senghor Seamount, 17°12.30'N 21°57.70'W, North transect, Core 1509 #01, shelly sand, 133 m, coll. SAMS, Oct 2009, SMF 22963.

Description. One anterior end of 9 segments, 1.2 mm long, 0.9 mm wide. Very small bodied, body fragmented after pharynx level. Prostomium quadrate, with two pairs of large, entire eyes; two small lateral antennae visible on anterior edge of prostomium, median antenna broken, two ventrolateral palps with subulate tips, moderate length. Elongate, single lobe present on posterior margin of mouth; elongate pharynx with pair of slender, red-brown stylets; everted proboscis with ring of small papillae.

Anterior segments: very reduced, achaetose segment I with 2 pairs of long dorsal cirri, ventral cirri bases evident; segment II biramous with notochoetae, long dorsal cirri, neurochaetae, no ventral cirri; notopodia of segment III with notochoetae, dorsal cirri, neuropodia with neurochaetae, small, subulate ventral cirri, not extending past neuropodial tip.

Notochaetal spines moderate length with two rows of spinelets; compound neurochaetae with slender shafts, slender, finely serrate blades, minute blade tips unidentate to bifid.

Remarks. Overall anterior end and chaetal characters agree between the shallow and deep *Dysponetus* individuals, but the smaller *Dysponetus* sp. 1 possesses two pairs of large red eyes, and all *D. caecus* material from both shallow and deep waters have been described in the literature as lacking eyes.

The only dysponetid described with eyes from the NE Atlantic is *Dysponetus joeli* Olivier, Lana, Oliveira & Worsfold, 2012 recorded from the English Channel in a maerl, shallow-water habitat. Without examining original *Dysponetus joeli* material, it is not possible to compare the single Senghor Seamount specimen based on the poorly preserved material figured and described in the literature.

Habitat. *Dysponetus* sp. 1 is found at 133 m at Senghor Seamount among coarse sediments.

Arichlidon Watson Russell, 1998

Arichlidon hanneloreae Watson Russell, 1998: 160, Figs 1–4 [type species]

Arichlidon reyssii (Katzmann, Laubier & Ramos, 1974)

Figures 4A, B.

Bhawania reyssii Katzmann, Laubier & Ramos, 1974: 313–317, Fig. 1A–G. Type locality: Adriatic Sea.

Paleanotus heteroseta Rullier, 1964: 142–3. Cape Verde Islands.

Chrysopetalum debile Cazaux, 1968: 536–541. Arcachon, France (larvae).

Arichlidon reyssii Watson Russell, 1998: 159–176, Figs 4C, 6G, H. Adriatic, Mediterranean, Cape Verde Islands.

Arichlidon reyssii Watson Russell, 2000: 465–477, Fig. 1A–D. Eastern Mediterranean

Material examined: NE Atlantic, Cape Verde Archipelago, Senghor Seamount, East summit, 17°12.30'N 21°53.12'W, shelly sand, 133.6 m, Core 1510 #08, coll. SAMS, 14, NMS.Z.2013.160.02; 17°10.62'N 21°56.83'W, 103.1 m, coarse sediment, Core 1531 #11, coll. SAMS, 3, NMS.Z.2013.160.03; 17°12.29'N 21°57.69'W, 132.4 m, Core #01, coll. DZMB, 4, NMS.Z.2013.160.04; 17°10.62'N 21°56.84'W, 103.1 m, Core #01, coll. DZMB, 3, NMS.Z.2013.160.05; 17°10.62'N 21°56.82'W, 102.7 m, Core #01, coll. DZMB, 1, NMS.Z.2013.160.06; East summit, 17°12.30'N 21°57.70'W, 133.6 m, shelly sand, Core 1510 # 12, coll. SAMS, 2, NMS.Z.2013.160.07; East summit, 17°12.30'N 21°57.70'W, shelly sand, 133 m, Core 1509 #02, coll. SAMS, 2, NMS.Z.2013.160.08; 17°09.66'N 21°53.12'W, dead coral, 1656.5 m, Core 1517 #08, coll. SAMS, 2, NMS.Z.2013.160.09; East summit, 17°12.30'N 21°57.70'W, shelly sand, 133.6 m, Core 1510 #10, coll. SAMS, 3, NMS.Z.2013.160.01; 17°10.62'N 21°56.82'W, Core #04, 102.7 m, coll. DZMB, 2, SMF 22965; 17°12.10.62'N 21°56.84'W, Core #05, 103.1 m, coll. DZMB, 6, SMF 22966; 17°12.29'N 21°57.69'W, Core #07, 132.4 m, coll. DZMB, 17, SMF 22967; 17°10.62'N 21°56.84'W, Core #08, 103.1 m, coll. DZMB, 2, SMF 22968; 17°10.62'N 21°56.82'W, Core #10, 102.4 m, coll. DZMB, 8, SMF 22969; 17°12.29'N 21°57.69'W, Core 864 #02, 132.4 m, coll. DZMB, 10, NTM W 025386; East summit, 17°12.30'N 21°57.70'W, Core 1509 #01, shell sand, 133 m, coll. SAMS, 3, NTM W25387.

