

A review of extant *Tudivasum* Rosenberg & Petit, 1987 (Neogastropoda: Turbinellidae) and description of three new species from Western Australia

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ABSTRACT

Tudivasum Rosenberg & Petit, 1987 is a morphologically distinct gastropod genus of low diversity. All but one species are known from Australia and they occur from the intertidal zone down to hundreds of metres on the continental shelf. These carnivorous gastropods are thought to have intracapsular development. The six currently recognized extant species are reviewed here and their geographical ranges clarified. Two new species, *Tudivasum chaneyi* n. sp. and *T. ashmorense* n. sp., are described from Ashmore Reef, Western Australia, and are characterized by differences in protoconch colour and shell sculpture. The third new species, *T. westrale* n. sp., is described from the mid-west coast of Western Australia, where it has long been misidentified as *T. spinosum* (H. Adams & A. Adams, 1864). We generated a molecular phylogeny based on mitochondrial DNA sequence data to test morphological species concepts and reconstruct relationships among four of the described species. High levels of divergence within one of the new species could indicate an additional cryptic species.

INTRODUCTION

The genus *Tudivasum* is a member of the Turbinellidae Swainson, 1835, a neogastropod family comprised of four extant subfamilies: Columbariinae, Turbinellinae, Vasinae and Tudiclinae (MolluscaBase, 2017; although see Harasewych, 2011 for reasons to exclude Tudiclinae). The genus *Tudivasum*, formerly *Tudicula* (H. Adams & A. Adams, 1864), consists of six Recent species: *Tudivasum armigerum* (A. Adams, 1856), *T. inerme* (Angas, 1878), *T. spinosum* (H. & A. Adams, 1864), *T. zanzibaricum* (Abbott, 1958), *T. rasilistoma* (Abbott, 1959) and *T. kurtzi* (Macpherson, 1964). Recent *Tudivasum* are characterized by shells of medium size that are pyriform or fusiform shaped and generally low spired. The last adult whorl is most often globose or rounded with a prominent keel, with or without spines. Except for *T. zanzibaricum*, all species are variable in both shell size and sculpture, often leading to confusion among species.

Current understanding of the evolutionary history of *Tudivasum* is poor. Despite much recent work on the evolution of Neogastropoda (e.g. Cunha, Grande & Zardoya, 2009; Couto *et al.*, 2016 for Fascioliidae; Modica *et al.*, 2011 for Cancellariidae; and Fedosov *et al.*, 2018 for Mitridae), as well as recent work on Tonnoidea (Strong *et al.*, 2019), there are also no existing phylogenies examining the relationships among extant *Tudivasum* species. Furthermore, while it is well established that turbinellids have a fossil record extending back to the Palaeocene (e.g. Columbariinae from the Wangaloan of New Zealand; Harasewych, 2011) and the genus *Vasum* in the Vasinae subfamily is generally well represented in the fossil record

(e.g. Darragh & Kendrick, 2010), there are no known fossils for *Tudivasum*. Both Abbott (1959) and Wilson (1994) have mentioned a single Pliocene species, *Tudicula sinotecta* Ludbrook, 1941, from South Australia. Rosenberg & Petit (1987) retained this species in *Tudicula* (Röding, 1798), because Ludbrook (1941) described *T. sinotecta* as having one columellar fold, while all other species of *Tudivasum* usually have three and rarely four columellar folds.

Prior to 1987, the name *Tudicula* H. & A. Adams, 1864 had been used for *Tudivasum* (not to be confused with *Tudicula* Röding, 1798). Abbott (1959) was the first to conduct a modern review of *Tudicula* (as part of his larger work on Vasidae), which was then accepted as a family-level taxon. He recognized four species, namely *Tudicula armigera* (A. Adams, 1856), *T. inerme* (Angas, 1878), *T. spinosa* (H. & A. Adams, 1864) and *T. zanzibarica*, and described a fifth, *T. rasilistoma* Abbott, 1959.

Tudicula kurtzi Macpherson, 1964 was later described from off Darwin, Northern Territory, Australia, but the author did not discuss the composition of the genus. The brevity of the original description led Abbott & Dance (1982) to consider *T. kurtzi* as a subspecies of *T. armigera*. Rosenberg & Petit (1987) showed that *Tudicula* was preoccupied and proposed *Tudivasum* as a replacement. They also raised *T. kurtzi* from a subspecies to a species-level taxon. Rosenberg & Petit (1987) referred to an unidentified *Tudivasum* reported from the east coast of Tasmania by Cochran (1986) but made no further comment regarding this isolated specimen. Wilson (1994) was the next to examine the Australian members of the renamed *Tudivasum*. He discussed and illustrated four species

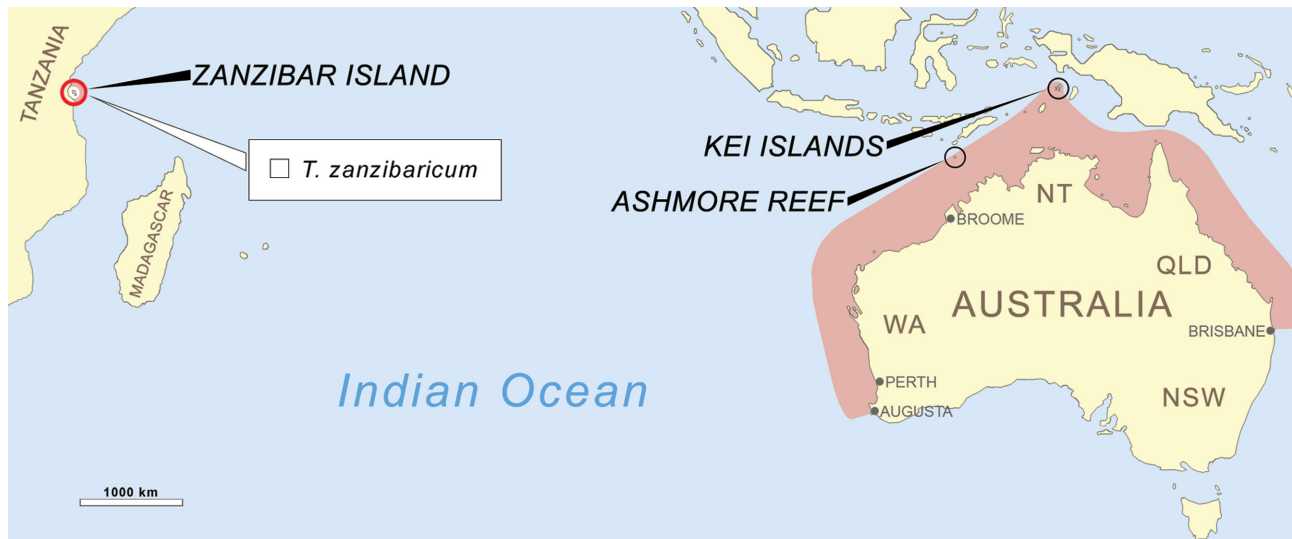


Figure 1. Disjunct distribution of *Tudivasum* in the Indo-West Pacific. Most of the species are found in Australian waters but also extend to Indonesia. The exception to this is *T. zanzibaricum*. Red circle denotes type locality.

(*T. armigerum*, *T. inerme*, *T. rasilistoma* and *T. spinosum*), and noted the existence of the Tasmanian shell, but made no further comments.

Most Recent species of *Tudivasum* are relatively rare and little is known of their preferred habitat. At least two are found in intertidal waters (*T. inerme* and *T. armigerum*), while all others occur at depths ranging from 15 to 250 m along the upper continental shelf. All are associated with coarse sand, in the case of shallow water species, or with sandy mud at bathyal depths. Abbott (1959) stated that all species of *Tudivasum* are carnivorous and Harasewych (1998) reported a possible diet of endobenthic animals, such as tube-dwelling polychaetes, sipunculans and gaping bivalves. As with most neogastropods, turbinellids are gonochoristic, with internal fertilization and the production of some form of egg capsule (Harasewych, 1998).

Recent members of the genus *Tudivasum* are found in the Indo-West Pacific (IWP) and some species have wide distributions, while others are much more restricted. *Tudivasum zanzibaricum*, found exclusively in Zanzibar and Tanzania in the Western Indian Ocean (Fig. 1), is the most isolated species. All of the other currently known species have ranges that are entirely Australian (e.g. *T. rasilistoma*, *T. armigerum* and *T. inerme*), or restricted to the central IWP, including Australia (*T. kurtzi* and *T. spinosum*). The northwest of Western Australia has three of the described species (*T. inerme*, *T. spinosum* and *T. kurtzi*), as does Queensland (*T. armigerum*, *T. spinosum* and *T. rasilistoma*).

This study was initiated to clarify uncertainty in the identity and distribution of species of *Tudivasum* in Western Australia, and to test these concepts with molecular tools. Specifically, the distribution of *T. armigerum* is unclear; Wilson (1994) stated that it was found as far west as Adele Island in Western Australia, but this may have been complicated by the presence of the morphologically similar *T. kurtzi*, which was then unknown from the area. Close examination of the illustrations of *T. spinosum* in Wilson (1994: vol. 2, pl. 8: fig. 9a–c) has revealed two different species, thus highlighting the need for careful study of the Western Australian Museum collections. Our study has also been spurred by the discovery of a new and large species of *Tudivasum* at isolated Ashmore Reef in the far north of Western Australia. Here, we review all taxa, clarifying the current taxonomy and distributions of the genus *Tudivasum*. Three new taxa are described from Western Australia. Morphological species delimitations and phylogenetic relationships among available taxa are assessed using two mitochondrial genes.

MATERIAL AND METHODS

Institutional abbreviations

AIMS	Australian Institute of Marine Science, Townsville, Australia
ANSP	Academy of Natural Sciences, Drexel University, Philadelphia, PA, USA
CSIRO	Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia
HM coll.	Hugh M. Morrison collection, Perth, Australia
LSGB	Laboratory of Shellfish Genetics and Breeding, Fisheries College, Ocean University of China, Qingdao, China
MAGNT	Museum and Art Gallery of the Northern Territory, Darwin, Australia
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, UK
NMV	Museums Victoria, Melbourne, Australia
PRI	Paleontological Research Institute, Ithaca, NY, USA
QM	Queensland Museum, Brisbane, Australia
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, CA, USA
WAM	Western Australian Museum, Welshpool, Australia

Morphological taxonomy

Most material examined was from the WAM collection, with additional material and types examined from the NHMUK, MNHN, SBMNH, MAGNT and NMV as well as private collections. The following shell measurements were taken for adult shells (i.e. with developed parietal shield, unless otherwise noted), using a precision digital calliper to two decimal points: shell height (*H*), maximum length of shell from apex to tip of anterior canal, and shell width (*W*), maximum width of body whorl of teleoconch, excluding any spines and perpendicular to *H*. The protoconch was measured using a standard binocular microscope at 16× magnification; we measured the maximum diameter before the protoconch–teleoconch boundary. Mean and standard deviations for these measurements were calculated in Excel, based on specimens that reside in state and private collections. The raw data are available from the authors on request. Scanning electron microscopy was carried out by D. Geiger using standard protocols, including

Table 1. Specimens of *Tudivasum* and *Vasum* used in the phylogenetic analysis, with relevant collection data, registration and GenBank accession numbers.

