Description of three new species of *Amphitritides* Augener, 1922 (Terebellida, Annelida) from the coast of Namibia (South West Africa)

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Abstract

Three new terebellid species with two pairs of arborescent branchiae, serrated notochaetae with bulbous wings and avicular uncini in completely separate double rows are described from the Namibian coast, SW Africa, found during different expeditions between 2004 and 2022. These species were assigned to the genus *Amphitritides*, *A. jirkovi* sp. nov., *A. namibiensis* sp. nov. and *A. skeletonensis* sp. nov. The main diagnostic characters of these species are discussed, especially in the light of the ongoing discussion of synonymising *Amphitritides* with *Amphitrite* and *Paramphitrite*. The features of the three newly described species are compared in a table. An identification key for all known species of *Amphitritides* is also provided.

Key words: Identification key, morphology, Namibia, new species, Polychaeta, SW Africa, systematics, taxonomy, Terebellidae

Introduction

The temperate southern African region (according to Spalding *et al.* 2007) is poorly studied in terms of biological diversity research (Konar *et al.* 2010) and also in terms of polychaete fauna, including Terebelliformia (Hutchings *et al.* 2021a). This study is part of an ongoing inventory of biodiversity off the coast of West and Southwest Africa. Other studies recently reported on marine macrozoobenthic species from this region are those on amphipods (Zettler *et al.* 2018, 2022), bivalves (e.g. Zettler & Hoffman 2022), cumaceans (Bochert & Zettler 2011), gastropods (e.g. Massier & Zettler 2009) and holothurians (Thandar *et al.* 2010).

During several expeditions conducted between 2004 and 2022 with four research vessels, about 1,600 specimens of Terebellidae Johnston, 1846 were found in depths between 20 m and 2,513 m off the coast of SW Africa. About 250 specimens of these terebellids have two pairs of stalked arborescent branchiae on segments two and three, distally serrated notochaetae with bulbous wings on the shaft, and avicular uncini in completely separated double rows. These species are described in this first contribution of a planned series on the taxonomy and distribution of the terebellids of this region.

Terebellidae is a monophylum within Terebellida sensu Rouse *et al.* 2022, and is characterized mainly by the possession of multiple grooved buccal tentacles, or palps, that cannot be fully retracted into the oral cavity and are used for selective deposit feeding on the sediment surface. These tentacles are prostomial in origin. However, the exact status of this taxon continues to be debated. Especially the phylogenetic relationship of the subfamilies within the Terebellidae is currently a matter of discussion. As a result of a comprehensive phylogenetic analysis based on morphological characters, Nogueira *et al.* (2013) concluded that the subfamilies should be raised to family rank. They distinguished four families within the Terebellidae *sensu lato*: Polycirridae Malmgren, 1866, Thelepodidae Hessle, 1917, Thelothelepodidae Nogueira, Fitzhugh & Hutchings, 2013, and Terebellidae *sensu stricto* Johnston, 1846. Trichobranchidae Malmgren, 1866 was also integrated into Terebellidae *sensu lato* (e.g. Hutchings *et al.*
2021a, b, Nogueira et al. 2013). In contrast, Stiller et al. (2020) concluded, based on transcriptomes, molecular, and morphological data, that Trichobranchiidae and Terebellidae are sister groups. Accordingly, within the Terebellidae there are two subfamilies, the Terebellinae and the Thelopodinae. One representative of the Thelopodopodiidae was nested within the Thelopodinae, and Polycirridae within Terebellinae. In addition, Stiller et al. (2020) found four well-defined clades within the Terebellinae, which are ranked as tribes, namely Proleini, Polycirrini, Terebellini and Lanicini.

The exact delimitation and definition of some genera within the Terebellidae respectively within the Terebellinae or Terebellini is similarly problematic. This applies, among others, to the genus Amphitritides Augener, 1922. Augener (1922) established this subgenus, to the genus Amphitrite O.F. Müller, 1771, for two species, both originally assigned to Terebella Linnaeus, 1767: A. (A.) gracilis (Grube, 1860) and A. (A.) bruneocoma (Ehlers, 1887). Later, Hartman (1959) elevated this subgenus to genus level. Three characters characterize the species of Amphitritides, the presence of two pairs of arborescent branchiae with distinct stalks on segments two and three, double rows of uncini on most of abdominal neuropodia and distally serrated notochaetae (Augener 1922, Hutchings et al. 2021b). However, Jirkov (2020) proposed a synonymising Amphitritides with Amphitrite (including Neoamphitrite Hessle, 1917). He argued that the presence of double rows of uncini in abdominal neuropodia and the presence of two pairs of branchiae also occur in some species currently assigned to Amphitrite. In contrast, Lavesque et al. (2021) pointed out that the presence of double rows of uncini on different neuropodia does not only occur within these two genera, but also within other genera of the Terebellidae, and that this character must therefore rather be regarded as a convergence. Furthermore, the lack of lateral lobes on the first segments in the species of Amphitritides is supposed to separate this genus from Amphitrite, whose species are always supposed to have well-developed lateral lobes on segments two to four. In our opinion, it is not completely clear which diagnostic characters are really relevant for the definition of the genera of the Terebellidae. For example, the genus Paramphitrite Holthe, 1976, with the presence of two pairs of branchiae and with double rows of uncini on first abdominal neuropodia, was recently synonymised with Amphitritides (Jirkov 2020) or considered a valid genus (e.g. Holthe 1986, Hutchings et al. 2021b, Lavesque et al. 2021), based on a different assessment of the number and shape of branchiae, number of thoracic segments and number of neuropodia with double rows of uncini. However, the species of both genera have lateral lobes on segments two to four.

In addition to these five characters, the number of genital papillae and ventral glandular areas (=ventral shields), as well as the shape of the notochaetae and uncini are of significant diagnostic importance for the species of the genera mentioned above, and also for most terebellid species (Hutchings et al. 2021a, b, Rouse et al. 2022).