Description. Largest individual measuring 50 segments, length 5.0 mm and width 1.1 mm. Body relatively short, broad, with silver to pale-golden palaeal fans, often with brownish scale bands, covering dorsum. Prostomium with two pairs of violet-black eyes often fused, forming rectangular block visible beneath palaea of anterior segments (fig. 4A). Segment I with two pairs of dorsal and ventral tentacular cirri; segment II with palaeal notochoetae, dorsal cirri, neurochaetae, ventral cirri absent. Lateral palaea fascicle intergrades smoothly with main palaea fascicle; distinctive group of asymmetrical ornate median palaea interlock middorsal line forming smooth convex ridge. From segment VI median group palaea number 3–5. Long lateral-most median palae appears first at segment VI and continues down body as tallest palae in entire fan (fig. 4B). Dorsal surface of notochaetal palae with tubercles and raised serrate ribs. Neurochaetae comprising superior group of spinigers; mid group with strongly dentate falcigers; inferior group falcigers with short, broad, curved articles with smooth to minutely serrate margin and blunt tip.

Remarks. One character, not reported on previously, and observed in 67 individuals of *Arichlidon reyssii* at Senghor Seamount and in material of all other re-examined *Arichlidon* species, is a distinctive paired structure at a level near the top of the pharynx. It is composed of two small, brownish,