Species	Museum/collection registration no.	Locality	Depth (m)	GenBank acc. no.	
				COI	16S rRNA
<i>T. armigerum</i>	QM SBD004318_1	Great Barrier Reef, QLD	59	MF782558	–
<i>T. armigerum</i>	QM SBD004318_2	Great Barrier Reef, QLD	59	MF782559	MF782589
<i>T. armigerum</i>	QM SBD006804_1	Great Barrier Reef, QLD	20	MF782563	MF782594
<i>T. armigerum</i>	QM SBD020459_1	Great Barrier Reef, QLD	66	MF782560	MF782590
<i>T. armigerum</i>	QM SBD020459_2	Great Barrier Reef, QLD	66	MF782562	MF782591
<i>T. armigerum</i>	QM SBD022930	Great Barrier Reef, QLD	56	–	MF782593
<i>T. armigerum</i>	QM SBD023231_1	Great Barrier Reef, QLD	52	MF782561	MF782592
<i>T. armigerum</i>	QM SBD002198A	Great Barrier Reef, QLD	–	MF782556	MF782587
<i>T. armigerum</i>	QM SBD002198B	Great Barrier Reef, QLD	–	MF782557	MF782588
<i>T. inerme</i>	WAMS90821	Exmouth Gulf/Muiron Islands, WA	17	MF782581	MF782611
<i>T. inerme</i>	WAMS90850	Exmouth Gulf/Muiron Islands, WA	18	MF782582	MF782615
<i>T. inerme</i>	WAMS90867	SE Barrow Islands, WA	100	MF782586	MF782612
<i>T. inerme</i>	WAMS99026	Point Cloates, WA	100	MF782583	MF782613
<i>T. inerme</i>	WAMS99027	Point Cloates, WA	100	MF782584	MF782616
<i>T. inerme</i>	WAMS99028	Point Cloates, WA	100	MF782585	MF782614
<i>T. spinosum</i>	WAMS11610	Ningaloo, WA	165	MF782576	MF782606
<i>T. spinosum</i>	WAMS99030	Ningaloo, WA	106	MF782579	MF782609
<i>T. spinosum</i>	WAMS99031	Ningaloo, WA	106	MF782580	MF782610
<i>T. spinosum</i>	WAMS99037	Muiron Islands, WA	55	MF782577	MF782607
<i>T. spinosum</i>	WAMS99038	Muiron Islands, WA	55	MF782578	MF782608
<i>T. westrale</i> n. sp.	WAMS99023	Point Cloates, WA	100	MF782569	MF782605
<i>T. westrale</i> n. sp.	WAMS99024	Point Cloates, WA	100	MF782571	MF782599
<i>T. westrale</i> n. sp.	WAMS99025	Point Cloates, WA	100	MF782570	MF782596
<i>T. westrale</i> n. sp.	WAMS11607	Ningaloo, WA	202	MF782564	MF782595
<i>T. westrale</i> n. sp.	WAMS11608	Ningaloo, WA	105	MF782566	MF782604
<i>T. westrale</i> n. sp.	WAMS43233	Marmion Marine Park, WA	150	MF782575	–
<i>T. westrale</i> n. sp.	WAMS43708	Ningaloo, WA	113	MF782565	MF782597
<i>T. westrale</i> n. sp. holotype	WAMS99033	Ningaloo, WA	102	MF782573	MF782603
<i>T. westrale</i> n. sp.	WAMS99034	Ningaloo, WA	100	MF782568	MF782598
<i>T. westrale</i> n. sp.	WAMS99035	Ningaloo, WA	100	MF782572	MF782600
<i>T. westrale</i> n. sp.	WAMS99036	Ningaloo, WA	100	MF782574	MF782601
<i>T. westrale</i> n. sp.	WAMS99250	Ningaloo, WA	40	MF782567	MF782602
<i>V. turbinellus</i>	LSGB23801	China	–	HQ834084	HQ833957
<i>V. globulus</i>	MNHN-IM-2013-8329	Guadeloupe	–	KU986430	KU873939
<i>V. muricatum</i>	MNHN-IM-2013-20017	Guadeloupe	–	KU986431	KU873940

sonication in a mild detergent and mounting on double-sided carbon adhesives.

Listed synonymies include only those references that have discussed the species; references to illustrations or checklists have been excluded. The exception to this is *Tudivasum kurtzi*, which has been illustrated but not described. Three species new to science are described in this work (*T. ashmorense* n. sp., *T. chaneyi* n. sp. and *T. westrale* n. sp.); these are attributed to Morrison in Morrison, Kirkendale and Wilson.

Molecular systematics

Our molecular phylogenetic analyses included four morphologically defined species of *Tudivasum*, *T. armigerum*, *T. inerme*, *T. spinosum* and *T. westrale* n. sp.; tissue samples of the other *Tudivasum* species examined in this paper could not be obtained. Details of specimens sampled are provided in Table 1. DNA was extracted from tissue clips using a DNeasy Blood & Tissue Kit (Qiagen) according to manufacturer's instructions. The extractions were then used in 25- μ l reactions to amplify fragments of the mitochondrial cytochrome oxidase *c* subunit I (COI) and 16S rRNA genes. We used the universal primers LCO/HCO (Folmer *et al.*, 1994) and

16SarL/brH (Simon *et al.*, 1994). All PCRs included a denaturation step at 95 °C for 3 min and a final extension at 72 °C for 5 min. For COI, amplicons were created either with a simple PCR (95 °C for 20 s; 45 °C for 30 s; 72 °C for 40 s) \times 40 or by using an initial stage of cycling as above but only for 5 cycles, followed by (95 °C for 20 s; 50 °C for 30 s; 72 °C for 40 s) \times 35. 16S rRNA amplicons were derived by a protocol of (95 °C for 20 s; 50 °C for 30 s; 72 °C for 40 s) \times 35.

Amplified products were outsourced to the Australian Genome Research Facility (Perth) for bidirectional sequencing. These were assembled in Geneious v. 9 (Kearse *et al.*, 2012) and edited by eye as necessary. Consensus sequences were aligned using MAFFT v. 7 (Katoh *et al.*, 2002). Data for each gene fragment were analysed separately in a maximum-likelihood (ML) framework and then with both genes concatenated but partitioned, applying a GTR + G model of evolution in RAxML v. 1.0 (Stamatakis, 2006; Silvestro & Michalak, 2011). ML analyses were carried out independently for each gene using 10 replicate runs with 100 bootstrap replicates. The concatenated analysis was performed using 10 replicate runs with 1,000 bootstrap replicates. The outgroup consisted of three species of Vasiniae and these sequences were obtained from GenBank (Table 1). A branch/clade was considered to be strongly

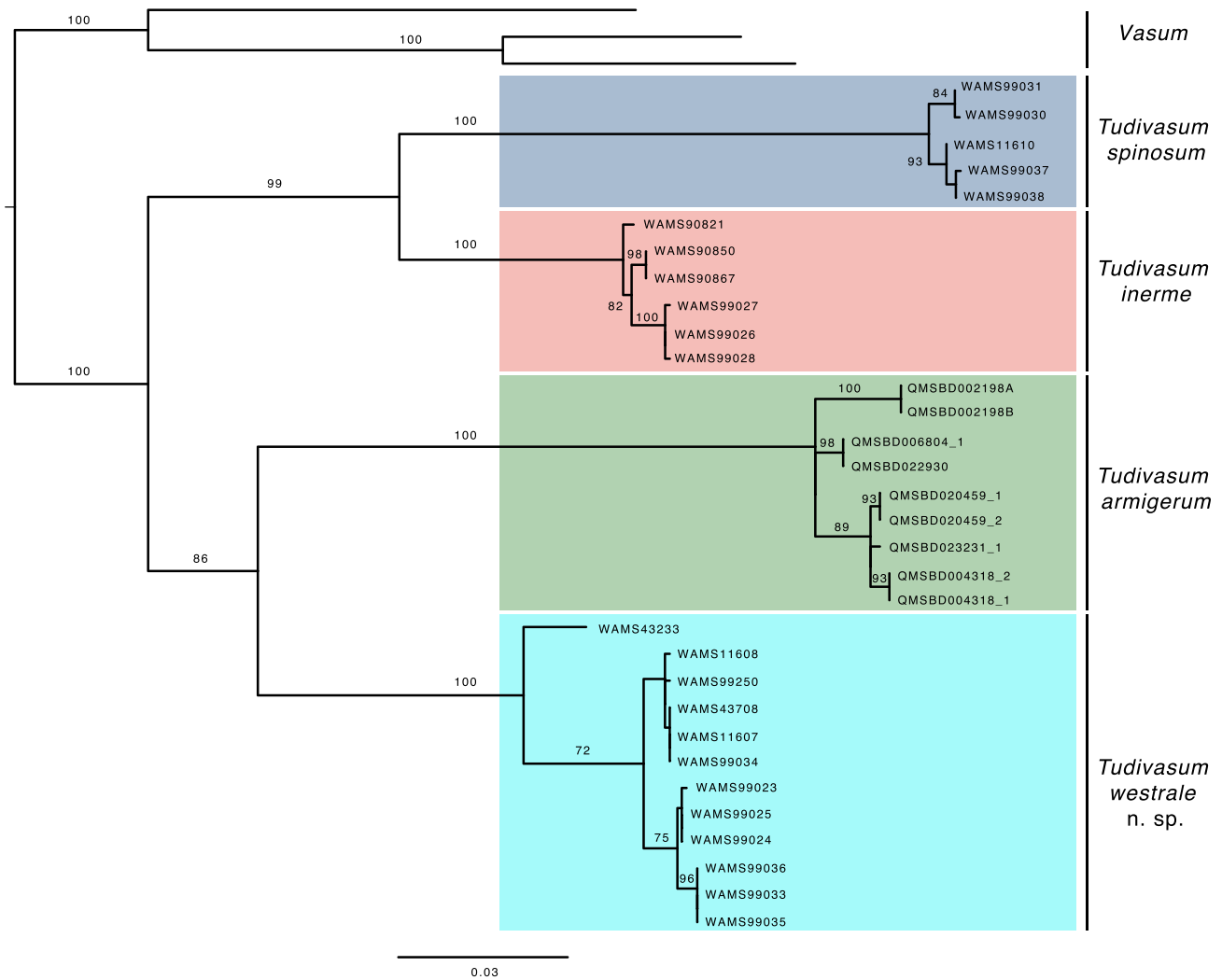


Figure 2. ML tree for selected *Tudivasum* species, based on concatenated COI and 16S rRNA DNA sequence dataset data. Scale bar indicates substitutions per site.

supported if bootstrap support (BS) values were $\geq 70\%$ (Hillis & Bull, 1993). Intra- and interspecific distances were calculated in MEGA v. 7.026 (Kumar, Stecher & Tamura, 2016) and corrected using the maximum composite likelihood model for the COI gene.

RESULTS

Both single-gene analyses (Supplementary Material Figs S1, S2) showed the same topology as the ML tree based on the concatenated dataset, so only the results of the concatenated COI + 16S rRNA dataset are discussed in the following section. The topology of the concatenated ML tree (Fig. 2) revealed four fully supported and deeply diverged clades that correspond with the morphologically defined species *Tudivasum armigerum*, *T. inerme*, *T. spinosum* and *T. westrale* n. sp.

We found that *T. spinosum* was sister to *T. inerme* (BS = 99%) and, in turn, that the clade comprising these two species was sister to a strongly supported (BS = 86%) clade composed of *T. westrale* and *T. armigerum*.

The maximum intraspecific distance for COI was 4.5% (*T. westrale* n. sp.). Interspecific distances ranged from 10.2% to 13.2%. The strongly supported *T. westrale* clade comprised two lineages, one consisted of a single specimen from near Perth, for which no

16S rRNA sequence data could be generated. The other three *Tudivasum* species each comprised at least two (*T. spinosum* and *T. inerme*) or three (*T. armigerum*) strongly supported clades.

SYSTEMATIC DESCRIPTIONS

Family TURBINELLIDAE Swainson, 1835

Genus *Tudivasum* Rosenberg & Petit, 1987

Tudivasum Rosenberg & Petit, 1987: 59 (type species: *Tudicla armigera* A. Adams, 1856, SD, Wenz, 1943: 1303).

Tudicla (*Tudicula*)—H. Adams & A. Adams, 1864: 439 (type species: *Tudicula armigera* A. Adams, 1856, SD, Wenz, 1943: 1303; invalid junior homonym of *Tudicula* de Ryckholt, 1862).

Tudicula—Angas, 1878: 610. Smith, 1887: 465. Abbott, 1959: 27. Macpherson, 1964: 209.