We follow here the views of Hutchings et al. (2021b) and Lavesque et al. (2021) who proposed the separation of Amphitrite and Amphitritides, and the synonymisation of Neoamphitrite with Amphitrite. However, we see the urgent need for a revision of this group of genera, including Paramphitrite, based on type or topotype material using both morphological and molecular data. But a revision of these genera is beyond the scope of this paper.

There are nearly 400 described species of Terebellidae s. str. worldwide, occurring from the eulittoral to more than 4,000 m depth (Hutchings et al. 2021a, b). A hotspot of distribution is the central Indo-Pacific with over 90 species. In contrast, only 12 species occur in the temperate Southern Africa region, but no Amphitritides species (Hutchings et al. 2021a). However, it is assumed that the low number of species in these regions is due to collection activity rather than actual species diversity.

The aim of this paper is to describe the terebellids with two pairs of arborescent branchiae, serrated notochaetae with bulbous wings on the shaft and avicular uncini in completely separate double rows found in the above-mentioned region. In addition, the diagnostic characters of these species will be discussed, considering their importance for the taxonomic assignment of the species. Finally, the distribution of these species in terms of depth and some abiotic factors are also discussed. An identification key for all known species of the genus Amphitritides completes this study.

Material and Methods

The material used in this study was sampled off Namibia during several expeditions with the research vessels Alexander von Humboldt (AHAB8), Maria S. Merian (MSM07, MSM18, MSM105), Meteor (M131 and M157) and Mirabilis (RgNO) in the years 2004, 2008, 2011, 2016, 2019 and 2022. A map shows the type localities and distribution of the species described in this paper (Fig. 1). Samples were taken using van Veen grabs, multi-corers
and dredges. The samples were sieved by washing with seawater on board retaining specimens larger than 1 mm. These specimens were fixed in 4% formalin and preserved in 70% EtOH after being sorted in the laboratory. Selected specimens were colour-photographed using a stereo microscope (Zeiss Discovery.V8) and light microscope (Zeiss Axio Lab.A1). Digital microphotographs were made using an AxioCam 105 colour (Carl Zeiss MicroImaging GmbH, Jena) and AxioVision software (Carl Zeiss Imaging Solutions GmbH, Jena).

![Figure 1](image_url)

**FIGURE 1.** Map of the study area, with the records of the three newly described *Amphitritides* species. Type localities are marked with a star.
Specimens were stained with methyl blue or Shirlastain A to visualize specific body regions and structures. For that purpose, ethanol-preserved specimens were first transferred into distilled water and then dipped into a methyl blue or Shirlastain A solution, respectively. The staining fades completely when the specimens are returned to ethanol.

For scanning electron microscopy (SEM) analyses, several specimens were dehydrated in a graded ethanol series and finally in acetone; they were dried in a critical point drier (K850 EMITECH) and were then attached to a stub and sputter-coated with gold palladium. Scanning electron microscopy was carried out using a Zeiss DSM 960A microscope.

All figure plates were edited using the graphic software Adobe Acrobat 9 Pro.

Specimens are deposited in the Zoological Collection of University of Rostock (ZSRÖ) and in the Marine Evertrebraten II collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt/Main (SMF).

**Results**

**Taxonomic Account**

Terebellidae Johnston, 1846 *sensu stricto*

*Amphitritides* Augener, 1922

Type species: *Terebella gracilis* (Grube, 1860), by subsequent designation.

**Diagnosis** (after Hutchings *et al.* 2021b, slightly emended (*in bold*)). The diagnoses of the genera *Amphitritides* and *Amphitrite*, for which a synonymisation is discussed (see Introduction), are similar in many characters. *Amphitritides* is distinguished from *Amphitrite* by the characters in *italics* below.

Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots may be present, **but may fade when stored in alcohol**; distal part shelf-like. Buccal tentacles all usually uniformly cylindrical. Peristomium forming lips and continuing dorsally for short extension, not forming a complete ring; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded, slightly or distinctly undulated; narrow, rectangular, mid-ventral lower lip. Peristomial shield marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal shields. Two pairs of short, arborescent branchiae, on segments two and three, with short or long main stalks. Rectangular to conical notopodia beginning on segment 4, extending a variable number of segments; notochaetae all medially winged and finely serrated distally, **with or without basally bulbous wings**. Neuropodia beginning on segment 5, as low, sessile ridges throughout; neurochaetae as short-handled avicular uncini, in completely separate double rows, beak-to-beak arrangement, from segment 11 until **termination of notopodia** or posterior body. Nephridial papillae on segment 3, genital papillae on some anterior segments, beginning from segment 6, **between parapodial lobes or at anterior bases of notopodia**.

**Remarks.** In addition to the presence of lateral lobes on the anterior segments, the serrated notochaetae are also described as having no bulbous wings at the base and the uncini are arranged in partially intercalated double rows in *Amphitrite*. But there is also an overlap in the presence of these uncini double rows in the neuropodia. In *Amphitrite*, they are supposed to be present almost exclusively in the thorax region, while in *Amphitritides* they extend to the posterior end of the body. However, there are several exceptions. In *Amphitrite rubra* (Risso, 1826) and *A. vigintipes* (Grube, 1870) (but *Neoamphitrite vigintipes* in WoRMS, Read & Fauchald 2024b), for example, the double rows of uncini extend almost to the posterior end (Jirkov 2020), whereas in *Amphitritides pectinobranchiata* Hartmann-Schröder, 1965 they are only present in the thoracic region (Hartmann-Schröder 1965).

As described in the introduction, we follow here the views of Hutchings *et al.* (2021b) and Lavesque *et al.* (2021) who proposed the separation of *Amphitrite* and *Amphitritides*, and a synonymisation of *Neoamphitrite* with *Amphitrite*.

Amphitritides jirkovi sp. nov.
(Figs 2, 11F–J, R)

Material examined. Holotype. Off Namibia: 17.3158°S 11.7232°E, depth 26 m, 05.03.2008, complete specimen (ZSRO-P2674).