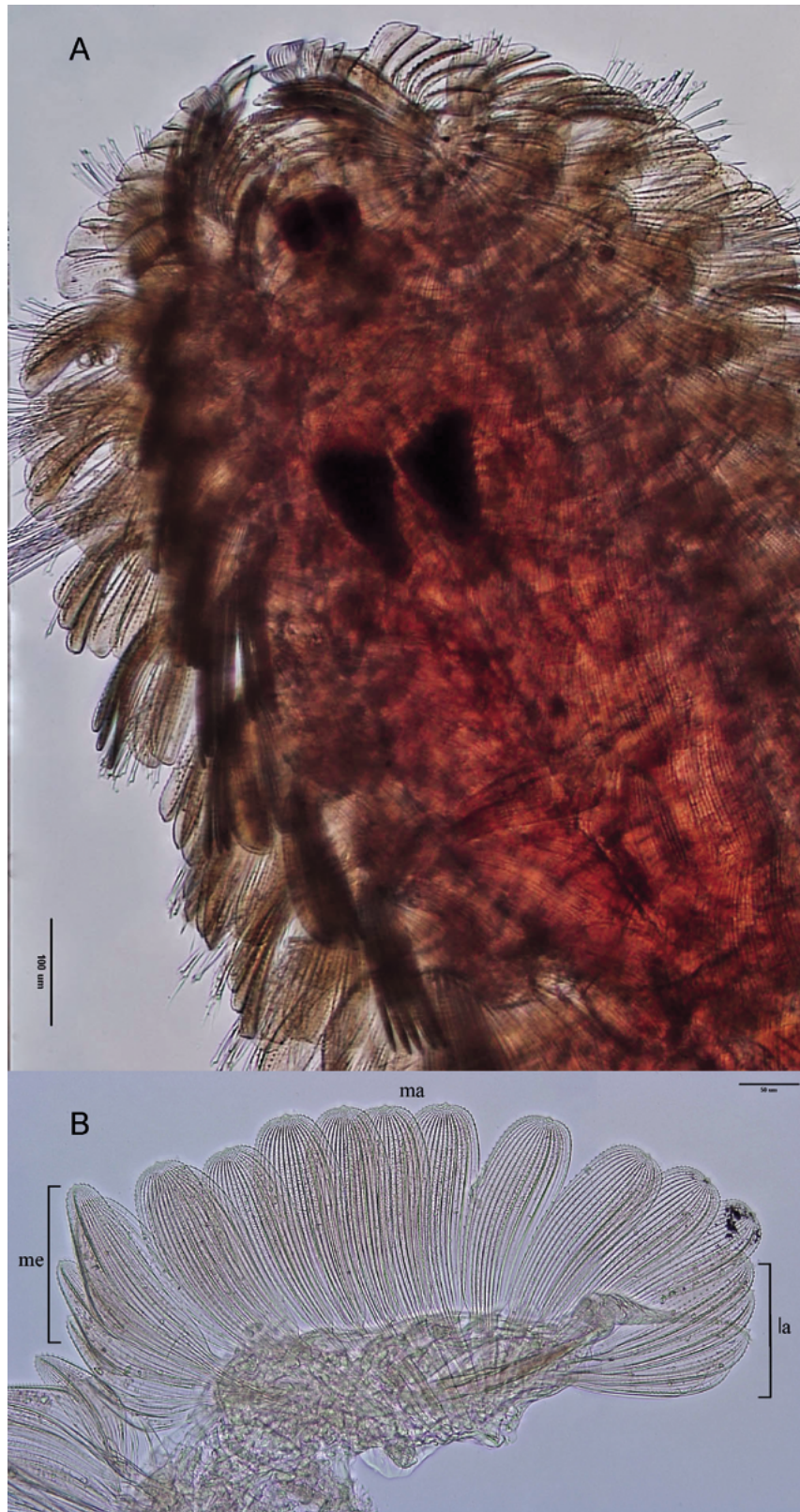


Figure 4. A–B: *Arichlidon reyssei*, adult, Senghor Seamount, NMS.Z.2013.160.09, slide preparations. A, Anterior end; B, mid-body notopodium from anterior end. Scalebars: A, 100 µm; B, 50µm.

triangular structures sitting opposite each other, either side of the pair of stylets (fig. 4A). When dissected they spill out densely packed, tiny, golden-brown globules; function currently unknown. They are reminiscent of the oil globules common to many chrysopetalid species that occur as larger, singular globules inside parapodia (Watson, 2012).

Epitokous swimming neurochaetae, described from both benthic and planktonic adults in all nominal *Arichlidon* species (Watson Russell, 1998, 2000), were not seen in any *Arichlidon reyssii* individuals in the present study.

Adult specimens of *Arichlidon reyssii* from the Cape Verde Archipelago (Maio, Brava and Boavista Islands) in sponge, shell and sediment samples, depth 20–425 m, were included in the description of the new genus *Arichlidon* and a redescription of *A. reyssii* from the Adriatic and Mediterranean Seas and NE Atlantic (Watson Russell, 1998). *Arichlidon reyssii* specimens observed in this present study from Senghor Seamount morphologically agree with the former Cape Verde material examined in all characters of body shape, size, colouration, notochaetal and neurochaetal characters, including numbers of palaeal ribs and chaetal types.

Previously, *Arichlidon reyssii* have been collected in moderately large numbers (e.g. 82 individuals from one station) and over large depth ranges (10–4000 m) in the Eastern Mediterranean (Watson Russell, 1998). At Senghor Seamount, *A. reyssii* ranges from the summit at 102 m to mid-slope depths of over 1000 m. In both cases, no discernible morphological differences were found between individuals at different depths.

Arichlidon is one of a number of chrysopetalid taxa that possess primarily cryptic species with a very conservative morphology. Watson Russell (2000) described a new species, *Arichlidon gathofi* from the western Atlantic, and compared it with *A. reyssii* on the basis of one character in particular. In *A. reyssii*, the long lateral-most median palae, with a higher number of ribs, is taller than the main fan (fig. 4 B); in *A. gathofi*, the lateral-most median palae, with a slightly lesser number of ribs, is the same height or shorter than the main fan (fig. 6E). This singular median-palae is evident in mid-body segments in juvenile and adult material examined and dissected from both species (Watson Russell, 2000: 476). In order to identify chrysopetalid larvae to species, it is essential to study chaetal patterns throughout the entire body. In the interests of distinguishing Atlantic *Arichlidon* larvae to species, and to elaborate on the sequence of changes in the morphology of planktonic to benthic individuals, larvae of *A. reyssii* and *A. gathofi* are described below.

Distribution and habitat. Benthic adults of *Arichlidon reyssii* are found from the Mediterranean, NE Atlantic coast, and the islands and seamount of the Cape Verde Archipelago. Among the Senghor Seamount chrysopetalid fauna, *A. reyssii* comprises the largest number of individuals, which predominantly dwell in coarse sediments at the summit at ~100 m, among the largest polychaete biomass recorded. There is also one record from mid-slope at 1651 m.

Arichlidon reyssii metatrochophore planktonic larvae

Figures 5A–F.

Material examined: NE Atlantic, France, Arcachon, from plankton outside Marine Station, Nov 1987, coll. C. Cazaux, 3 entire specimens all 6 segments.

Description based on planktonic specimens. 1: Length 480 μm , width 440 μm ; 2: length 640 μm , width 440 μm ; 3: length 720 μm , width 520 μm ; NTM W25385.