Diagnosis: Shell medium sized (maximum height 100 mm in *T. armigerum* and *T. kurtzi*), moderately solid, usually pyriform or fusiform, with low spire and often with long, narrow anterior



Figure 3. *Tudivasum armigerum* and *T. kurtzi*. **A–G.** *Tudivasum armigerum*. **A, B, G.** Old Reef, Queensland (WAM S99342). **C, D.** Bait Reef, Queensland (WAM S99343). **E, F.** Holotype of *Tudicla armigera*, Moreton Bay, Queensland (NHMUK 1992160). **G.** Detail of protoconch. **H–K.** *Tudivasum kurtzi*. **H, I.** Holothuria Banks, Western Australia (NHMUK 92.1.293835). **J, K.** Adele Island, Western Australia (WAM S70624). **K.** Detail of protoconch. Scale bars: **A–F, H–J** = 20 mm; **G, K** = 5 mm.

siphonal canal. Last adult whorl often globose or rounded, with prominent keel; with or without spines but always with fine spiral threads. Nuclear whorls large, almost mammillate in some species; parietal shield well developed, with all species having at least 3 (rarely 4) columellar plaits. Operculum corneous, brown, with terminal nucleus.

***Tudivasum armigerum* (A. Adams, 1856)**
(Fig. 3A–G)

Tudicla armigera A. Adams, 1856: 221, fig. 3E, F (Moreton Bay, Australia; holotype NHMUK 1992160). Abbott, 1959: 27. Abbott & Dance, 1982: 210.

Turbinella (Tudicula) armigera—E. A. Smith, 1884: 53, pl. 5: fig. G. Abbott, 1959: 27; pl. 9: figs 9, 10.

Tudivasum armigera—Harasewych, 1998: 844. Wilson, 1994: 59, pl. 8: fig. 11a, b. Beesley *et al.*, 1998: 824, fig. 15158M–O.

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell pyriform, globose; last adult whorl sculptured with row of long, hollow spines along keel and two rows of spines on anterior canal; colour cream with mottled brown patches.

Description: $H = 52\text{--}100$ mm (up to 100 mm; J.P. Barbier, personal communication). Shell pyriform, last teleoconch whorl globose, siphonal canal long, straight; spire of medium height; mammillate protoconch of $1\frac{1}{2}$ whorls (mean \pm SD = 3.19 ± 0.24 mm, $n = 22$). Teleoconch whorls with row of long (5–16 mm), hollow spines on shoulder keel; fine spiral ribs (usually with small spines) and 10–12 indistinct axial folds over remainder of whorls. Base of siphonal canal has spiral row of long, often curved hollow spines, with further row surrounding canal at its midpoint. Spiral rows of long, often curved hollow spines. Aperture smooth but may show weak crenulations within outer lip; parietal shield erect, solid; columella with 3 (rarely 4) strong plaits. Exterior mottled cream to white, sometimes with darker patches, rarely with salmon-orange or red-brown axial streaks. Parietal shield, interior of aperture and columella white; protoconch mottled tan.



Figure 4. Distribution of *Tudivasum kurtzi*, *T. armigerum* and *T. rasilistoma*. Red circles denote type localities. Note that for *T. kurtzi* this is a reported type locality only.

Habitat and distribution: *Tudivasum armigerum* is found on clean sand from the intertidal zone to depths of 50 m. Most often taken by trawlers, this species is locally common. Abbott (1959) cited Queensland as the range, but Wilson (1994) greatly extended this from Moreton Bay in Queensland to Adele Island in Western Australia, based on a single juvenile specimen (WAM S70624), dredged at 80 m, which is here shown to be a juvenile *T. kurtzi* (Fig. 3J). Our evidence restricts the range to the Queensland coast, from Cape Cleveland (19°10.55'S) south to Moreton Bay (Fig. 4).

Remarks: *Tudivasum armigerum* is a well-defined species; its sister taxon *T. kurtzi* is morphologically similar to it, but the two species have allopatric ranges. *Tudivasum armigerum* only occurs in Queensland, and *T. kurtzi* is found over the northwest and northern coast of Australia. *Tudivasum armigerum* is variable in both colour and size ($H = 50\text{--}100$ mm in adults), but the basic structure of the shell remains constant throughout.

***Tudivasum kurtzi* (Macpherson, 1964)**
(Fig. 3H–K)

Tudicula kurtzi Macpherson, 1964: 209, pl. 210 (Shoal Bay, Darwin, Northern Territory, Australia; holotype, NMV F 23320).

Tudicula armigera kurtzi—Abbott & Dance, 1982: 210.

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell pyriform with inflated last adult whorl; 7–9 very long hollow spines along keel and 2–3 rows of smaller spines on anterior canal; exterior and aperture white with orange-tinted protoconch.

Description: H up to 103.9 mm (largest recorded; J.P. Barbier, personal communication). Shell largest in genus, pyriform, with globose adult whorl, straight tapering siphonal canal (40% of overall shell length); spire short; centrally pitted protoconch of $1\frac{1}{4}\text{--}1\frac{1}{2}$ whorls, largest in genus (3.84 ± 0.19 mm, $n = 18$). Teleoconch of 5 rounded whorls; 2 post-nuclear whorls sculptured with axial growth lines crossed by 2–3 spiral cords, creating cancellate appearance, becoming nodulose, then spinose by third whorl; spines on prominent adapical spiral cord becoming progressively longer as cord

continues towards body whorl, with number of spiral cords increasing to 3–4 adapically of prominent cord and 10–12 abapically. Body whorl has 7–9 shoulder spines reaching to $c. 30$ mm in length, while remaining cords have very short (2–3 mm long), closely spaced spines. Anterior canal clearly delineated by second prominent row of spines of $c. 25$ mm length; this row followed by further 1–2 rows with much shorter spines, interspersed by 8–12 cords with smaller spines typical of body whorl. Aperture oval while tapering anteriorly; lip simple with strong lirae within, corresponding to spiral cords of body whorl; columella concave with 3 strong plaits anteriorly, followed by 2 indistinct folds posteriorly; parietal shield prominently erect, giving aperture tubular appearance. Exterior cream or white; aperture and interior glossy and white. Protoconch cream with orange-brown rays or blotches radiating from the central pit.

Habitat and distribution: All specimens with accurate data have been trawled or dredged on a sandy mud bottom at depths greater than 70 m. A specimen from Tanimbar Island (Timur Laut, Indonesia; MNHN) was dredged at 235–250 m; this species and *T. spinosum* are the deepest dwelling members of the genus. Macpherson (1964) cited Shoal Bay, Darwin, Northern Territory as the type locality. Recent findings now extend the range from the Kimberley (WAM S70624, Adele Island, and WAM S98307, Lynher Bank) to the Rowley Shoals in Western Australia and northwards through the Joseph Bonaparte Gulf and the Arafura Sea. One specimen was trawled as far north as Tanimbar Island (MNHN Stn CP79 03NOV91) and another from the seas around Aru Island, eastern Indonesia (WAM S70539).

Remarks: Morphologically, *T. kurtzi* is similar to *T. armigerum*. It is, however, found only in the Northern Territory and northwest Western Australia, while *T. armigerum* is restricted to Queensland. The similarity in morphology has caused some confusion among modern workers. Abbott & Dance (1982) considered *T. kurtzi* to be a subspecies of *T. armigerum*, while Wilson (1994), who did see examples of *T. kurtzi*, assumed that *T. kurtzi* in Western Australia was a range extension of *T. armigerum*. Recently, many more specimens of this once rare shell have become available and the study of this material has confirmed this as a valid species with more constant features than the variable *T. armigerum*. *Tudivasum kurtzi* can be separated from *T. armigerum* because the former is always white, has a more spiny appearance overall, with much longer spines on the

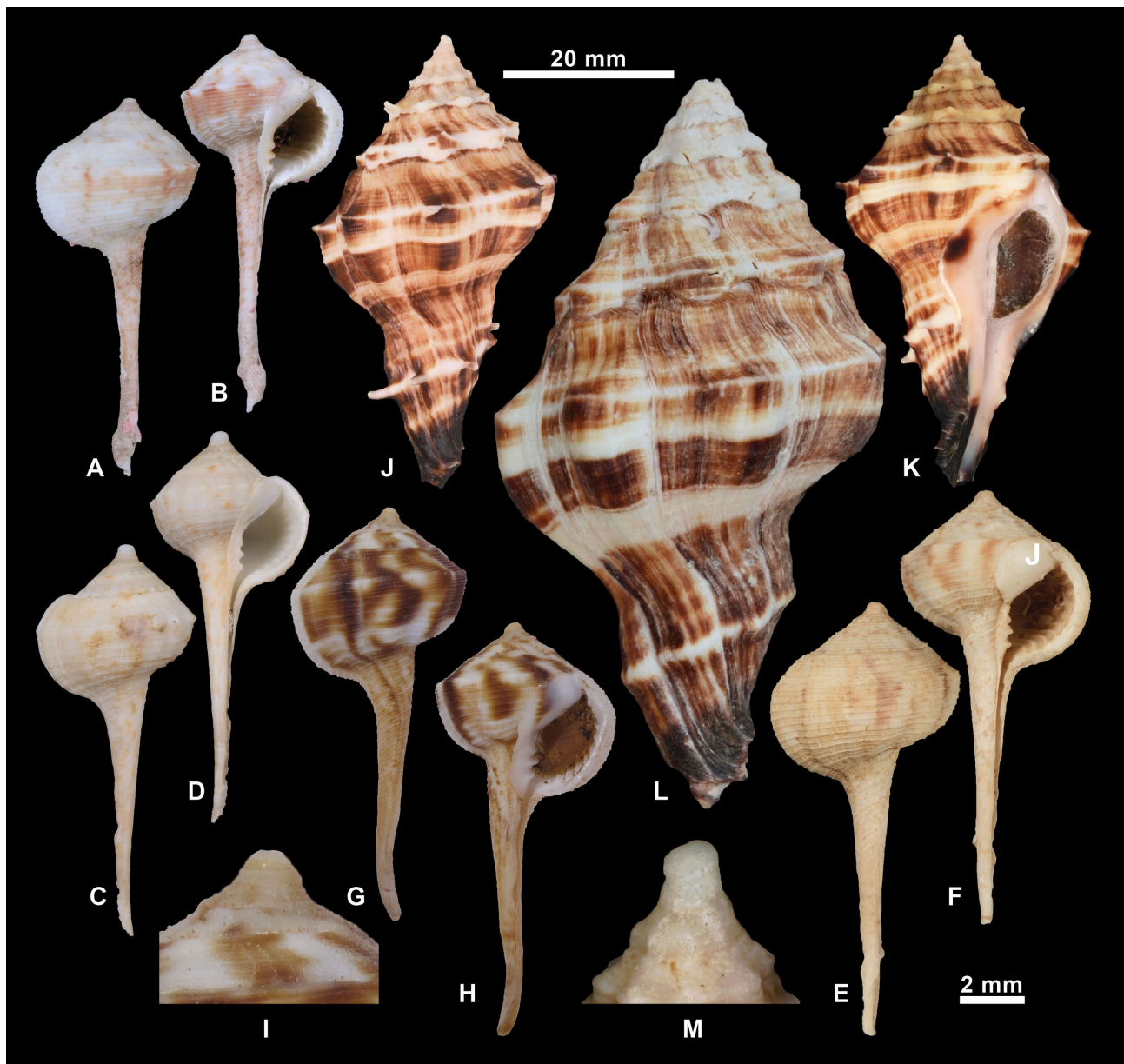


Figure 5. *Tudivasum inerme* and *T. rasilistoma*. **A–I.** *Tudivasum inerme*. **A, B.** Adele Island, Western Australia (WAM S50160). **C, D.** Rowley Shoals, Western Australia (WAM S38117). **E, F.** 235 km north of Cape Leveque, Western Australia (NMV F 227286). **G–I.** Cooke Point, Port Hedland, Western Australia (WAM S99344). **J–M.** *Tudivasum rasilistoma*. **J, K, M.** Off Noosa, south Queensland (WAM S99345). **L.** Off Fraser Island, south Queensland (WAM S99424). Scale bars: **A–H, J–L** = 20 mm; **I, M** = 2 mm.

last adult whorl (28–30 mm), and has a larger and more prominent protoconch. The protoconch of *T. kurtzi* has an average diameter of 3.85 ± 0.19 mm ($n = 18$), while that of *T. armigerum* is smaller. The protoconch of *T. kurtzi* is the only coloured part of the shell (i.e. has radiating brown lines from the centre of the protoconch) and has a knobbly appearance (Fig. 3K); the protoconch of *T. armigerum* is more evenly coloured with a smooth appearance (Fig. 3G). *Tudivasum kurtzi* is larger than *T. armigerum* ($H > 90$ mm, with both body and anterior canal spines extending to over 20 mm).