Diagnosis. Distal part of prostomium as shelf-like tentacular membrane with distinct lateral lobes. Two pairs of arborescent branchiae with short stem; first and second pairs of branchiae about same length, slightly more than half the body width. Prostomium with lateral lobes. Without lateral lobes on anterior segments, but midventral lobe on segment 1 present. 25–26 thoracic segments. One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Ten pairs of genital papillae on segments 6–15, originating from anteriorly bases of corresponding notopodia and aligned to them. Notochaetae with bulbous wings in the middle of longer chaetae, distally serrated. Neuropodia from segment 5, double rows of uncini from segment 11 almost to end of body. Pygidium with crenulated margin.

Description of holotype. Large species, complete specimen 60 mm long, 5 mm wide, for about 120 segments. Anterior part of body not distinctly swollen.

Body surface of dorsal and ventral sides throughout different from each other. Ventral side with glandular structure, well stained with methylene blue; true ventral shields, i.e. clearly separated from the lateral sides by furrows, from segments 3 or 4–14; last ventral shields are slightly longer (anterior-posterior axis), but narrower; mid-ventral groove begins after segments with ventral shields, initially shallow (Fig. 2C). Dorsal side papillose; papillae arranged in more or less distinct rows, in single row up to about segments 4–5, 2 rows on segments 6–7, 3 rows on segments 8–13, and 4–5 rows thereafter; rows of papillae continuing through abdomen, segments appearing secondarily annulated as a result (Fig. 2A, B, D).

Prostomium at base of upper lip; basal part without eyespots; distal part forming shelf-like tentacular membrane with lateral lobes and numerous filiform and deeply grooved, ciliated buccal tentacles (Fig. 2A–C).

Peristomium well developed, with conspicuous hood-like upper lip, with corrugated anterior margin, upwards curved; lower lip swollen, pharyngeal organ visible (Fig. 2C).

Segment 1 dorsally narrow, conspicuous developed ventrally, forming a mid-ventral lobe, with swollen flanges ventrolaterally, anterior margin concave and corrugated. Segments 2 and 3 without any lobes (Fig. 2B–C).

Two pairs of arborescent branchiae on segments 2 and 3 with short stem and wide medial gap; first and second pairs of branchiae about same length, slightly more than half body width; branchiae about 3–4 mm long; main stem thick, with irregular dichotomous branching; branches start shortly above the base and terminate by short filaments (Fig. 2A–C).

Notopodia starting from segment 4 and extending for 22 (left body side) and 23 (right body side) segments, i.e. up to segments 25 and 26; first pair same size as following ones, but more dorsally arranged; from second pair of notopodia, all laterally aligned; notopodia short, rectangular to conical; notopodia and neuropodia clearly separated (Fig. 2B). Notochaetae indistinctly arranged in two or more rows, chaetae of first row shorter; limiation indistinctly or absent basally; bulbous wings in the middle of longer chaetae present; tips serrated, base of serrated tip distinctly wider; no difference observed between notochaetae of anterior and posterior thoracic segments (Fig. 11F–G, R).

Neuropodia beginning from segment 5; thoracic and abdominal neuropodia as long lateral ridges distinctly raised from body surface, almost reaching the ventral shields on thorax, reaching the ventral groove on the abdomen (Fig. 2B–D). Uncini arranged in double rows, in face-to-face arrangement, from segment 11 almost to end of body, only last 12 segments with single rows; rows completely separated from each other. Fully developed avicular uncini, 37–45 µm wide and 48–56 µm high; short triangular or rounded heel, distally pointed prow downwardly directed; barely visible dorsal button inserted halfway between base of main fang and tip of prow, dorsal button sometimes absent; convex base; uncini with 3–4 more or less distinct rows of apical teeth above main fang, with about 2–3 on first, 3–6 on second and more than 10 teeth on rows 3 and 4; dental formula MF: 2–3: 3–6: >10 (>10); thoracic and abdominal uncini similar (Fig. 11H–J).

One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Ten pairs of tubular genital papillae on segments 6–15, originating anterior to base of the notopodia and aligned with them; genital papillae distinctly shorter than corresponding notopodial lobe, last 2–3 papillae shorter than previous ones (Fig. 2E–F).

Pygidium terminal, margin crenulated (Fig. 2D).
**FIGURE 2.** Amphi"tritis jirkovi sp. nov. A. Anterior end, dorsal view. B. Anterior end, lateral view. C. Anterior end, ventral view. D. Posterior end, dorsolateral view. E. Segments 3 to 10, lateral view, Shirlastain-A staining (note: nephridial and genital papillae). F. Genital papillae on segments 8 to 10, Shirlastain-A staining. Scale bars. A–D 1 mm, E, F 500 μm. Abbreviations: gp genital papillae, ll lower lip, np nephridial papilla, po pharyngeal organ, ul upper lip, numbers refer to segments.
**Remarks.** *Amphitritides jirkovi* sp. nov. differs from *A. namibiensis* sp. nov. and *A. skeletonensis* sp. nov. (see below) by the presence of distinctly shorter branchiae, the larger number of genital papillae (10 pairs vs 3 pairs), and double rows of uncini on most abdominal segments, which are completely absent on abdominal segments in *A. namibiensis* sp. nov. and which are present only on the first 6–7 abdominal segments in *A. skeletonensis* sp. nov. The number of thoracic segments also differs in these 3 species (see Table 1).