Broad, ovoid bodies filled with dense oily droplets; conspicuous fascicles of long, brown, latero-anteriorly directed transitory notochaetal spines in first chaetigerous segment (fig. 5A). Smallest larva 1 with notochaetal fans more folded and bare mid dorsal line; larvae 2 and 3 with notochaetal palaeal fans spread over dorsum from segments II–VI; compound falcigerous neurochaetae from segments II–VI. All larvae possess large rounded epispheres with three pairs of eyes; largest pair in anterodorsal position with apparent lenses, smaller pairs more dorsal. Larva 1 prostomium with small, unpaired, anterolateral cirrus (developing lateral antenna?); larva 3 with circular hyaline patch mid-episphere and developing mouth. No median antennae, palps or nuchal organs visible.

Small ciliate ‘buds’ present each side of body at posterior latero-dorsal edges of episphere at dividing line between head and trunk (nascent adult segment 1). Larval segment I with two pairs of larval tentacular cirri, longer than following cirri; inserting at the same level as the transitory notochaetae. Transitory notochaetae insert in large, rounded dorso-lateral lobe with 2 aciculae; number ~15, with larger spinelets along entire lateral edge and minor spinelets in another plane along part of length (figs 5A–D).

Segment II, ventral view: very small neuropodial rami present and directed towards mid-body ventral line i.e. not laterally; with fascicles of spinigerous neurochaetae, ventral cirri absent. Neuropodia III–VI with subulate ventral cirri (fig. 5C).

Notopodia of segments II–III with larval primary palaea types only: with 2–4 lateral palaea, 1–3 short spines, 4 large symmetrical main palaea and 2 broad asymmetrical palaea in medial-most position. Notopodium of segment III with 2 lateral palaea with 8–12 ribs, 5–7 main palaea with 17–21 ribs and 4 symmetrical median palaea. Larval main palaea distally rounded. Subsequent notopodia with 1 small spine overlying dorsal aciculum; notopodia of segments II–VI with relatively short, subulate dorsal cirri (fig. 5B).

Segments IV–VI notopodium with adult chaetal types replacing larval types. Notopodia of segment IV with 4 lateral palaea with 6–14 ribs; 4–5 main palaea with 15–19 ribs, including large, slightly asymmetrical subunit 1 palae with 19–20 ribs and 3 raised serrated ribs; 5–6 median palaea grading in size and degree of asymmetry with 7–14 ribs, including tall lateral-most one with 2–3 raised and serrated ribs as tall as or taller than main palaea group) (fig. 5E). Notopodia of segment V with 3 lateral, 4 main and 5 median; notopodia 6 with small notosetal fascicle comprising 1–2 slender lateral, 2 main and 3 short median palae. Adult main palae distally squarer (fig. 5F).