***Tudivasum inerme* Angas, 1878**

(Fig. 5A–I)

Tudicula inermis Angas, 1878: 610, 2 text figs [‘Singapore’ (in error); holotype PRI 19232]. E. A. Smith, 1887: 465. Abbott, 1959:

30, pl. 8: figs 4–6. Abbott & Dance, 1982: 210. Cochran, 1986: 1.

Tudivasum inermis—Wilson, 1994: 59, pl. 8: figs a, b.

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell globose with long straight siphonal canal; last adult whorl adorned with well-developed keel, which may have only low projections or may produce large protruding spines with discrete spiral cords above and below.

Description: Shell globose, with short, almost truncate spire, long, straight siphonal canal and mammillate protoconch of $1\frac{1}{4}$ whorls (2.04 ± 0.21 mm, $n = 22$). Teleoconch whorls with spiral threads and axial striae; shoulder or keel generally smooth or weakly nodulose. Aperture with 9–10 strong lirae; parietal shield erect in adults



Figure 6. Distribution of *Tudivasum chaneyi* n. sp., *T. ashmoreense* n. sp., *T. spinosum* and *T. inermis*. Red circles denote type localities. Ashmore Reef (encircled in red) is the type locality for both *T. chaneyi* n. sp. and *T. ashmoreense* n. sp.; these two species are currently only known from this locality.

and columella with 3 strong plaits. Colour of exterior generally cream, brown or fawn with brown axial streaks or blotches; interior white. Adult specimens vary substantially in size ($H = 30\text{--}52$ mm).

Habitat and distribution: Typical ‘toffee apple’-shaped shells are often found intertidally on clean sand and shell rubble and can be seen in large numbers (Fig. 5G, H). Deeper water specimens (depths up to 100 m) are usually associated with muddy sand and are found relatively rarely alive. Abbott (1959) cited the range as Exmouth Gulf to Broome, while Wilson (1994) extended the range south to the Abrolhos Islands ($28^{\circ}43'S$, $113^{\circ}47'E$) (Fig. 6). Recent dredging operations around the Rowley Shoals and Ashmore Reef have yielded shells from deep water (i.e. 80–100 m); these are similar to typical inshore shells but are more sharply keeled. These deep-water specimens, provisionally identified here as *T. inermis*, may prove to be a new species. *Tudivasum inermis* and *T. spinosum* are morphologically similar (Fig. 5A–D).

Remarks: The Tasmanian specimen of *Tudivasum* illustrated by Cochran (1986) is clearly *T. inermis* (Fig. 5E, F). The specimen is in the NMV collections (F227286), and when compared with deep-water material from the WAM, no significant morphological differences could be found. C. Crowley (NMV) has raised significant doubts about the accuracy of the data associated with this specimen. He has confirmed that T. Cochran was not involved with either the collection or cataloguing process and has suggested that it is likely that the Tasmanian locality is incorrect, and that a wrong station number was likely allocated. The specimen label cites the accession number 84/6, which belongs to the RV ‘Soela’ cruise SO1/84, a location on the northwest shelf of Western Australia. However, the station number SO3/84-74 written on the same label belongs to RV ‘Soela’ cruise SO3/84, a southeast Australian location. The accession number assigned to material collected from the South East Australian Cruise (SO3/84) is 84/16. The single-digit difference between ‘84/6’ (northwest Western Australia) and ‘84/16’ (southeast Tasmania) could be the source of the error in assigning cruise locations. On further investigation, the distance offshore and depth cited by Cochran (1986) do not appear to match either the accession or station numbers on the label for *T. inermis* (Fig. 5E, F). Given the similarity between the accession and cruise numbers, Crowley has speculated that if the specimen was collected on cruise SO1/84, and not SO3/84, the actual collection

locality would be station SO1/84-74, located c. 235 km north of Cape Leveque, Western Australia ($14^{\circ}17'S$, $122^{\circ}35'E$).

C.C. Lu, who was a curator at NMV in 1984, has indicated to us that while he is confident that the specimen was collected off Tasmania, he is of the view that it was trawled at a distance of 20 miles offshore not 254 km offshore, as was cited by Cochran (1986). The collection data C.C. Lu supplied indicate a bottom depth of 320–480 m, with a conflicting trawl depth of 320–540 m. If true, this would substantially exceed the greatest depth ever recorded for any specimen of the genus *Tudivasum*. These data need to be verified, particularly as *T. inermis* is otherwise known to occur only at much shallower depths.

In this species, there appears to be a wide variability in size even within populations, but no geographical patterns of variation are discernible. While in the shallow-water forms the last adult whorl is more rounded, in deeper water forms it is sharply keeled.

***Tudivasum spinosum* (H. & A. Adams, 1864)**
(Fig. 7A–N)

- Tudicula* (*Tudicula*) *spinosa* H. & A. Adams, 1864: 429, fig. 7A–D (Port Curtis, Australia; syntype NHMUK 1992159).
Turbinella (*Tudicula*) *spinosa*—E. A. Smith, 1884: 54, pl. 5: fig. H. Abbott, 1959: 29, pl. 9: figs 5, 6.
Tudivasum spinosa—Wilson, 1994: 60, pl. 8: fig. 9a–c.
Tudicla inermis—Kuroda, 1932: 117, fig. 3, 114 (not Angas, 1878).
Tudivasum inermis—Dharma, 2005: 157, pl. 53, fig. 13a, b (not Angas, 1878).

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell globose with long, straight siphonal canal; last adult whorl adorned with well-developed keel that often shows large protruding spines; aperture with 9 or 10 lirae on inner lip.

Description: Shell with globose-shaped last adult whorl, long, straight spine-like siphonal canal and low spire. Protoconch of $1\frac{1}{4}$ whorls, prominent and mammillate (1.87 ± 0.14 mm, $n = 22$). Teleoconch whorls sculptured with fine axial striae and low axial folds; sometimes bearing single row of spines along keel and low, often scaly, spiral cords. Siphonal canal generally smooth; aperture oval

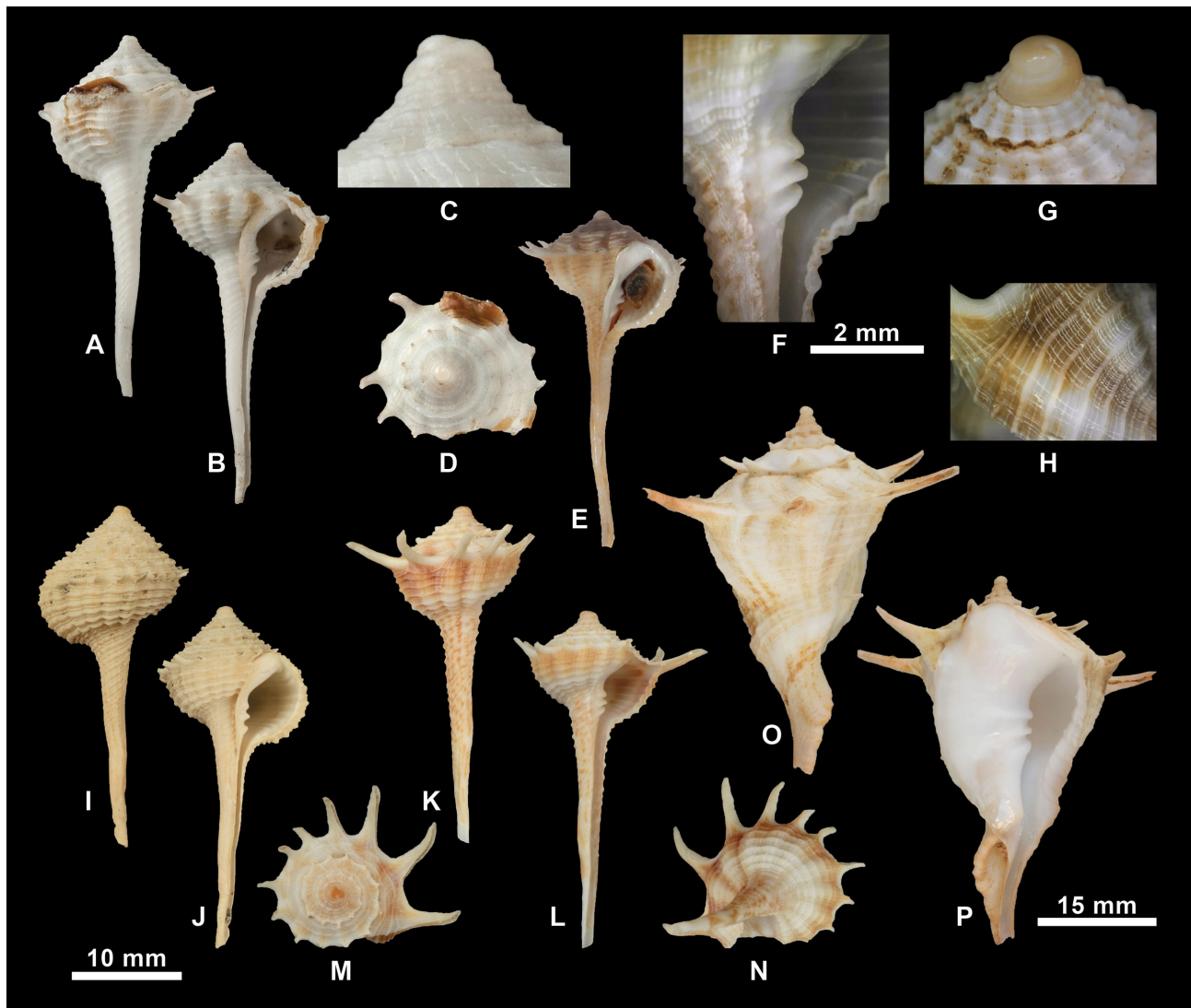


Figure 7. *Tudivasum spinosum* and *T. zanzibaricum*. **A–D.** *Tudivasum spinosum*. **A–D.** Syntype, Port Curtis, Queensland (NHMUK 1992159). **E, F, H.** Holothuria Reef, northwest Western Australia (NHMUK 1892.1.29.46–47). **G.** Ningaloo Reef, Western Australia (WAM S11610). **I, J.** Tanimbar Island, Indonesia (MNHN CW80). **K–N.** Gulf of Carpentaria, north Queensland (MNT P007882). **O, P.** *Tudivasum zanzibaricum*. Leven Bank, Zanzibar Island, Tanzania (WAM S99346). Scale bars: **A, B, D, E, I–N** = 10 mm; **C, F–H** = 2 mm; **O, P** = 15 mm.

with 8–10 distinct lirae on inner lip; parietal shield solid and erect in adults; columella with 3 strong plaits. Protoconch pale cream to orange; teleoconch and last adult whorl cream to pale tan, occasionally with darker blotches.