### Table 1. Diagnostic characters of three newly described *Amphitritides* species off Namibia, SW Africa.

<table>
<thead>
<tr>
<th></th>
<th><em>A. jirkovi</em> sp. nov.</th>
<th><em>A. namibiensis</em> sp. nov.</th>
<th><em>A. skeletonensis</em> sp. nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of first branchiae</td>
<td>more than half the body width</td>
<td>longer than body width</td>
<td>longer than body width</td>
</tr>
<tr>
<td>Number of thoracic chaetigers</td>
<td>22 – 23</td>
<td>usually 21 (16 – 21)</td>
<td>25 – 27 (rarely 28)</td>
</tr>
<tr>
<td>Number of thoracic segments</td>
<td>25 – 26</td>
<td>usually 24 (19 – 24)</td>
<td>28 – 30 (rarely 31)</td>
</tr>
<tr>
<td>Position of genital papillae</td>
<td>segments 6 – 15</td>
<td>segments 6 – 8</td>
<td>segments 6 – 8</td>
</tr>
<tr>
<td>Double row of uncini</td>
<td>almost up to end of abdomen</td>
<td>up to end of thorax</td>
<td>up to 6. or 7. (rarely 4. or 5.) abdominal segment</td>
</tr>
<tr>
<td>Anterior abdominal segments with papillae-like structure above neuropodia</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
</tbody>
</table>

*Amphitritides jirkovi* sp. nov. 60 mm in length, is among the seven largest *Amphitritides* species known worldwide, including *A. namibiensis* sp. nov. and *A. skeletonensis* sp. nov. described in this paper. The three remaining species are about 20 mm long. These larger species include *A. bruneocoma* (Ehlers, 1887) (84 mm long), *A. carawa* Nogueira & Hutchings, 2007 (41 mm long), *A. gracilis* (Grube, 1860) (120 mm long) and *A. kuehlmanni* Arvanitidis & Koukouras, 1995 (50 mm long). Of these larger species *A. bruneocoma* has more pairs of notopodia than *A. jirkovi* sp. nov. (27 vs. 22 or 23) and also significantly more genital papillae (15 vs. 10); in addition, the bases of notochaetae are narrow and not swollen, and the uncini in the double rows are partially intercalating. *Amphitritides carawa* is distinctly smaller, and has also more genital papillae (14 pairs); in addition, the first pair of branchiae is twice as long as the second pair. *Amphitritides gracilis* is twice as long as *A. jirkovi* sp. nov. but has fewer pairs of notopodia (17–21 pairs) and genital papillae (8 pairs); genital papillae are located between parapodial lobes, instead of being at the anterior base of notopodia as found in *A. jirkovi* sp. nov. *Amphitritides kuehlmanni* is somewhat smaller, but has considerably more segments (177 segments); this species also has 12 pairs of genital papillae, and the first pair of branchia is also larger than the second.

There are also no species in the genus *Amphitrite* and *Paramphitrite* to which the characters of *A. jirkovi* sp. nov. apply, i.e. the number of branchiae and genital papillae, as well as segments with notopodia and uncini in double rows (see Jirkov 2020).

Since only one specimen was available, no SEM-photos could be made.

**Etymology.** This species is dedicated to Igor A. Jirkov, for his great contribution to polychaete taxonomy especially the Terebellidae.

**Distribution.** Only known from the type locality. We found this specimen at a shallow water station (26 m depth) in front of the mouth of the Kunene River.

**Habitat.** The salinity of the bottom water was 35.7 psu and the oxygen content was 54 µmol/l. Bottom water temperature was 17.8 °C. No information is available on the sediment conditions and the tube shape.

*Amphitritides namibiensis* sp. nov. (Figs 3–7, 11A–E, P)

**Material examined.** Holotype. Off Namibia: 20.013°S 12.984°E, depth 44 m, 30.08.2011, complete specimen (ZSR-O-P2675). Paratypes. Off Namibia: 20.013°S 12.984°E, depth 44 m, 30.08.2011, 47 specimens (ZSR-O-P2676); 20.010°S 13.004°E, depth 33 m, 27.08.2011, about 80 specimens (ZSR-O-P2677); 20.022°S 12.969°E, depth 56 m, 30.08.2011, 4 specimens (SMF 329075); 19.998°S 13.010°E, depth 30 m, 27.08.2011, 10 specimens (SMF
32976); 20.003°S 12.971°E, depth 41 m, 04.11.2016, 15 specimens (ZSrO-P2678); 20.000°S 12.999°E, depth 33 m; 10.05.2019, 5 specimens (ZSrO-P2679). **Additional material.** Off Namibia: 20.013°S 12.984°E, depth 44 m, 30.08.2011, about 50 specimens (ZSrO-P2680); 20.010°S 13.004°E, depth 33 m, 27.08.2011, 5 specimens (ZSrO-P2681); 17.267°S 11.724°E, depth 31.5 m, 04.03.2008, 1 specimen (ZSrO-P2684); 17.2671°S 11.7241°E, depth 33 m, 31.08.2019, 1 specimen (ZSrO-P2685); 19.0000°S 12.4483°E, depth 26 m, 23.01.2022, 1 specimen (ZSrO-P2686).

**Diagnosis.** Two pairs of stalked arborescent branchiae; first pair distinctly longer than second pair, often longer than body width. Without distinct lateral lobes on anterior segments, but midventral lobe on segment 1 present. Twenty-four thoracic segments. One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Three pairs of genital papillae on segments 6 to 8, located anteriorly to base of the corresponding notopodia and aligned with them. Notochaetae with bulbous wings in the middle of longer chaetae or basally, distally serrated. Neuropodia from segment 5, double rows of uncini only on thoracic segments, beginning on segment 11. Anterior abdominal segments with papillae-like structures situated dorsally above the neuropodia. Pygidium with crenulated margin.

**Description.** Large species, complete holotype 63 mm long, 4.1 mm wide for about 105 segments. Paratypes 25–110 mm long, and 1.8–6.4 mm wide, maximum 100–110 segments, but most specimens incomplete. Anterior body not distinctly swollen.

Body surface of the dorsal and ventral side very different from each other, especially on thorax. Ventral side glandular, and well stained with methylene blue, with well-developed ventral shields, i.e., clearly separated from the lateral sides by furrows, on segments 5 to segment 12–14 usually, last ventral shields narrower and shorter; midventral groove usually beginning after few transitional segments, without clearly marked ventral shields. Dorsal side papillose throughout, papillae in more or less distinct rows, up to about segments 4–6 in 2 rows, 3 rows until segment 11, and, from segment 12 onwards 4 rows of papillae; segments secondarily annulated as a result (Figs 3B, C, E; 4A; 5A–F).