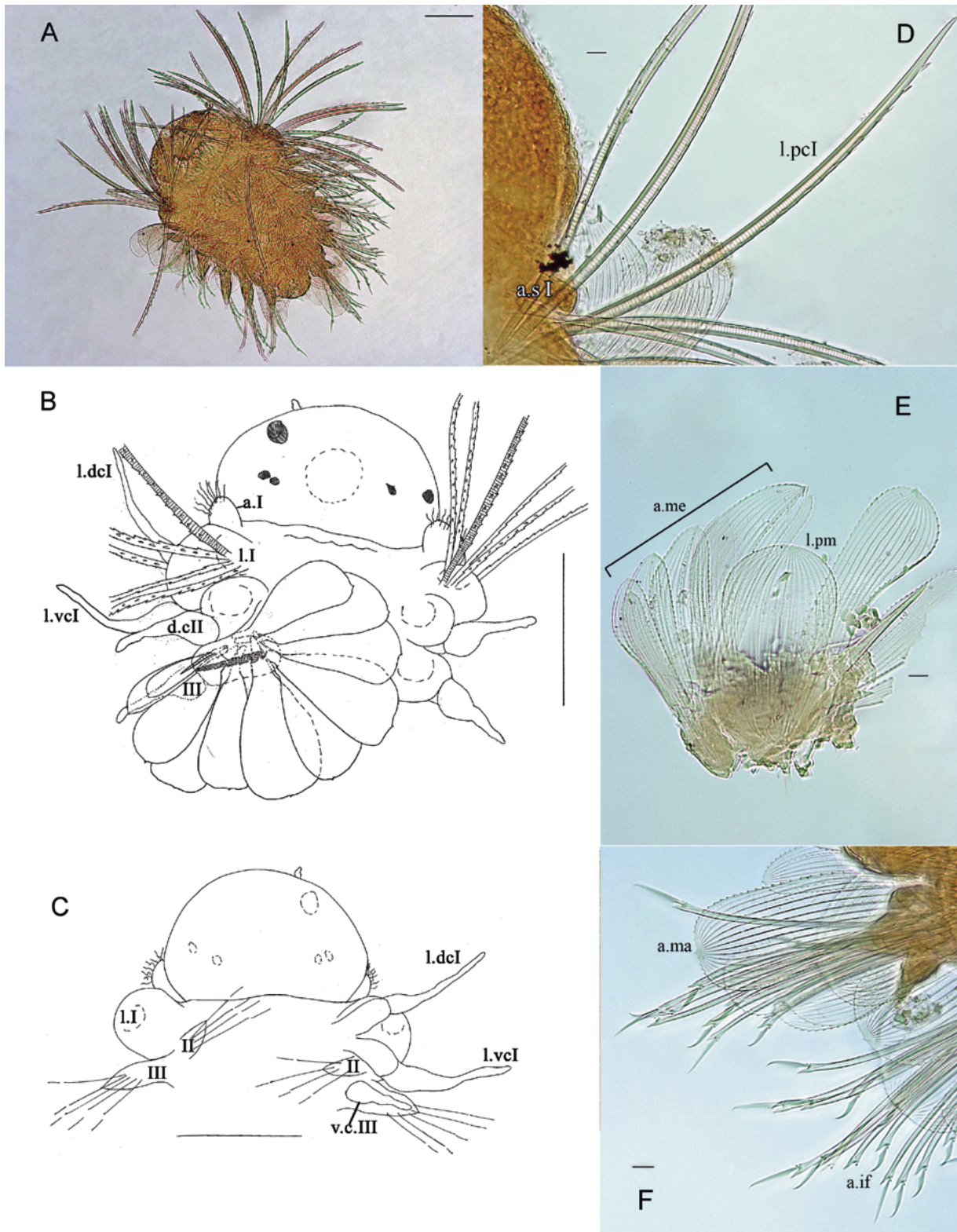


Figure 5. A–F: *Arichlidon reysyi* 6-segmented larva, Arcachon, NE Atlantic, NTM 25385; A, D–F: slide preparations. A, Entire larva, dorsal view; B, anterior end, dorsal, left side detail (transitory chaetae drawn in part); C, anterior end, ventral view, left side detail; D, detail of anterior end of fig. 5A; E, notopodium segment IV; F, neuropodia segments IV and V. Scalebars: A, 50 μm ; B–C, 100 μm ; D–F, 10 μm .

Segment III neuropodia mainly with falcigerous neurochaetae with slender, narrow blades; recognisable adult chaetae and adult types from neuropodia of segments IV–VI. Neuropodium of segment IV with 1 superior spiniger, 2–4 mid-superior falcigers with long blades, 4 mid-inferior falcigers with shorter blades and 6–8 inferior falcigers with typical adult smooth, short, curved blades (fig. 5F). Neuropodium of segment VI with 1–2 superior long, narrow-bladed falcigers and 2–3 lower falcigers with shorter, slender blades. All neuropodia with 1 short, simple spine overlying ventral acicula. Pygidium composed of ventral median conical protruberance and dorsal rounded structure with two lateral anal cirri.

Remarks. Cazaux (1968) provided detailed figures of the early development of a species he identified as *Chrysopetalum debile*, collected at different stages from the plankton at Arcachon, NE Atlantic. The '*C. debile*' identification was based on one of a number of chrysopetalid species present in the region, and original material was subsequently lost. Study of recent material of metatrochophore chrysopetalid larvae from the same locality and described in this paper, confirms Cazaux's material as most likely belonging to the species *Arichlidon reyssii*.

Behavioural observations in Cazaux's 1968 paper include a description of the planktonic larvae not feeding but living on their reserves and at the slightest touch rolling into a ball, becoming bristly like a 'Chaetosphaera' larvae. He observes there is a planktonic duration of at least three weeks between metatrochophore 1 to nectochaete 1, and their presence in stations located between the ocean and inner estuary of the Bay of Arcachon between October and December. Bhaud *in litt.* mentions their presence in the Western Mediterranean between August and October.

Distribution. Planktonic larvae of *Arichlidon reyssii* have been reported from the Mediterranean and NE Atlantic coast.

Arichlidon gathofi benthic nectochaete larvae

Figures 6A–F.

Arichlidon gathofi Watson Russell, 2000: 465–477

Figures 1–5.

Material examined: Paratypes. USA, off North Carolina, western Atlantic, Stn. 2606, 34° 35'N 75° 52'W, 45 m, coll. RV *Albatross*, 18 Oct 1885, USNM 186017. Note: 148 individuals were collected; among these were 36 juveniles and 4 late nectochaete larvae, the latter described herein.

Description based on benthic specimens. 7 segments: length 520 μm , width 500 μm (fig. 6A, B); 7 segments: length 460 μm , width 460 μm ; 8 segments: length 540 μm , width 460 μm ; 10 segments: length 700 μm , width 500 μm ; 11 segments: length 840 μm , width 52 μm ; 14 segments: length 920 μm , width 520 μm .