Habitat and distribution: *Tudivasum spinosum* has the largest distribution of any member of the genus. The shallowest record for this species is 9–10 m off Wathumba, Queensland (MNT P035232). [Abbott \(1959\)](#) recorded specimens dredged at 9 fathoms (16.5 m), but most specimens have been dredged below 40 m; the maximum collection depth is 235–250 m, off Tanimbar Island, eastern Indonesia. The species lives on fine sand and shell rubble substrate and has been recorded from off Perth in southwest Western Australia to Moreton Bay in southern Queensland. MNHN dredgings in eastern Indonesia have extended the range outside of Australia to at least 9°16'S. [Dharma \(2005\)](#) illustrated two specimens of this species (wrongly identified as *T. inermis*) from the Arafura Sea; these clearly show the peripheral spines characteristic of *T. spinosum*.

Remarks: *Tudivasum spinosum* is the most morphologically variable species within the genus. The syntype measures 37.58 mm. Speci-

mens from Stn CP65, Tanimbar Island, Indonesia (MNHN) range from 22 to over 53 mm. This disparity in size is found within single populations throughout the range of this species. The syntype shows small, sharp spines along the periphery of the last adult whorl, but specimens with large, erect and hollow spines are also found near the type locality (Fig. 7K–N). The spines on the latter shells contrast significantly with the barely discernible spines often seen on deeper water specimens (Fig. 7I, J). The label of the syntype has the word ‘holotype’ crossed out and ‘syntype’ written next to it as “the original author never mentioned that they based their description on a single specimen and therefore the type should be a syntype not a holotype” (A. Salvador, Senior Curator, Mollusca Section, NHMUK, personal communication).

There are some specimens that are morphologically difficult to assign to either *T. spinosum* or *T. inermis*. [Abbott \(1959\)](#) suggested that *T. inermis* may prove to be a western form of *T. spinosum*, but the range of the latter species overlaps with that of *T. inermis*, and ‘typical’ specimens of each species are substantially different. Our molecular phylogeny (Fig. 2) suggests that *T. spinosum* and *T. inermis* are sister species, but future molecular systematic studies

should include individuals that are morphologically intermediate to 'typical' *T. spinosum* and *T. inerme*.

***Tudivasum rasilistoma* Abbott, 1959**
(Fig. 5J–M)

Turbinella (Tudicula) rasilistoma Abbott, 1959: 29, pl. 4: fig. 2; pl. 10: figs a–c (Tweed Heads, northern New South Wales, Australia; holotype NMV F18189).

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell fusiform with broad attenuated siphonal canal, last adult whorl showing 2 rows of nodules (these becoming spinose on central portion of anterior canal) and columella marked by 2 brown blotches.

Description: Shell solid, fusiform, high spired, with tapered last adult whorl and broad, attenuated siphonal canal. Protoconch (when present) of 1½ whorls and small (1.88 ± 0.04 mm, $n = 7$). Teleoconch whorls with weak spiral cords and axial growth striae. Last adult whorl with 2 closely set peripheral rows of blunt nodules or, in some specimens, row of stout, fairly long, open-faced spines. Aperture smooth or weakly lirate; parietal shield heavy but low; columella with 3 strong plaits. Overall colour of shell generally pink or cream, overlaid with areas of light to mid-brown; anterior tip dark brown, interior white and columella pinkish, with 1 or 2 large black blotches opposite aperture of adult shells.

Habitat and distribution: Traditionally trawled by shrimp boats, this species has been recently taken by a small shell dredge, at 60–80 m depth off Mooloolaba, on coarse sand and rubble substrate (V. Harris, personal communication). This species ranges from Mooloolaba in southern Queensland to northern New South Wales (Fig. 4).

Remarks: *Tudivasum rasilistoma* appears morphologically very different from the other members of the genus and its generic assignment needs to be confirmed with molecular data. This species has the shortest geographical range of any member of the genus in Australia and as yet little is known regarding its anatomy or habitat. Only the equally little known *T. zanzibaricum* may have a more restricted range. *Tudivasum rasilistoma* has two distinct adult size groups, both of which show a fully developed parietal shield (Fig. 5K). The shell length of the large-shelled group varies between 60 and 80 mm, while in the small-shelled group it ranges from 45 to 60 mm. The large-shelled group almost never has an intact protoconch, while c. 50% of individuals in the smaller group show an intact protoconch. When present, the nucleus of the protoconch always appears eroded (Fig. 5M). The discrepancy in shell size could be evidence of sexual dimorphism.

***Tudivasum zanzibaricum* Abbott, 1958**
(Fig. 7O, P)

Tudicula zanzibarica Abbott, 1958: 1–4, figs 1–7 (Zanzibar Island, Zanzibar; holotype ANSP No. 225261). Abbott, 1959: 31, pl. 8: figs 1–3; pl. 9: figs 7, 8. Abbott & Dance, 1982: 210.

Material examined: See Supplementary Material Table S1.

Diagnosis: Shell subtriangular with last adult whorl sculptured with 6–8 prominent spines and aperture with well-developed parietal shield covering most of ventral shell surface.

Description: Shell solid, subtriangular and spinose; spire moderately elevated, consisting of c. 6 whorls. Last adult whorl strongly shoul-

dered posteriorly, with 6–8 large, flattened spines; sides of whorl flat or slightly concave. Protoconch 1–1¼ whorls, rather large (1.83 ± 0.09 mm, $n = 3$), bulbous and protruding. Teleoconch whorls with weak spiral cords that become obsolete on the siphonal canal. Anterior half of the last whorl in the central region of the siphonal canal bears 1 or 2 rows of elongate spines, which may become obsolete with the development of the aperture, resulting in only 1 spine being visible behind the columellar shield. Aperture long, wider posteriorly, gradually becoming constricted over the siphonal canal. Parietal shield well developed and raised. Columella bears 3 weak plicae. Overall colour is white with cream or tan highlights on tips of spines and extremity of siphonal canal. Aperture cream or white to pale orange in fresh shells. Abbott's (1959) drawing of the radula shows a tricuspid central tooth and bicuspid laterals. The operculum is corneous, unguiculate and brown.

Habitat and distribution: Abbott (1959) gave a depth of 8 fathoms (14.6 m) on a bottom of sand, broken shell and seagrass. Recent specimens in private collections suggest a deeper depth range extending to at least 90 m. *Tudivasum zanzibaricum* has only been found around the northern waters of Zanzibar Island with large numbers being taken recently from the Leven Bank area by local fishermen (Fig. 1).

Remarks: This species cannot be confused with any of its congeners. Most of the specimens recorded are between 40 and 52 mm in shell length. However, Abbott (1959) cited a paratype with a shell length of 28 mm, which may have been a subadult. Compared with many other species of *Tudivasum*, this species is not very variable in size; the most variable character appears to be the length of the spines on individual shells. The range of this species lies well outside the ranges of all the other species, and future genetic work will be key to understanding its phylogenetic placement.

***Tudivasum chaneyi* Morrison new species**
(Fig. 8A–I)

Type material: Holotype: WAM S70625, Ashmore Reef (north-east corner, outside reef), Western Australia, 12°11'14.0"S, 123°07'11.0"E. Taken live at night at 15–25 m depth, on sand and coarse shell rubble (Fig. 8A–G). Paratype 1: SBMNH 142888, same locality as holotype but dead collected (Fig. 8H, I). Paratype 2: WAM S12430, same locality as holotype but dead collected.

ZooBank registration: urn:lsid:zoobank.org:act:6E5861C7-CCD6-4540-8FF8-B759009991D8.

Etymology: This species is named in honour of Henry Chaney of SBMNH.

Diagnosis: Shell low spired, globular, with a projecting, dull white protoconch, very long straight siphonal canal and single row of spoon-like nodules on prominent keel of last adult whorl.

Description (holotype): Shell medium to large sized, napiform, with globose last adult whorl, very long, relatively straight siphonal canal and raised spire. Protoconch of 1¼ smooth whorls, large; boundary with teleoconch indistinct (2.56 ± 0.12 mm, $n = 3$). Teleoconch with 4 whorls, sculptured with fine axial striae and low axial folds. Single row of nodules begins on shoulder of second teleoconch whorl, then develops into round-topped, scoop-like structures on last adult whorl, becoming larger towards the aperture; all teleoconch whorls exhibit fine spiral cords, which diminish towards tip of siphonal canal. Aperture oval with 11 sharp, fine spiral lirae running inwards from outer lip; parietal shield raised, with 3 well-developed plicae at base of columella. Siphonal canal c. 65% of total shell length; anterior third becoming smooth, while twisting

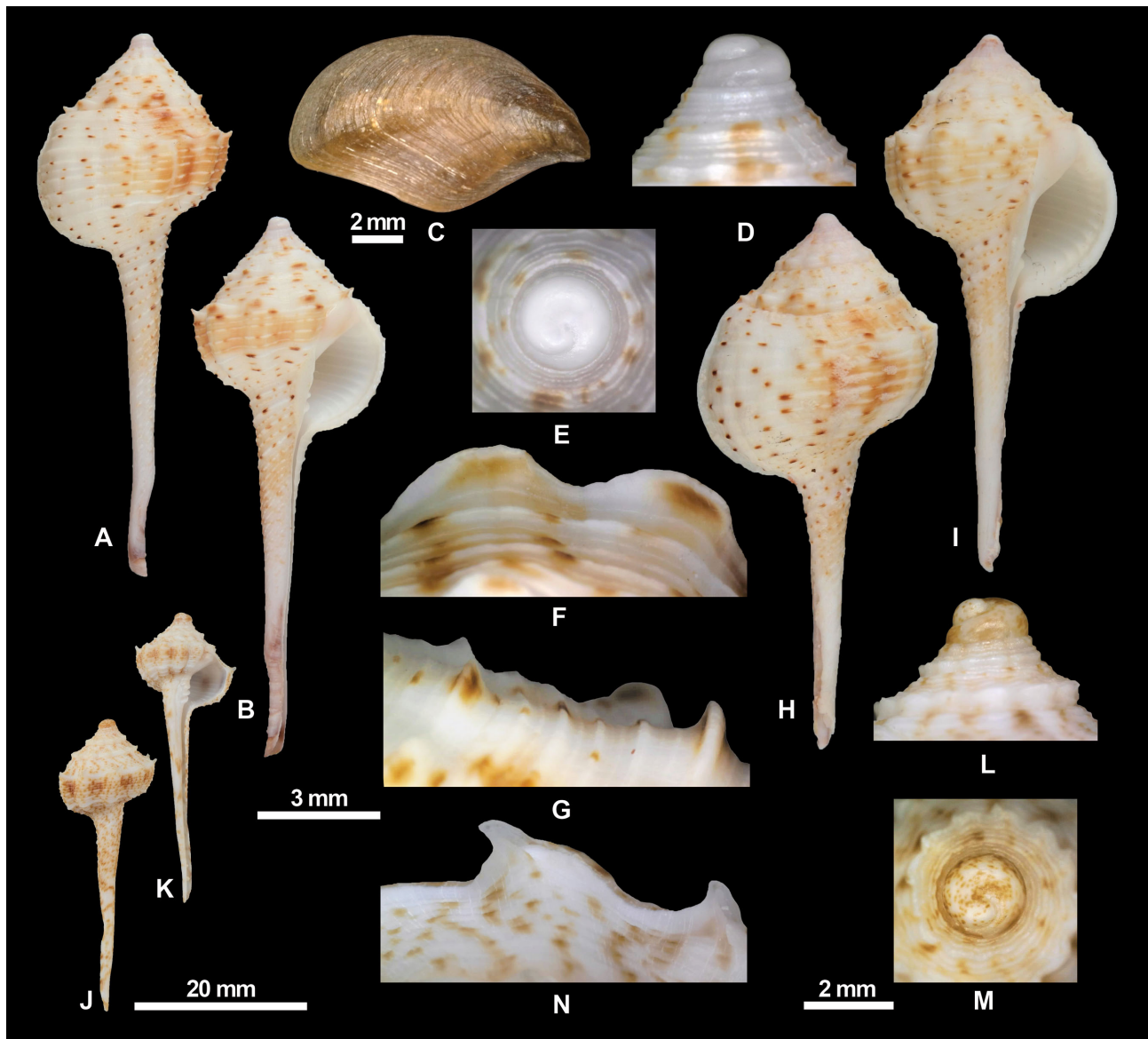


Figure 8. Comparison of *Tudivasum chaneyi* n. sp. and *T. ashmorense* n. sp. **A–I.** *Tudivasum chaneyi* n. sp. **A–G.** Holotype (WAM S70625), Ashmore Reef, Western Australia. **C.** Detail of operculum. **D, E.** Detail of protoconch. **F, G.** Detail of sculpture, showing unadorned scoops on the last adult whorl. **H, I.** Paratype 1 (SBMNH 142888), Ashmore Reef, Western Australia. **J–N.** *Tudivasum ashmorense* n. sp. **J, K.** Holotype (WAM S82970), Ashmore Reef, Western Australia. **L, M.** Detail of protoconch. **N.** Detail of sculpture showing sheathed scoops on last adult whorl. Scale bars: **A, B, H, I, J, K** = 20 mm; **C** = 2 mm; **D, E, F, G, N** = 3 mm; **L, M** = 2 mm.

slightly from vertical axis. Protoconch dull white, teleoconch white with discrete orange or brown spots on upper teleoconch whorls, these spots becoming larger band of orange on dorsum of last adult whorl; upper siphonal canal pale orange with fine spots along spiral cords, fading to pinkish purple at tip; aperture white. Body of animal pure white with no discernible pattern; black eyes on white stalks (Fig. 9A); operculum corneous, unguiculate, pale orange or brown, leaf-like and thin; radula with tricuspid central and bicuspid lateral teeth (Fig. 9B).