Prostomium at base of upper lip; basal part without eyespots; distal part forming shelf-like tentacular membrane from which numerous filiform and deeply grooved, ciliated buccal tentacles originate (Figs 3A–C; 4A–C, F).

Peristomium well developed, with conspicuous hood-like upper lip, trilobate, with corrugated anterior margin, directed anteriorly or upwards curved; lower lip narrow and swollen, often with transverse groove separating the lower lip from the pharyngeal organ, visible posteriorly (Figs 3A, C; 4A–C; 5C).

Segment 1 dorsally narrow, conspicuously developed ventrally, forming mid-ventral lobe below lower lip, anterior margin concave and crenulated (Figs 3A, C; 4A, C). Segments 2 and 3 without any lobes but with small rounded dorsal projections (Figs 3A, E; 4A, C; 5C).

Two pairs of large arborescent branchiae on segments 2 and 3, with wide medial gap; first pair distinctly longer than second pair, usually about twice as long as second pair, often longer than body width; first pair about 6–9 mm (exceptionally 18–20 mm) long; second pair about 2–5 mm (exceptionally 10–12 mm) long, usually shorter than body width; thick main stem, with irregular dichotomous branching; branches end in short branchial filaments (Figs 3A, B, D, E, G; 4A, D).

Notopodia starting from segment 4, usually extending for 21 segments, until segment 24 (n=24 specimens); rarely also for 16 (until segment 19; n=1), 17 (until segment 20; n=1), 18 (until segment 21; n=3) and 19 (until segment 22; n=1) segments; first pair of notopodia same size as following pairs; notopodia short, rectangular to conical; all laterally aligned; notopodia and neuropodia clearly separated (Figs 3A, E; 4A, C; 5A; 6B–D). Notochaetae arranged indistinctly in two or more rows, chaetae of first row shorter; chaetae of each row with symmetrical limbation, bulbous wings in the middle of longer chaetae or basally; longer and shorter chaetae with serrated tips; no difference observed between notochaetae of anterior and posterior thoracic segments (Figs 5A; 6B–D, F; 7A–C; 11A–C, P).

First abdominal segments with papillae-like structures dorsally above neuropodia, visible on first 12–18 (10–25 among paratypes) abdominal segments (Fig. 6B, E).
**Figure 3.** *Amphitritides namibiensis* sp. nov. A. Anterior end, lateral view. B. Anterior end, dorsal view. C. Anterior end, ventral view. D. First and second branchiae, methyl blue staining. E. Anterior end, lateral view (note: nephridial and genital papillae). F. Posterior end, methyl blue staining (note: crenulated pygidium). G. Living individuals. Scale bars. A–E 1 mm, F 500 µm G 20 mm. Abbreviations: br1 branchia of first pair, br2 branchia of second pair, bt buccal tentacles, gp genital papillae, ll lower lip, ne abdominal neuropodia, np nephridial papilla, ul upper lip, numbers refer to segments.
FIGURE 4. Amphitritides namibiensis sp. nov. SEM micrographs. A. Anterior end, lateral view. B. Anterior end of a small specimen, frontal view. C. Anterior end, lateral view. D. Second branchia of a small specimen (note: short stalk and short filaments). E. Segment 3 (note: nephridial papilla). F. Buccal tentacles. Scale bars: A 1 mm, B, C 500 µm, D 200 µm, E 100 µm, F 50 µm. Abbreviations: br branchia, br1 branchia of first pair, br2 branchia of second pair, bt buccal tentacles, ch1 chaetiger 1 (=segment 4), ci ciliated groove, gp genital papillae, ll lower lip, np nephridial papilla, ul upper lip, numbers refer to segments.
Figure 5. Amphitritides namibiensis sp. nov. SEM micrographs. A. Segments 7–14, lateral view (arrows: start of secondary annulation on segment 13 or 14). B. Segments 12–14, dorsolateral view (arrows: start of secondary annulation on segment 13 or 14). C. Anterior end, ventral view. D. Pore openings on the ventral shield of segment 2. E. Abdomen, dorsal view. F. Abdomen, ventral view (note: mid-ventral groove). Scale bars. A, B, F 500 µm, C, E 200 µm, D,10 µm, F 50 µm. Abbreviations: ll lower lip, numbers refer to segments.
Neuropodia beginning from segment 5; thoracic and abdominal neuropodia as long lateral ridges, distinctly raised from body surface, almost reaching ventral shields on thorax, and reaching ventral groove on abdomen (Figs 3A; 4A, C; 5A; 6A); neuropodia of posterior thoracic and anterior abdominal segments slightly thickened at upper margin (Fig. 6B, E). Uncini arranged in double rows, in face-to-face arrangement, from segment 11 until end of thoracic region (usually up to segment 24); rows completely separated from each other (Figs 5A; 6A–E). Avicular uncini, 36–46 µm wide and 28–35 µm high; short triangular or rounded heel, rounded prow, to a great extent upwards directed, short dorsal button inserted closer to prow than to base of main fang, convex base; uncini with 3 more or less distinct rows of apical teeth above main fang, first row with about 2–3 teeth, 2–4 on second row, and 6–10 on third row; dental formula MF: 2–3: 2–4: 6–10; thoracic and abdominal uncini all similar, the latter slightly narrower (Figs 7D; E; 11D, E).


One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Three pairs of tubular genital papillae on segments 6–8, present anterior to base of corresponding notopodia and aligned with them; all genital papillae of same size, and much longer than corresponding notopodia (Figs 3A, E; 4A, C, E).

Pygidium terminal, margin crenulated (Fig. 3F).

Live individuals purple in colour, with red-orange branchiae; pale after preservation (Fig. 3A–C, E–G).

No specimen with gametes observed.