Larvae of 7 segments with broad, ovoid body shape with palaeal fans fully extended over dorsum, neurochaetae extending out beyond palaeae; dense oil globules in gut. Rounded prostomium with faint red eye pigment visible; short, stout median antenna inserts on anterior edge of prostomium;

lateral antennae, palps and nuchal fold absent. Segments I–III in adult configuration (figs 6A, B). Segment I more visible in ventral view, with two pairs of dorsal and ventral tentacular cirri (fig. 6B).

Notopodium of segment II with 2 narrow palaeae, 6–8 ribs. Notopodium of segments II–IV include primary, expanded palaeae in medial position with 15–16 ribs (fig. 6C). Segments V–VII with adult type, slimmer, asymmetrical median palaeae, numbering 2–3, shorter than main fan, with 11–14 ribs (fig. 6D). Broad, asymmetrical medial-most, subunit 1, main palaeae (*A. gathofi* species character) present posterior segments VI–VII. Prominent, curved notochaetal spine originating from lateral group (continues into adult); subulate dorsal cirri present on all notopodia (figs 6C, D).

Neurochaetae of segment II all spinigers; neurochaetae of segments III–VII include 2–3 superior spinigers; adult groupings of mid-superior and mid-inferior falcigers; typical short, curved articles of inferior falcigers. Pygidium composed of slender ventral cone and dorsal structure with two filiform anal cirri.

Post-larvae and juveniles 8–14 segments with body slightly tapered anteriorly and posteriorly; neurosetae not extending out beyond palaeae. Prostomium smaller with two pairs of eyes, longer, subulate median antenna, two lateral antenna and two ventral, long, cylindrical palps. Triangular mouth fold posterior to palps, pair of stylets evident in pharynx; raised glandular nuchal fold present posterior to prostomium. Increasing numbers of adult main palaeal notochaetae and neurochaetae with increasing body segments.

Remarks. Chrysopetalid notochaetal palaeae, spines and neurochaetal shafts are composed of internal longitudinal ribs and horizontal diaphragms (Westheide and Watson Russell, 1992). The appearance of the first chaetae arises in the trochophore after initiation of the first larval segment. These long, brown, spinulose provisional chaetae are internally striated. The metatrochophore 4-segmented larvae develop compound falcigerous neurochaetae with striated shafts, and the generation of the sixth segment initiates primary, laterally folded, notochaetal palaeal fans and spines, all striated internally (Cazaux, 1968; Watson Russell, 1987).

This construction of internally striated chaetae creates maximum strength and lightness for larvae and adults found mid-water. Adult chrysopetalids may also possess epitokous, swimming neurochaetae, as first described for *Arichlidon gathofi* collected from the plankton (Watson Russell, 2000, Fig. 5A, and reproduced in this paper as fig. 6F).

Mileikovsky (1962) observed that the long provisional chaetae found in chrysopetalid, sabellariid and some 'Chaetosphaera' spionid trochophore larvae are probable convergent structures suited to a similar pelagic mode of living, with larvae able to be transported very long distances. There is no record of chrysopetalid teleplanic larvae, but chrysopetalid metatrochophore larvae have been collected from vertical plankton tows from the surface down to 100 m, in 3000–4000 m depth in the Gulf Stream, NW Atlantic (Mileikovsky, 1962). Original material was lost but its identity is inferred from his figures as belonging to either the genus *Arichlidon* or the deep-sea-dwelling *Strepternos* (see Watson Russell, 1997).