Habitat and distribution: Only known from the type locality. The three specimens of *T. chaneyi* n. sp. were collected by divers at night, at a depth of 15–25 m near the base of a near-vertical wall of coral and limestone. The live specimen was crawling on clean sand and shell rubble near larger boulders.

Remarks: The two paratypes are very similar. Paratype 1 (SBMNH 142888) is a larger, heavier shell, but as it has part of the siphon missing it is difficult to gauge the true size of the shell. Paratype 2 (WAMS 12430) has significantly damaged body whorl and is slightly smaller than the holotype and paratype 1. As the holotype was taken live, it shows no wear of sculpture or fading of colour. *Tudivasum chaneyi* n. sp. can only be confused with *T. ashmorense* n. sp. (Fig. 8) and *T. spinosum* (Fig. 6). The large, white protoconch, unsculptured scoops on the periphery of the last adult whorl and the shallow habitat differentiate *T. chaneyi* n. sp. from *T. ashmorense* n. sp., while the much larger size, presence of scoop-like structures on the last adult whorl and large protoconch separate *T. chaneyi* n. sp. from *T. spinosum*. *Tudivasum spinosum* is only found in deep water in Western Australia, while *T. chaneyi* n. sp. appears to be a shallow-water species.

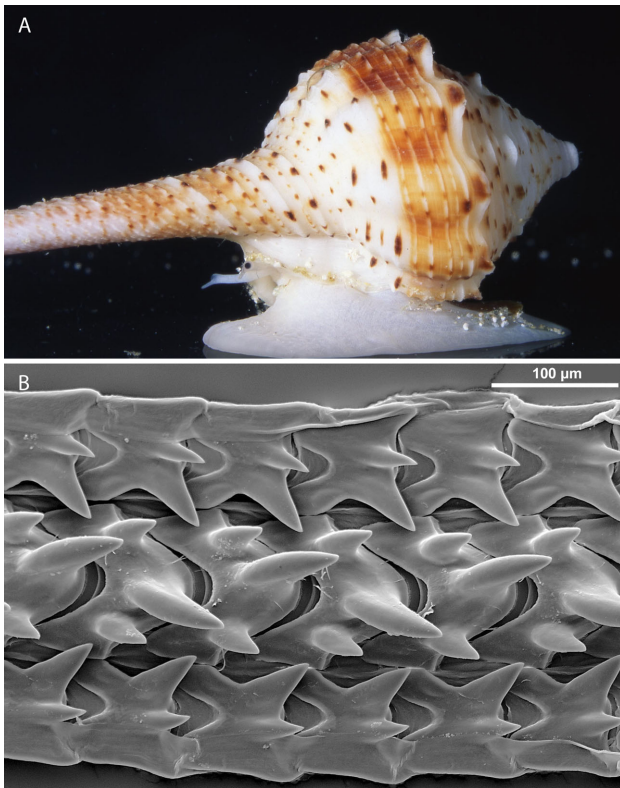


Figure 9. *Tudivasum chaneyi* n. sp., holotype (WAM S70625). **A.** Shell. **B.** Radula.

***Tudivasum ashmoreense* Morrison new species**
(Fig. 8J–N)

Type material: Holotype ($H = 31.45$ mm, $W = 10.43$ mm): WAM S82970, off Ashmore Reef, Commonwealth Marine Reserve, Ashmore and Cartier Islands, northwest Western Australia, 12.4324°S, 123.5964°E to 12.4344°S, 123.4344°E; taken dead by CSIRO, RV ‘Southern Surveyor’, Stn SS0507/196, 111 m (Fig. 8J–N).

ZooBank registration: urn:lsid:zoobank.org:act:25AA0ACA-564C-4C84-9CC4-D6F2D33B9B7.

Material examined: Only known from the type material.

Etymology: This species is named after the type locality, Ashmore Reef, northwest Western Australia.

Diagnosis: Shell low spired, globular, with projecting, mottled brown protoconch, slightly deviating siphonal canal and row of spoon-like nodules covered with sharp sheath-like hollow spine.

Description: Shell subadult, medium sized for genus, napiform with globose last adult whorl, long, straight, almost needle-like siphonal canal deviating to the left when viewed dorsally and raised spire. Protoconch of $1\frac{1}{4}$ whorls (1.89 mm, $n = 1$), depressed at apex;

boundary with teleoconch well defined. Teleoconch with 3 whorls, sculptured with fine axial striae and axial folds; each axial fold supporting a low, shallow scoop overlaid with sheath-like hollow spine facing posteriorly. Last adult whorl bearing secondary spiral ridge below prominent keel and sculptured only with axial folds, giving wavy appearance; remainder of whorl crossed by fine spiral cords that cease at juncture of aperture with siphonal canal. Aperture oval with 9 or 10 fine lirae running inwards from incompletely developed outer lip; no evidence of parietal shield; 3 well-developed plicae at base of columella; siphonal canal $c.$ 65% of overall shell length. Protoconch mottled brown, with finer spots of brown towards teleoconch; remainder of shell cream or white, with orange or tan highlights between axial folds, giving a slightly banded appearance; aperture white, siphonal canal streaked with tan.

Habitat and distribution: This species is only known from the type locality. The habitat appears to be silty sand and shell rubble at a depth of 111 m.

Remarks: Although the description of a new species based on a single subadult shell is controversial, the decision is warranted because the specimen is in good condition and its features are sufficiently distinct. That two very similar species are found within 30 nautical miles of each other is mirrored by the distributions of *T. spinosum* and *T. westrale* n. sp. over the latter species’ entire range. Several trawls have recovered both species suggesting they are sympatric. Along the northwest coast *T. spinosum*, *T. inerme* and to some extent *T. westrale* n. sp. are found close together, although often inhabiting different depths. The single specimen of *T. ashmoreense* n. sp. was found at over 100 m depth, while *T. chaneyi* n. sp. has only been found by divers at 15–25 m.

The primary features distinguishing *T. ashmoreense* n. sp. from *T. chaneyi* n. sp. are the size and colour of the protoconch (Table 2). *Tudivasum chaneyi* n. sp. has a larger and whiter protoconch, while *T. ashmoreense* n. sp. exhibits a smaller and mottled brown protoconch (compare Fig. 8D, E with Fig. 8L, M). Similarly, the post-nuclear teleoconch whorls and the spiral cords of *T. ashmoreense* n. sp. are more coarsely sculptured, with the axial folds progressing into scoops at a much earlier stage. As both holotypes are not worn or abraded, these features do not alter with maturity. There is no evidence of the hollow, sheath-like spines enveloping the scoops on the keel of *T. chaneyi* n. sp. This feature could conceivably alter with age or wear, but some trace of it should be visible (Fig. 8N). Additionally, the secondary keel on the last adult whorl of *T. ashmoreense* n. sp. is not present on any specimens of *T. chaneyi* n. sp., which has a much rounder, smoother appearance. *Tudivasum ashmoreense* n. sp. superficially resembles *T. spinosum*, but the presence of scoops along the keel of the former and its more angular shape, together with differences in the protoconch and the colour of the last adult whorl, clearly separate these two species (Table 2).

***Tudivasum westrale* Morrison new species**
(Fig. 10A–M)

Tudivasum spinosa Wilson, 1994: 60, pl. 8: fig. 9a (not H. & A. Adams, 1864).

Type material: Holotype ($H = 26.16$, $W = 10.81$ mm): WAM S99033, Ningaloo Marine Park, Western Australia, 22°14’55”S,

Table 2. Comparison of shell morphological features among similar species of *Tudivasum*.

Species	Average size (mm)	Protoconch size (mm)	Sculpture	Protoconch colour
<i>T. chaneyi</i> n. sp.	59.9 ($n = 3$)	2.56 ± 0.12 ($n = 3$)	Spiral cords with scoops	White
<i>T. ashmoreense</i> n. sp.	Unknown	1.89 ($n = 1$)	Spiral cords, hollow spines over scoops	Mottled brown
<i>T. spinosum</i>	44 ($n = 72$)	1.87 ± 0.14 ($n = 22$)	Single row of spines or nodules on keel of last adult whorl	White or pale orange

Measurements are shown with associated SD values and sample sizes.