**Remarks.** *Amphitritides namibiensis* sp. nov. differs from the seven already known *Amphitritides* species (Read & Fauchald 2024a) and the two species described in this paper (see Table 1) by the combination of the following...
characters: number of thoracic segments, complete absence of uncini in double rows on abdominal segments and number of genital papillae (see Arvanitidis & Koukouras 1995; Nogueira & Hutchings 2007). There is only one other species within this genus that lacks double rows of uncini on abdominal segments, A. pectinobranchiata Hartmann-Schröder, 1965, which Arvanitidis & Koukouras (1995) suggested should be transferred to Paramphitrite. All species of Paramphitrite have lateral lobes on the first anterior segments, particularly on segment 2, segment 1 is reduced dorsally, and the branchiae are much shorter than body width, mainly due to the lack of a distinct stem (Day 1963, Holthe 1976, Hutchings et al. 2021b, Jirkov 2020, Lavesque et al. 2021). Apart from a small midventral lobe on segment 1, A. namibiensis sp. nov. has no lobes on the anterior segments, segment 1 is not reduced dorsally, and the branchiae are rather long, with a well-developed stem. Amphitritides namibiensis sp. nov. also differs from A. pectinobranchiata in the number of thoracic segments (A. namibiensis sp. nov. with usually 24 and A. pectinobranchiata with 20 segments), the number of pairs of notopodia with notochaetae (A. namibiensis sp. nov. with usually 21 and A. pectinobranchiata with 13 pairs) and in the size of sexually mature individuals (A. namibiensis sp. nov. 110 mm long and A. pectinobranchiata 33 mm long). In these three characters A. namibiensis sp. nov. also differs clearly from all three accepted Paramphitrite species (see Day 1963, Holthe 1976, Jirkov 2020, Lavesque et al. 2021). There are also no other species in the genus Amphitrite to which the above characters apply (see Jirkov 2020).

Moreover, within the genera mentioned above, there is no species that has papillae-like structures situated dorsally above the neuropodia of the first abdominal segments. These papillae could represent reduced notopodia.

There are only minor differences between large (width 5–6 mm) and small (width 2 mm) individuals. The uncini in small immature specimens are smaller in general (18–22 µm high, 28–30 µm wide), especially shorter than those in larger mature individuals. In contrast, the genital papillae are clearly visible even in the smallest immature individuals.

**Etymology.** The specific epithet namibiensis is named after the type locality off Namibia.

**Distribution.** Only known from the northern part of Namibia (Kunene region) between 17° and 20°S in water depths between 26 and 56 m.

**Habitat.** The salinity was marine (35.1–35.7 psu). Depending on the season, the bottom water temperature fluctuated between 12.4 and 17.8 °C, and the oxygen content of the bottom water was very low to low and varied between 3.74 and 174 µmol/l. The mean grain size of the sediments was between 35 and 103 µm, while the organic content was between 1 and 10 %.

**Amphitritides skeletonensis** sp. nov.
(Figs 8–10; 11K–O, S)

**Material examined.** Holotype. Off Namibia: 18.000°S 11.650°E, depth 125 m, 30.08.2019, complete specimen (ZSrO-P2689). Paratypes. Off Namibia: 18.000°S 11.650°E, depth 125 m, 30.08.2019, 1 specimen (ZSrO-P2690; 22.499°S 13.533°E, depth 156 m, 18.09.2011, 1 specimen (ZSrO-P2691); 20.2225°S 12.6288°E, depth 154 m, 24.08.2011, 2 specimens (SMF 32973); 20.175°S 12.710°E, depth 133 m, 24.08.2011, 4 specimens (ZSrO-P2692), 1 specimen (SMF 32974); 20.079°S 12.872°E, depth 101 m, 06.09.2011, 1 specimen (ZSrO-P2693). Additional material. 25.0000°S 13.9168°E, depth 187 m, 07.09.2019, 3 specimens (ZSrO-P2694).

**Diagnosis.** Two pairs of stalked arborescent branchiae; first pair distinctly longer than second pair, often longer than body width. Without distinct lateral lobes on anterior segments, but midventral lobe on segment 1 present. Thorax with 28–31 segments. One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Three pairs of genital papillae on segments 6–8, occurring at the anterior base of the corresponding notopodia and aligned with them. Notochaetae distally serrated. Neuropodia from segment 5, double rows of uncini on thoracic and first 6–7 abdominal segments, beginning on segment 11. Pygidium with crenulated margin.

**Description.** Large species, complete holotype 60 mm long, 6 mm wide, for 71 segments. Paratypes between 8 mm and 75 mm long, and 1.5 mm and 12 mm wide. Maximum 60–75 segments, but most individuals are incomplete. Anterior body usually distinctly swollen (Fig. 8A, D).
Figure 8. *Amphitritides skeletonensis* sp. nov. methyl blue staining. A. Anterior end, lateral view. B. Anterior end, dorsal view. C. Anterior end, ventral view. D. Anterior end, ventrolateral view. E. Posterior end, lateral view. F. Segments 3–6, lateral view (note: nephridial and genital papillae). Scale bars. A 1 mm, B–E 2 mm, F 500 μm. Abbreviations: br1 branchia of first pair, br2 branchia of second pair, bt buccal tentacles gp genital papillae, np nephridial papilla, vs ventral shield.
Body surface of dorsal and ventral sides very different from each other, especially on thorax. Ventral side with glandular structure, well stained with methylene blue; well-developed ventral shields, i.e., clearly separated from the lateral sides by furrows, from segments 5 to segment 14–15 usually; last shields may be narrower and shorter; mid-ventral groove usually begins immediately after last ventral shield (Fig. 8C, D). Dorsal side papillose; papillae arranged in more or less distinct rows, up to about segments 8–12 in 2 rows, thereafter 3 and later 4 rows of papillae per segment, segments appearing secondarily annulated as a result (Figs 8A, B, E; 9A, B).

Prostomium at base of upper lip; basal part without eyespots; distal part forming shelf-like tentacular membrane from which numerous filiform and deeply grooved, ciliated buccal tentacles originate (Figs 8B, C; 9A).