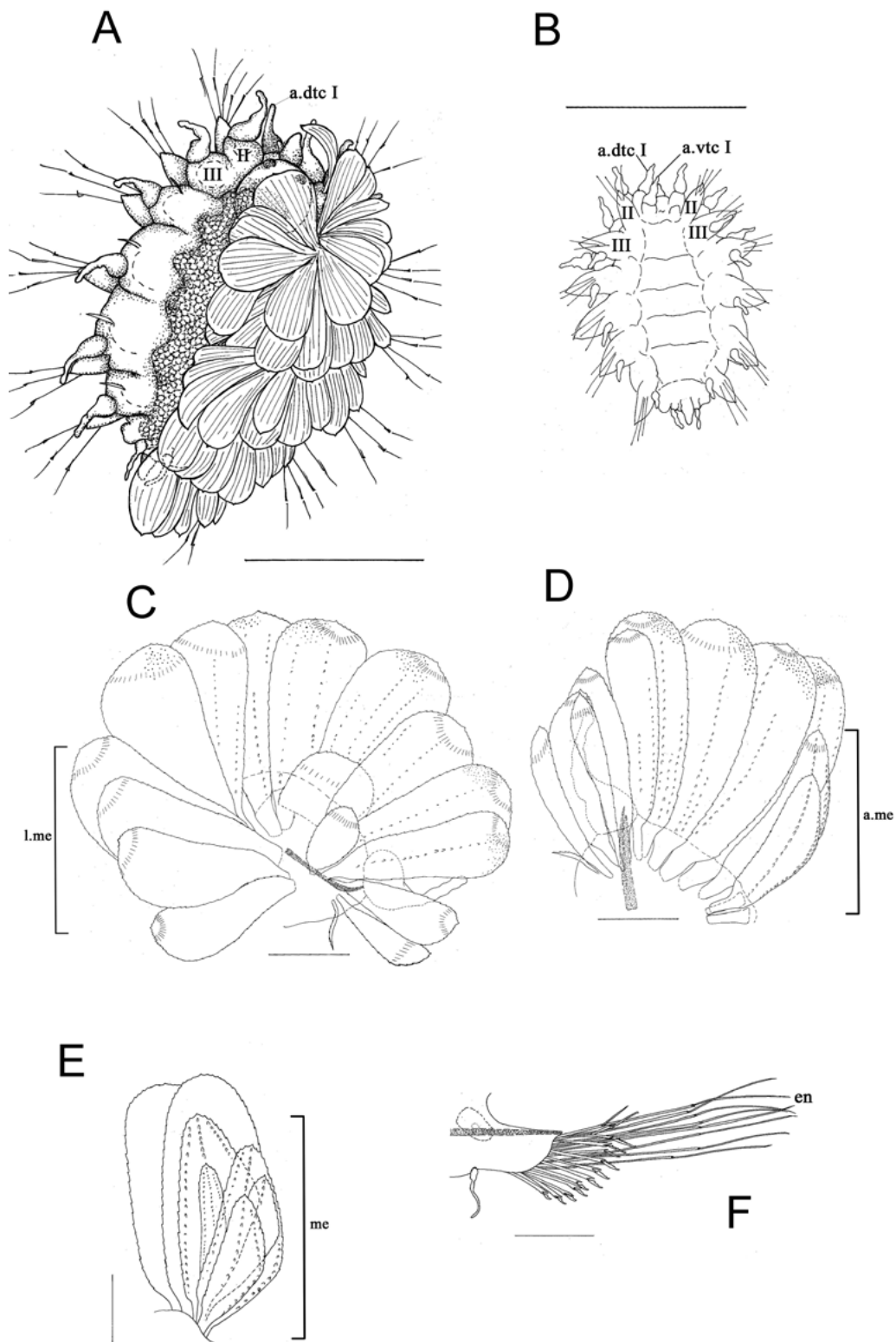


Figure 6. A–F: *Arichlidon gathofi*, 7-segmented larva, Carolina, West Atlantic, USNM 186017. A, Entire larva, dorsal view; B, ventral view of A; C, notopodium segment IV; D, notopodium segment VI (figs A, C, after Watson Russell, 1987: Figs 28.4, 6: as ‘new genus 1’). E, *A. gathofi*, adult, mid-body notopodium, detail median fascicle; F, mid-body neuropodium with epitokous swimming neurochaetae (figs E, F after Watson Russell, 2000: Figs 1D, 5A). Scalebars: A, 200 μ m; B, 350 μ m; C–E, 40 μ m; F, 100 μ m.

Distribution and habitat. *Arichlidon gathofi* is found from North Carolina, USA to Panama, Central America, western Atlantic. Benthic habitat varies from silty sands in the Gulf of Mexico to algal, sea-grass, shell and coral rubble substrates of the islands of the north and south Caribbean; 1–106 m.

Remarks on the larval morphology and development of Arichlidon reyssi and A. gathofi. Metamorphosis at the 6–7-segment stage occurs at benthic settlement and includes loss of larval notopodia I (comprising larval pair of cirri and transitory, provisional chaetae, figs. 5A–D) and development of adult segment I in a dorsal/ventral plane. The episphere reduces in size as it differentiates into a more adult prostomium and its appendages develop. Concurrent with these changes is development of adult notopodia II and III with forward rotation and part fusion, particularly evident in dorsal view; larval primary palaea are lost on notopodia II and replaced by a few, short adult palaea (fig. 6A). The nuchal fold begins to take shape as a result of these former changes and forms part of the retraction mechanism of the anterior end. A discreet caruncle, as postulated by Cazaux (1968), is found primarily in *Chrysopetalum* and is not present in *Arichlidon* species.

Adult segment I is developed from the ciliate buds seen in the larvae at the conjunction of the episphere and trunk (fig. 5A–D). From a 7-segmented larvae onwards, this segment I appears reduced and fused in part to the prostomium. It supports a pair of dorsal and ventral cirri that are often more visible in ventral view. These later-formed adult cirri are shorter than the larval pair and are approximately the same size as those dorsal cirri seen in segment II (fig. 6A, B). At no developmental stage are chaetae present on adult segment I in *Arichlidon* species, and the term ‘tentacular’ is therefore retained as a descriptor for the cirri of this segment.