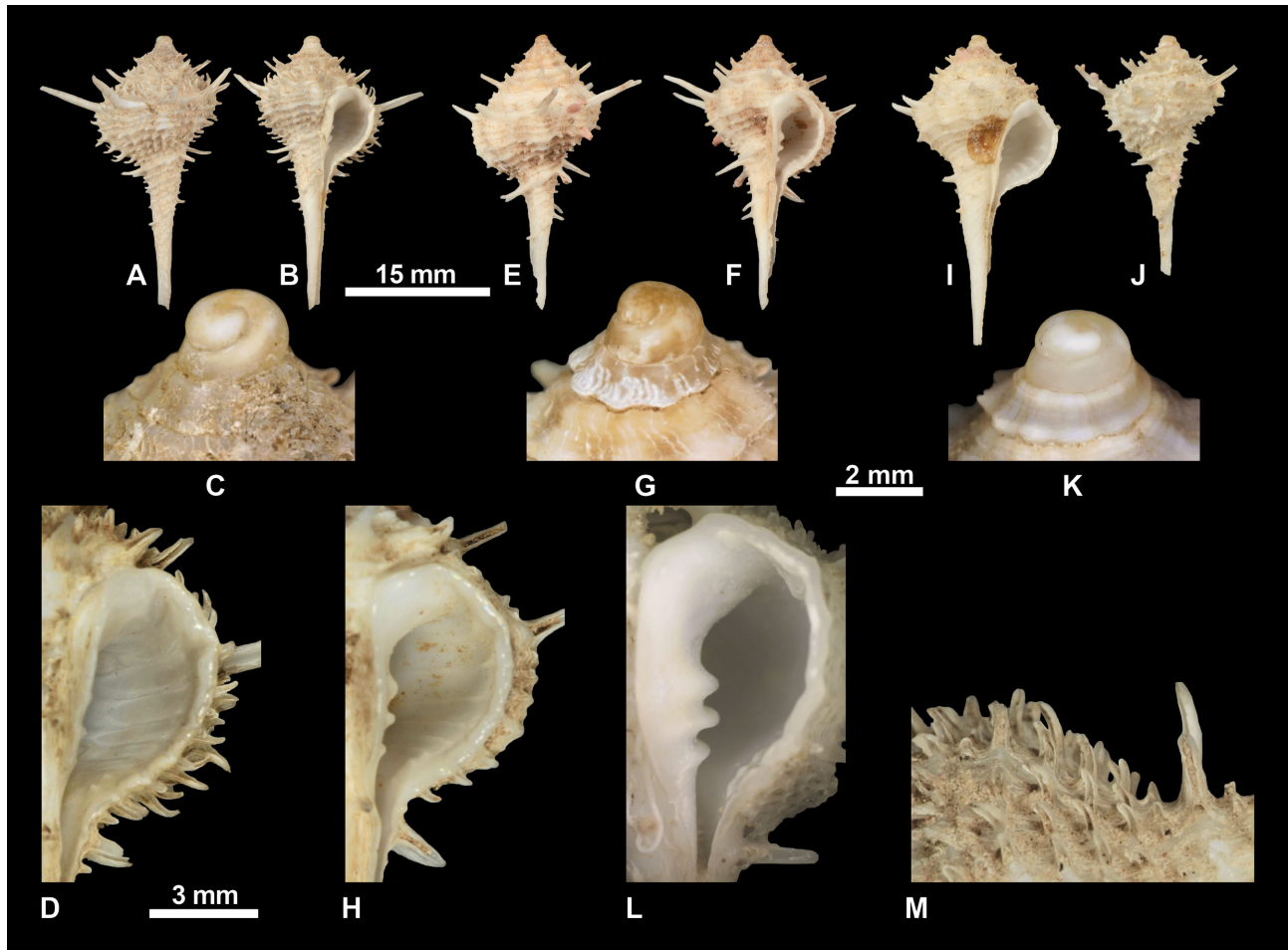


Figure 10. *Tudivasum westrale* n. sp. **A–D, M.** Holotype (WAM S99033), Ningaloo Reef, Western Australia. **E–H.** Paratype 1 (WAM S99393), Ningaloo Reef, Western Australia. **I.** Paratype 2 (HM coll.), Dongara, Western Australia. **J, L.** Paratype 3 (MNT P010248), Bernier Island, Western Australia. **K.** Paratype 4 (WAM S70637), Rottnest Island, Western Australia. Scale bars: **A, B, E, F, I, J** = 15 mm; **C, G, K** = 2 mm; **D, H, L, M** = 3 mm.

113°45'26"E to 22°16'20"S, 113°45'11"E, RV 'Cape Ferguson' Ningaloo Survey, Stn CF 4010 and 11-DOO, 99.7–104 m (Fig. 10A–D, M). Paratype 1: WAM S99393, off Ningaloo Reef (south), Western Australia, 22.0365°S, 113.8220°E to 22.0389°S, 113.8220°E. Paratype 2: HM, c. 80 nautical miles west of Dongara, Western Australia, 29°10'S, 114°10'E. Paratype 3: PO10248, 13 nautical miles west of Bernier Island, entrance to Shark Bay, Western Australia, 28°12.1'S, 113°22.5'E. Paratype 4: WAM S70637, northwest of Rottnest Island, Western Australia, 32°00'S, 115°30'E. Paratype 5: MNHN-IM-2014-6075, west of Ningaloo Reef, Western Australia, 21°48'S, 113°10'E. Paratype 6: JC, west of Ningaloo Reef, Western Australia, 21°48'S, 113°10'E. Paratype 7: WAM S70632, c. 73 km west of Cliff Head, Western Australia, 29°31.7'S, 114°15.5'E to 29°32.5'S, 114°16.2'E. Paratype 8: WAM S92091, northwest of Rottnest Island, Western Australia, 32°00'S, 115°30'E. Paratype 9: WAM S92090, 129 nautical miles northeast of Cape Lambert, Western Australia, 18°38.6'S, 118°07'E to 18°36.3'S, 118°08.5'E. Paratype 10: WAM S92093, seaward of Osprey Sanctuary Zone, Ningaloo Marine Park, Western Australia, 22°15'48"S, 113°44'58"E to 22°15'37"S, 113°45'1"E. Paratype 11: HM, west of Coral Bay, Western Australia, 23°6'15.0"S, 113°05'19.8"E. Paratype 12: HM, west side of Muiron Islands, north of North West Cape, Western Australia, 21°39'33.5"S, 114°12'17.8"E. Paratype 13: NHMUK 20160420, same locality as paratype 12.

ZooBank registration: urn:lsid:zoobank.org:act:75FDEBF2-BBF4-4BDD-B695-35E32E6E3EA7.

Material examined: See Supplementary Material Table S1.

Etymology: This beautiful species is named after Western Australia, as its range occupies the majority of the west coast of the state.

Diagnosis: Shell small, globose with straight, tapered siphonal canal; each whorl with single row of prominent spines, interspersed with rows of short hollow scale-like spines giving distinctly prickly appearance.

Description (holotype): Shell small for genus, napiform, with globose last adult whorl, straight, tapering siphonal canal, c. 50% overall shell length and short spire. Protoconch of $1\frac{1}{4}$ whorls, very small for genus (1.62 ± 0.12 mm, $n = 20$) but still mammillate. Three teleoconch whorls and last adult whorl sculptured with 2 spiral ribs, becoming 3 on penultimate whorl. Row of sharp hollow spines beginning on post-nuclear whorl, gradually increasing in length to reach 4.5–5 mm on last adult whorl. Last adult whorl also sculptured with 3 spinose spiral ribs between shoulder and suture and 7 spiral ribs below shoulder; another set of large spines at juncture of aperture and siphonal canal; then more spinose spiral ribs on upper half of the canal; all interspaces between ribs bearing

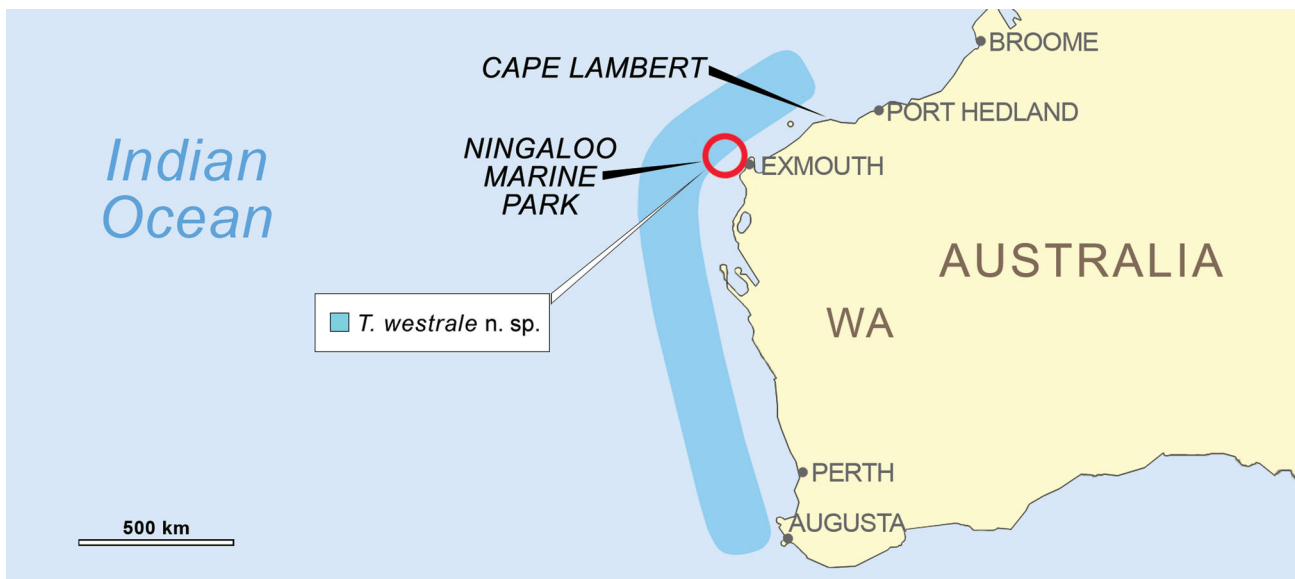


Figure 11. Type locality and range of *Tudivasum westrale* n. sp. Red circle denotes the type locality of *T. westrale* n. sp. from Ningaloo Marine Park. Both *T. westrale* n. sp. and *T. spinosum* have been recovered at the type locality and off Cape Lambert.

large lamellae, giving shell a distinctly prickly appearance. Anterior half of siphonal canal smooth; aperture oval but tapering anteriorly, strongly liriate with 2 distinct nodules near entrance to canal, which become 6 (rarely 7) lirae over remainder of inner lip; parietal shield strongly erect; columella with 3 strong plaits. Exterior cream or white, protoconch cream or pale orange, aperture white.

Habitat and distribution: The holotype was live collected by trawling on a sand and mud bottom at 99.7–104 m and was found in association with echinoderms and other molluscs. Other records of this species, albeit dead collected, indicate a much wider depth distribution (40–206 m).

Tudivasum westrale n. sp. has recently been taken off the southwest coast of Western Australia, near Augusta (34.3823°S, 115.1354°E), by a remotely operated vehicle (R. Walker, personal communication). Its range extends northwards to 129 nautical miles off Cape Lambert (18°38'S) in the northwest of Western Australia (Fig. 11). This species is largely sympatric with the western part of the range of *T. spinosum*: the two species co-occur north of Perth and have been taken together during trawls off Ningaloo and south of Port Hedland in Western Australia (denoted by red circles, Fig. 11).

Remarks: The animal of this species is known only from preserved specimens in the WAM. Due to the confusion surrounding the identity of *T. westrale* n. sp., observations of the living animal are lacking. Preserved material appears white with black eyes on a white stalk. The operculum is pale brown, leaf-like and thin, while still maintaining the features of the genus. As with most members of the genus, the shell of *T. westrale* n. sp. is variable in both length and degree of spinosity. The largest specimen measured is 40.20 mm (paratype 7), while the smallest adult (taken off Ningaloo Reef) is 21.46 mm. The average length is 29.4 mm ($n = 37$), making *T. westrale* n. sp. the smallest member of the genus. Larger shells have longer spines and appear less 'prickly'; however, the overall number of spinose ribs remains much the same. *Tudivasum westrale* n. sp. has been taken in scientific trawls dating back to the 1960s, often with *T. spinosum* in the same haul. Due to the variability of *T. spinosum*, it has always been assumed that the 'tiny, prickly specimens' were just extreme examples of the more common but larger species, *T. spinosum*. During the 'Southern Surveyor' expeditions, sufficient numbers of *Tudivasum* specimens were collected to finally enable analysis. It is now apparent that the smaller shells all have a tiny protoconch

(1.60 mm, $n = 38$) (Fig. 10C, G, K), lirae within the aperture (Fig. 10D, H, L) and spines extending along the siphonal canal (Fig. 10A, B, E, F, I, J); even shell fragments could be determined using these features. The only other comparable member of the genus is the co-occurring *T. spinosum*. These shells are larger, with an average protoconch size of 1.87 mm, 9 or 10 lirae within the aperture (Fig. 7F, J) and a totally smooth siphonal canal (Fig. 7A, B, I, J, K, L). Some specimens of *T. spinosum* exhibit large spines around the periphery of the last adult whorl but never multiple rows of spines.

Tudivasum inerme is similar in size to very large specimens of *T. westrale* n. sp., but it has a larger protoconch, 9 or 10 (rarely 11) apertural lirae, is usually strongly coloured with tan and brown (Fig. 5A–I), and lacks spines. The other members of the genus are either much larger (*T. armigerum* and *T. kurtzi*) or bear no resemblance to *T. westrale* n. sp. (*T. chaneyi* n. sp., *T. ashmoreense* n. sp. and *T. rasilistoma*).