Peristomium well developed, with conspicuous hood-like upper lip, sometimes trilobate, with corrugated anterior margin, directed anteriorly; lower lip narrow and swollen; pharyngeal organ often visible (Figs 8C; 9A).

Segment 1 dorsally narrow, conspicuously developed ventrally, forming mid-ventral lobe below lower lip; anterior margin concave and corrugated; lobe as long as lower lip or shorter (Figs 8A, C, D; 9A, B). Segments 2 and 3 without any lobes (Figs 8A; 9A, B).

Two pairs of large arborescent branchiae on segments 2 and 3; first pair distinctly longer than second pair, usually about 2–4 times as long as second pair, often even longer than body width; first pair about 5–10 mm (exceptionally 14–16 mm) long; second pair always shorter than body width, about 2–4 mm long; main stems short and thick, irregularly branching dichotomously, with short branchial filaments terminally (Figs 8A–D; 9A, B).

Notopodia starting from segment 4 and extending usually for 25–27 segments, i.e. up to segment 28–30 (n=15 specimens), rarely also for 28 (up to segment 31; n=1 specimen) segments; first pair of notopodia smaller than following pairs; notopodia short, rectangular to conical; all notopodia laterally aligned; notopodia and neuropodia clearly separated (Figs 8D; 9A–C). Notochaetae indistinctly arranged in two or more rows; chaetae of both rows with symmetrical limbation and serrated tips, base of serrated tip distinctly wider; chaetae of first row shorter, serrated tip forms a distinct angle to the shaft; chaetae of second row longer, without angle to the shaft; bulbous wings in the middle of longer chaetae poorly developed; notochaetae of anterior and posterior thoracic segments all similar (Figs 9E; 10A–G; 11K–M, S).

Neuropodia beginning from segment 5; thoracic and abdominal neuropodia as long lateral ridges, distinctly raised from body surface, almost reaching ventral shields on thorax, reaching ventral groove on abdomen (Figs 8A, C–E; 9A, B). Uncini arranged in double rows, in face-to-face arrangement, from segment 11 until abdominal segment 6 (n=4 specimens) or 7 (n=6 specimens) usually, sometimes up to abdominal segment 4 (n=1 specimen) or 5 (n=1 specimen); rows completely separated from each other (Figs 9F, 11N). Avicular uncini; thoracic uncini 50–58 µm wide and 38–47 µm high, abdominal uncini 45–50 µm wide and 34–40 µm high; triangular heel, distally pointed prow downwardly directed, pointed dorsal button inserted closer to prow than to base of main fang, convex base; thoracic uncini with 3–4 distinct rows of apical teeth above main fang, about 2–4 teeth on first row, 2–4 on second and 4–5 teeth on third and four row; dental formula MF: 2–4: 2–4: 4–5: 4–5; abdominal uncini with 2–3 rows above main fang, 2–3 teeth on first and 3–5 on second and third row; dental formula MF: 2–3: 3–5: 3–5 (Figs 10H, I; 11N–O).

One pair of nephridial papillae on segment 3, inserted laterally and close to branchial stalk. Three pairs of tubular genital papillae on segments 6–8, originating at anteriorly base of the corresponding notopodia and aligned to them; all genital papillae of same size, clearly exceeding corresponding notopodia (Figs 8F; 9C, D).

Pygidium terminal, margin crenulated (Fig. 8E).

The specimens pale after preservation.

No specimen with gametes observed.

**Remarks.** *Amphitritides skeletonensis* sp. nov. most closely resembles *A. namibiensis* sp. nov. described above (see Table 1). Both species have very long branchiae and 3 pairs of distinct genital papillae at the anterior base of notopodia of segments 6–8. However, they clearly differ in the number of thoracic segments (*A. skeletonensis* sp. nov. with 28–31 and *A. namibiensis* sp. nov. with 24 segments), and the absence (*A. namibiensis* sp. nov.) or occurrence (*A. skeletonensis* sp. nov.) of double rows of uncini on the first abdominal segments. The uncini of *A. skeletonensis* sp. nov. are clearly larger than those in *A. namibiensis* sp. nov. and the thorax in *A. skeletonensis* sp. nov. is always clearly swollen, contrarily to *A. namibiensis* sp. nov.

*Amphitritides skeletonensis* sp. nov. differs from *A. jirkovi* sp. nov. mainly in that *A. jirkovi* sp. nov. has ten pairs of genital papillae, whereas *A. skeletonensis* sp. nov. has three pairs. In addition, *A. jirkovi* sp. nov. has neuropodia with double rows of uncini on all abdominal segments, whereas *A. skeletonensis* sp. nov. has only double rows on the anterior 4–7 abdominal segments (see Table 1).
Within the genera Amphitritides, Amphitrite (including Neoamphitrite) and Paramphitrite no species has 2 pairs of branchiae, 3 pairs of genital papillae and 28–31 thoracic segments. Amphitritides bruneocomata and A. kuehlmani, with a similar number of thoracic segments, also have 2 pairs of branchiae, but significantly more segments with genital papillae. Amphitritides bruneocomata has 15 and A. kuehlmani 11–13 pairs of genital papillae. In addition, both species have double rows of uncini on almost all abdominal segments. All other species of these 3 genera with a similar number of segments always have 3 pairs of branchiae and significantly more genital papillae.

There are only minor differences between large (width 8–12 mm) and small (width 2–4 mm) individuals. Thus, the uncini in small specimens are smaller in general (24–28 µm high, 31–60 µm wide). As in A. namibiensis sp. nov. genital papillae are always visible, even in the smallest specimens which are presumably juveniles.

**Etymology.** The specific epithet skeletonensis is derived from the northern part of coast of Namibia, the Skeleton Coast (type locality).

**Distribution.** Although this species is not common, it had the widest distribution of all three species, described from Namibia, occurring between 18°–25°S, in water depths between 101–187m.