A similar series of morphological changes has been described for the larval deep-sea chrysopetalid *Strepternos didymopyton* Watson Russell, 1991, which has the same anterior end schema, i.e. segment I with two pairs of tentacular cirri, segment II with notopodia, chaetae, neuropodia with chaetae, ventral cirri absent (Watson Russell, 1997). In *Strepternos* and *Arichlidon*, the small neuropodia I does not at any time possess ventral cirri (fig. 5C, 6B). It has been the contention of some authors, e.g. Perkins, 1987, that there has been loss of ventral cirri from this segment during ontogeny.

Identification of Atlantic Arichlidon larvae to species. Chaetal patterns in the midposterior body of chrysopetalid larvae can be used for identification to genus and species (Watson Russell, 1987). The shape of the main palaea (and particularly the inferior-most curved, falcigerous neurochaetae from posterior segments) identify the above larvae as belonging to the genus *Arichlidon* (fig. 5F). Adult lateral, main and median palaeal types are present from segments IV–VI, with the overall highest numbers of adult chaetal types present in segments IV–VI in *A. reyssi* and segments V–VII in *A. gathofi*. The tall lateral-most median palae—a distinguishing species character for *A. reyssi*—is clearly visible from segment IV (fig. 5E); the shorter, broader median palae visible from segment V in *A. gathofi* (fig. 6D).

Discussion

Dispersal mode and depth ranges of chrysopetalid species at Senghor Seamount

The polychaete fauna of the Cape Verde Islands represents West African species, American elements absent from the continental African plateau, small numbers of endemic species, and species from the southern limit of the NE Atlantic and Mediterranean (Ruillier, 1964). Senghor Seamount chrysopetalid species present in this study comprise a predominantly eastern Atlantic fauna. *Thrausmatos* species are deep-sea dwellers found only at depths greater than 1000 m, and the new species, *T. senghorensis*, is potentially a NE Atlantic seamount endemic. *Dysponetus caecus* and *Arichlidon reyssi* are regional benthic species: *A. reyssi* from the Mediterranean Sea and the NE Atlantic coast, including the Cape Verde Archipelago; *D. caecus* from the Mediterranean Sea, NE to SE Atlantic coast, including off West Africa.

Dispersal of chrysopetalid larvae and swimming adults to and from Senghor Seamount must largely be determined by regional and local hydrodynamic regimes. NE Atlantic water circulation near the surface does not favour transport of larvae from the European mainland towards seamounts (Surugi et al., 2008). Mediterranean water outflow occupies the NE Atlantic at depths of around 1000 m; one branch forms an eastern boundary slope current, the other forms isolated anticyclonic vortices, with velocities of up to 30 cm s⁻¹, referred to as Meddies. Meddies consist of lenses of warm, salty water with a diameter of around 60 km that move westwards at a depth interval of 800–1400 m. Those that do not collide with seamounts may have a lifetime of up to five years (Richardson et al., 2000). Meddy structures have been inferred at Senghor from 200 m (Christiansen et al., 2010). Planktonic larvae and swimming adults of *Arichlidon reyssi* and *Dysponetus caecus* hypothetically could disperse by passive travel in the deeper currents and Meddies in a ‘stepping stone’ fashion along continental margins and between islands and seamounts.

Deep-sea communities are known to be strongly influenced by bathymetric gradients, although the exact controls of depth zonation remain conjectural (Carney, 2005). *Arichlidon reyssi* shares records with *Dysponetus caecus* for extreme depth ranges (from shallow to abyssal waters) within the Mediterranean and NE Atlantic. At Senghor Seamount, individuals of *Arichlidon reyssi*, morphologically identical, are found at ~100 m and also at ~1600 m. This raises the question—are we dealing with the same species or a number of cryptic species over these depth ranges?

Bik et al. (2010) found low genetic divergence across vertical depths (~2800 m) among Antarctic taxa, and identical gene sequences recorded over a 680-m depth range in another taxon within the free-living marine nematodes. Genetic analyses suggest the same species is present between 400- and 1800-m depths in a poeobiid polychaete species off Central California (K. Osborn, pers. comm.), and results for cryptic species of phyllodocid polychaetes on the NE Atlantic continental shelf of between <100 m and >1000 m confirmed shallow and deep forms represented different species (Nygren et al., 2010).

DNA studies of *Arichlidon reysyi* and *Dysponetus caecus* benthic populations at different depths would help to resolve: (i) whether the same species has the ability to live and move between areas of very different depths; (ii) whether this is evidence of the existence of different species belonging to a number of clades that may be sympatric at different depths; or (iii) whether these are distinct species living at different depths with no apparent morphological distinguishing characters to separate them.

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