DISCUSSION

Examination of specimens of the nine species of *Tudivasum* reveals that regardless of size, and to some extent, shape or spinosity, seven of the species are clearly identifiable. However, two species (*Tudivasum inerme* and *T. spinosum*) show a wide and confusing variation in shell morphology. For example, potentially subtle adaptation to different environmental conditions throughout the large geographical range of *T. spinosum* (Fig. 6) may have resulted in the wide variability of size, shell shape and spinosity (Fig. 7B, E, J, L). In contrast, *T. inerme* appears to be morphologically more uniform, particularly in the case of inshore shallow populations. However, recent trawling in the far northwest of Western Australia and around the Rowley Shoals and Ashmore Reef has recovered shells that are more variable. These specimens, none of which have been live collected, blur the line between the pictured types of *T. inerme* and *T. spinosum* (compare Fig. 5E, F with Fig. 7I, J). Future genetic studies involving nuclear markers are needed to investigate whether individuals from these locations might be hybrids, or whether they expand the known extent of morphological variation for *T. inerme*.

The phylogeny presented here shows that *T. spinosum* and *T. inerme* are well-supported sister taxa, which is consistent with their morphological similarity (Fig. 2). With an incomplete phylogeny, however, it is premature to interpret broader patterns of speciation in the group. Additionally, this topology is based solely on

mitochondrial genes, so it needs to be confirmed with additional sampling of nuclear loci. The northern half of Australia contains many species pairs that are thought to be the result of the intermittent emergence of the Torres land bridge (see references in Mirams *et al.*, 2011). The widely distributed *T. spinosum* may have been split several times in the past, potentially giving rise to some of the more restricted east or west species. However, the greatest diversity of *Tudivasum* species occurs in the northwest, and multiple tectonic or sea-level change events may have driven speciation processes in this region (Wilson, 2013). Unfortunately, the poor fossil record for this group may never allow for robust molecular dating of divergence events.

A southern specimen of *T. westrale* n. sp. sequenced in this study (WAM S43233) shows a potential species-level divergence from the other sequenced specimens (all from near Ningaloo) (Fig. 2); this was reflected in *T. westrale* n. sp. having a higher level of intraspecific variation in COI (0–0.045) than was recorded for the other species. Other southerly records of this species should be considered provisional species assignments until further species delimitation work can be carried out. It may be that the addition of sequence data from specimens sampled at intermediate geographical areas (such as Jurien Bay or the Abrolhos Islands) could break down the currently observed reciprocally monophyletic relationship, or the divergence seen here could be preliminary evidence that an unrecognized southern species exists.

The simultaneous discovery of two new species from one location is surprising. However, as has been previously noted (Wilson, 2013), the remote nature of Ashmore Reef, which makes access difficult, coupled with proximity to the centre of diversity (Indo Malay/Coral Triangle) may have contributed to the evolution of a highly endemic molluscan fauna in the area. Ashmore Reef is part of a Commonwealth of Australia Marine Reserve and includes Cartier Reef and associated sand cays. It covers c. 150 km² and lies 320 km northwest off the coast of the Western Australian mainland. The closest land mass to Ashmore Reef is Rote Island in eastern Indonesia (Carrigy & Fairbridge, 1954). The large distance between the reef and mainland shore of Australia, and the surrounding deep water have created an isolated habitat with a high level of endemism (Wilson, 2013). Three volute species are endemic to the area, *Melo ashmorensis*, *Amoria spenceriana* and *Cymbiola baili*. Volute species lack a planktonic distribution phase in their larval life cycle (Wilson, 1994, 2013: 335–341) and this may favour allopatric speciation over relatively short distances (Castelin *et al.*, 2010).

On the basis of their protoconch morphology, Harasewych (1998) inferred that volutes and other vasines lack planktonic dispersal. *Tudivasum* has a similar protoconch to these taxa, suggesting that it too lacks planktonic dispersal, thus being more prone to speciation than taxa with a planktonic dispersal stage (Wilson, 1994, 2013: 335–341; Kay, Wells & Ponder, 1998: 592; Castelin *et al.*, 2010). The discovery of two new species of *Tudivasum* from the remote Ashmore Reef is consistent with this expectation. If specimens of the new species can be found that are suitable for genetic analysis, the relationship of these two species can be clarified. Similarly, the relationship of *T. zanzibaricum* to the Australian members of *Tudivasum* needs to be addressed in this way.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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REFERENCES

- ABBOTT, R.T. 1958. A new Recent species of *Tudicula* from Zanzibar (Gastropoda: Vasidae). *Notulae Naturae of the Academy of Natural Sciences of Philadelphia*, **305**: 1–4.
- ABBOTT, R.T. 1959. The family Vasidae in the Indo-Pacific. *Indo-Pacific Mollusca*, **1**: 15–32.
- ABBOTT, R.T. & DANCE, P. 1982. *Compendium of seashells*. E.P. Dutton, New York.
- ADAMS, A. 1856. Descriptions of twenty-five new species of shells from the collection of Hugh Cuming, Esq. *Proceedings of the Zoological Society of London*, **23**: 221–226.
- ADAMS, H. & ADAMS, A. 1864. Descriptions of new species of shells, chiefly from the Cumingian collection. *Proceedings of the Zoological Society of London*, **1863**: 428–435.
- ANGAS, G.F. 1878. Description of a new species of *Tudicula*. *Proceedings of the Zoological Society of London*, **1878**: 610–611.
- BEESELEY, P.L., ROSS, G.J.B. & WELLS, A. (eds). 1998. *Mollusca: the southern synthesis. Fauna of Australia*. Vol. 5. Part A. CSIRO Publishing, Melbourne.
- CARRIGY, M.A. & FAIRBRIDGE, R.W. 1954. Recent sedimentation, physiography and structure of the continental shelves of Western Australia. *Journal of the Royal Society of Western Australia*, **38**: 65–95.
- CASTELIN, M., LAMBOURDIERE, J., BOISSELIER, M.-C., LOZOUET, P., COULOUX, A., CRUAUD, C. & SAMADI, S. 2010. Hidden diversity and endemism on seamounts: focus on poorly dispersive neogastropods. *Biological Journal of the Linnean Society*, **100**: 420–438.
- COCHRAN, T. 1986. Tasmanian *Tudicula!* *Australian Shell News*, **54**: 1.
- COUTO, D.R., BOUCHET, P., KANTOR, Y.I., SIMONE, L.R.L. & GIRIBET, G. 2016. A multilocus molecular phylogeny of Fasciolaridae (Neogastropoda: Buccinoidea). *Molecular Phylogenetics and Evolution*, **99**: 309–322.
- CUNHA, R.L., GRANDE, C. & ZARDOYA, R. 2009. Neogastropod phylogenetic relationships based on entire mitochondrial genomes. *BMC Evolutionary Biology* **9**: 210.
- DARRAGH, T.A. & KENDRICK, G.W. 2010. Eocene molluscs from the Merlino Sandstone, Carnarvon Basin, Western Australia. *Records of the Western Australian Museum*, **26**: 23–41.
- DE RYCKHOLT, P. 1862. *Melanges Paleontologiques, 1851–1862*. Part 3, pl. 33 (privately printed).
- DHARMA, B. 2005. *Recent and fossil Indonesian shells*. ConchBooks, Hackenheim, Germany.
- FEDOSOV, A., PUILANDRE, N., HERRMANN, M., KANTOR, Y.I., OLIVERIO, M., DGEBUADZE, P., MODICA, M.V. & BOUCHET, P. 2018. The collapse of *Mitra*: molecular systematics and morphology of the Mitridae (Gastropoda: Neogastropoda). *Zoological Journal of the Linnean Society*, **183**: 253–337.

- FOLMER, O., BLACK, M., HOEH, W., LUTZ, R. & VRIJENHOEK, R. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, **3**: 294–299.
- HARASEWYCH, M.G. 1998. Family Turbinellidae. In: *Mollusca: the southern synthesis. Fauna of Australia, Vol. 5, Part B* (P.L. Beesley, G.J.B. Ross & A. Wells, eds), pp. 824–825. CSIRO Publishing, Melbourne, Australia.
- HARASEWYCH, M.G. 2011. The living Columbariinae (Gastropoda: Neogastropoda: Turbinellinae) of New Zealand. *Zootaxa*, **2744**: 1–33.
- HILLIS, D.M. & BULL, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, **42**: 182–192.
- KATOH, K., MISAWA, K., KUMA, K.I. & MIYATA, T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, **30**: 3059–3066.
- KAY, E.A., WELLS, F. & PONDER, W.F. 1998. Class Gastropoda. In: *Mollusca: the southern synthesis. Fauna of Australia, Vol. 5, Part B* (P.L. Beesley, G.J.B. Ross & A. Wells, eds), pp. 565–604. CSIRO Publishing, Melbourne, Australia.
- KEARSE, M., MOIR, R., WILSON, A., STONES-HAVAS, S., CHEUNG, M., STURROCK, S., BUXTON, S., COOPER, A., MARKOWITZ, S., DURAN, C., THIERER, T., ASHTON, B., MEN-TJIES, P. & DRUMMOND, A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, **28**: 1647–1649.
- KUMAR, S., STECHER, G. & TAMURA, K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, **33**: 170–1874.
- KURODA, T. 1932. An illustrated catalogue of the Japanese shells (appendix). *Venus*, **3**: 87–102.
- LUDBROOK, N.H. 1941. Gastropoda from Abattoirs Bore, Adelaide, South Australia together with a list of some miscellaneous fossils from the Bore. *Transactions of the Royal Society of South Australia*, **65**: 79–102.
- MACPHERSON, J.H. 1964. A new species of *Tudicula* from North Australia. *Memoirs of the National Museum of Victoria*, **26**: 209–210.
- MIRAMS, A.G.K., TREML, E.A., SHIELDS, J.L., LIGGINS, L. & RIGINOS, C. 2011. Vicariance and dispersal across an intermittent barrier: population genetic structure of marine animals across the Torres Strait land bridge. *Coral Reefs*, **30**: 937–949.
- MODICA, M.V., BOUCHET, P., CRUAUD, C., UTGE, J. & OLIV-ERIO, M. 2011. Molecular phylogeny of the nutmeg shells (Neogastropoda, Cancellaridae). *Molecular Phylogenetics and Evolution* **59**: 685–697.
- MOLLUSCABASE. 2017. Turbinellinae Swainson, 1835. World Register of Marine Species. Available at: <http://www.marinespecies.org/aphia.php?p=taxdetails&cid=23134>. Accessed 25 April 2017.
- ROSENBERG, G. & PETTIT, R.E. 1987. Ryckholt's Melanges Paleontologiques 1851–1862, with a new name for *Tudicula* H.A. Adams, non Ryckholt. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **139**: 53–64.
- SILVESTRO, D. & MICHALAK, I. 2011. RaxMLGUI: a graphical front end for RAXML. *Organisms, Diversity and Evolution*, **12**: 335–337.
- SIMON, C., FRATI, F., BECKENBACH, A., CRESPI, B., LIU, H. & FLOOK, P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, **87**: 651–701.
- SMITH, E.A. 1884. Mollusca. In: *Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H. M. S. Alert' 1881–2. Pt. I. The collections from Melanesia*, pp. 34–116, pls 4–7. British Museum, London.
- SMITH, E.A. 1887. Miscellaneous, note on *Tudicula inermis*. *Annals and Magazine of Natural History*, **19**: 465–466.
- STAMATAKIS, A. 2006. RAXML-VI-HPC: maximum likelihood based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**: 2688–2690.
- STRONG, E.E., PUILANDRE, N., BEU, A.G., CASTELIN, M. & BOUCHET, P. 2019. Frogs and tuns and tritons: a molecular phylogeny and revised family classification of the predatory gastropod superfamily Tonnoidea (Caenogastropoda). *Molecular Phylogenetics and Evolution*, **130**: 18–34.
- WENZ, W. 1943. Gastropoda. Allgemeiner Teil und Prosobranchia, Teil 6. In: *Handbuch der Paläozoologie* (O.H. Schindewolf, ed.), Band 6, pp. 1201–1506. Gebrüder Bornträger, Berlin.
- WILSON, B.R. 1994. *Australian marine shells*. Vol. **2**. Odyssey Publishing, Kallaroo, Australia.
- WILSON, B.R. 2013. *The biogeography of the Australian North West Shelf: environmental change and life's response*. Elsevier, Amsterdam.