**Habitat.** Bottom water salinity between 34.9–35.5 psu, oxygen content between 4–112 µmol/l. Bottom water temperature was between 11–13 °C. The sediments were silty mud with grain sizes ranging from 20–150 µm. The organic content varied between 4–26 %. No information is available on the shape of the tubes.

Two more specimens of Amphitritides were found, which clearly differ in important diagnostic features from the species described above and those already known. These two individuals also differ from each other. However, their poor conservation status prevents us from formally describing these species until better preserved material becomes available.

### Identification key to described species of Amphitritides

(Type locality in brackets)

1A. Double rows of uncini only on thoracic neuropodia ......................................................... 2
1B. Double rows of uncini on some anterior or most abdominal neuropodia ............................ 3

2A. 13 pairs of notopodia (Chile) ................................................. *A. pectinobranchiata* Hartmann-Schröder, 1965
2B. Usually 21 pairs of notopodia (Namibia) ............................................................... *A. namibiensis* sp. nov.

3A. Double rows of uncini only on some anterior abdominal neuropodia (Namibia) .............. *A. skeletonensis* sp. nov.
3B. Double rows of uncini on most abdominal neuropodia ................................................ 4

4A. Notopodia extending until posterior body (Australia, Queensland) .......................... *A. harpa* Hutchings & Glasby, 1988
4B. Notopodia only on thoracic segments ............................................................................. 5

5A. 27 pairs of notopodia; 15 pairs of genital papillae on segments 6–20 (USA, Florida) ....... *A. bruneocomata* (Ehlers, 1887)
5B. Number of notopodia and genital papillae in other combination ..................................... 6

6A. Very short branchial filaments with rugose tips; 22–26 pairs of notopodia; 11–13 pairs of genital papillae from segment 6 (Greece) ............................................................... *A. kuehlmani* Arvanitidis & Koukouras, 1995
6B. Branchial filaments long, tips filamentous; number of notopodia and genital papillae in other combination ................................................................. 7

7A. Genital papillae between parapodial lobes; 17–21 pairs of notopodia; 8 pairs of genital papillae on segments 6–13 (Great Britain) ................................................. *A. gracilis* (Grube, 1860)
7B. Genital papillae at anterior base of notopodia and aligned to them .................................. 8

8A. 22–23 pairs of notopodia; 10 pairs of genital papillae on segments 6–15 (Namibia) ........ *A. jirkovi* sp. nov.
8B. Number of notopodia and genital papillae in other combination ..................................... 9

9A. Small species with 18–20 pairs of notopodia and 9 pairs of genital papillae (Australia, Queensland) ............................................................. *A. ithya* Hutchings & Glasby, 1988
9B. Median-sized species with 19–22 pairs of notopodia and 14 pairs of genital papillae (Australia, NS Wales) ....................................................... *A. carawa* Nogueira & Hutchings, 2007

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**AMPHITRITIDES OF NAMIBIA**
Discussion

With the three species described here, 10 species of *Amphitritides* are now known worldwide. Table 1 shows some important diagnostic characters of the new species described in this paper. However, the separation of this genus from the similar currently recognized genera is not entirely clear, which is why the assignment of some species and the synonymisation of *Amphitritides* with *Amphitrite* have been debated repeatedly (Arvanitidis & Koukouras 1995, Jirkov 2020, Lavesque et al. 2021). One of the most important diagnostic characters of *Amphitritides* is the presence of double rows of uncini from segment 11 onwards (Hutchings et al. 2021b, Lavesque et al. 2021). This is true here only for *A. jirkovi* sp. nov. as double rows of uncini occur only on the anterior abdominal segments in *A. skeletonensis* sp. nov., while in *A. namibiensis* sp. nov. they terminate at the end of thorax. However, in *A. pectinobranchiata* the double rows of uncini are also restricted to the thorax, and *Amphitrite rubra* and *Amphitrite vigilintipes* have these double rows on most of abdominal neuropodia (Jirkov 2020). This character is not very helpful in every case to separate species of both genera with certainty. Another character that should separate species of the genera *Amphitrite* and *Amphitritides* is the presence or absence of lateral lobes on first thoracic segments. In the species described here these lobes are not present, however it must be verified if this is a useful character. The significance of this character has also been discussed by Jirkov (2020). However, a revision of these two genera and also *Neoamphitrite* and *Paramphitrite* is outside the scope of this study.

Because differences in the expression of characters often occur in juvenile and adult specimens within a species, we also looked for them in the species described with large and small individuals. There were indeed differences in the appearance of the upper lip, and sizes of the branchiae and uncini in *A. namibiensis* sp. nov. and *A. skeletonensis* sp. nov. between small and large specimens; in small specimens the upper lip is not folded and trilobed, and branchiae and uncini are generally smaller, but the uncini are similar to those of adults. Genital papillae are also already fully developed in small individuals of both species.

Although a sympatric occurrence of *A. namibiensis* sp. nov. and *A. jirkovi* sp. nov. would be possible in terms of water depth and geographical distribution, as both are rather shallow water species (< 56 m depth) in northern Namibia, they were not found together. *Amphitritides skeletonensis* sp. nov. occurred in deeper waters and was never found at depths shallower than 100 m depth. Apart from temperature (due to the greater water depths), the other abiotic parameters such as salinity, sediment grain size and organic content were similar to the habitats of both species, although there is a remarkable difference on the number of individuals found: *A. namibiensis* sp. nov. is by far the most common species, with more than 220 specimens (maximum density 420 ind./m²), only 16 individuals of *A. skeletonensis* sp. nov. were found, usually with 1–2 individuals per sample, and a single specimen of *A. jirkovi* sp. nov. was gathered. However, the occurrence of three *Amphitritides* species in a relatively small region is also noteworthy. This study seems to confirm the thesis that temperate southern Africa is still under-represented in the study of polychaete diversity (Hutchings et al. 2021a). However, these investigations should follow an integrated approach that includes both morphological and molecular analyses.

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