

## RECENT BRACHIOPODS FROM THE TONGA ISLANDS, SW PACIFIC: TAXONOMY AND BIOGEOGRAPHY

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To cite this article: Bitner M.A. (2019) - Recent brachiopods from the Tonga Islands, SW Pacific: taxonomy and biogeography. *Riv. It. Paleont. Strat.*, 125(3): 587-608.

**Keywords:** Brachiopoda; systematics; biodiversity; Pacific archipelagos; BORDAU 2.

*Abstract.* Twenty species of Recent brachiopods belonging to the genera *Neoancistrocrania*, *Basiliola*, *Basiliolella*, *Dyscolia*, *Abyssothyris*, *Xenobrochus*, *Terebratulina*, *Fallax*, *Septicollarina*, *Frenulina*, *Amphithyris*, *Annuloplatidia*, *Leptothyrella*, *Dallina*, *Campages*, *Thecidellina* and *Minutella* have been identified in the material collected during the French cruise BORDAU 2 to the Tonga Islands, South-West Pacific. Apart from *Frenulina sanguinolenta* all species represent the first records for the Tonga Islands. The investigated brachiopod fauna shows the greatest affinity to that from Fiji and New Caledonia, having 16 and 12 species in common, respectively. Although less affinity is observed with the New Zealand fauna, there are two species, *Terebratulina australis* and *Amphithyris buckmani* reported so far only from New Zealand, Fiji and Tonga. The biodiversity of brachiopods in Tonga is similar to that in Fiji but half as great as that in New Caledonia and New Zealand regions and much higher than in French Polynesia.

### INTRODUCTION

Since 1976 the South-West Pacific region has been intensively surveyed within the program Tropical Deep-Sea Benthos (formerly MUSORSTOM) established by the Muséum national d'Histoire naturelle (Paris, France) and the Institut de Recherche pour le Développement (Nouméa, New Caledonia). The present report focuses on the Tonga island group, explored during the cruise BORDAU 2 in 2000. The name of the cruise refers to the BORDER of the Indo-AUstralian plate (Bouchet et al. 2008). Tonga, comprising more than 170 islands, is an archipelago in the South Pacific Ocean close to Fiji, about two-thirds of the way from Hawaii to New Zealand (Fig. 1). It lies along the boundary of the Pacific and Indian-Australian tectonic plates and consists of two geologically different, parallel chains of islands; the western islands are of volcanic

origin, the eastern non-volcanic coral limestone. So far only two species, *Novocrania turbinata* (Poli, 1795) and *Frenulina sanguinolenta* (Gmelin, 1791) have been reported from Tonga (Saito & Endo 2001; Logan 2007; Robinson 2017). Although both species are well known and widely distributed in the western Pacific, in the studied material they are either absent (*N. turbinata*), or very rare (*F. sanguinolenta*). However, Robinson (2017) recognized *N. turbinata* in the University of Tokyo collection from Tonga. Among the 20 species identified in the studied material, 19 are reported for the first time from the Tonga Islands.

### MATERIAL AND METHODS

The material presented here was collected during the cruise BORDAU 2 (<https://expeditions.mnhn.fr/campaign/bordau2>) to the Tonga Islands, SW Pacific (Fig. 1). The expedition was organized by the Muséum national d'Histoire naturelle, Paris and by the Institut de la Recherche pour le Développement, Nouméa, New Caledonia

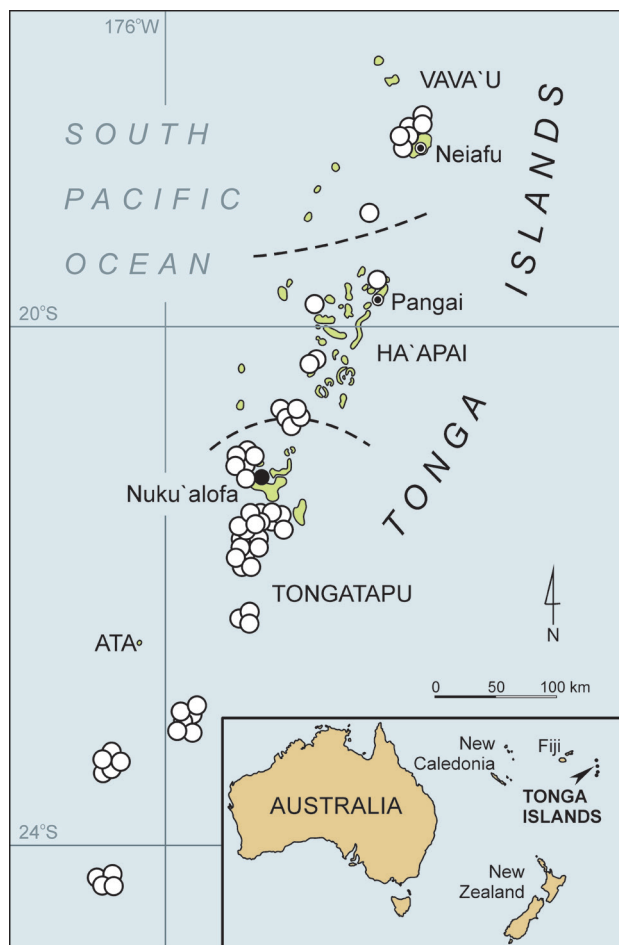


Fig. 1 - Map of Tonga Islands, showing location of the brachiopod-bearing stations.

on R.V. "Alis" and carried out from 31 May 2000 to 22 June 2000. Brachiopods were found in 69 out of 138 stations. The exact location, depth and species identified at each station are given in the Appendix. Although the collection is rich overall (1212 specimens), nine species are rare (3 or fewer specimens).

Samples were collected using a Warén dredge (DW) or a trawl (CP, CH). To remove soft tissues, specimens were treated with hypochlorite bleach, followed by a water wash. For scanning electron microscope (SEM) examination, the selected specimens were mounted on stubs, coated with platinum, and investigated using a Philips XL-20 microscope at the SEM laboratory of the Institute of Paleobiology, Warszawa. All the material is deposited in the collection of the Museum national d'Histoire naturelle, Paris, France under the catalogue number MNHN IB-2009-516 to IB-2009-562, IB-2009-1198, IB-2009-1240, IB-2013-678 to IB-2013-790.

## SYSTEMATIC PART

Phylum **BRACHIOPODA** Duméril, 1805  
 Subphylum **CRANIIFORMEA** Popov, Bassett,  
 Holmer & Laurie, 1993

Class **CRANIATA** Williams, Carlson, Brunton,  
 Holmer & Popov, 1996

Order **Craniida** Waagen, 1885

Superfamily Cranioidea Menke, 1828

Family Craniidae Menke, 1828

Genus *Neoancistrocrania* Laurin, 1992

Type species - *Neoancistrocrania norfolki* Laurin, 1992, by original designation of Laurin (1992: 344)

### *Neoancistrocrania norfolki* Laurin, 1992

Fig. 2A-C

1992 *Neoancistrocrania norfolki* Laurin, pp. 344-346, pl. 1, figs. 1-6, pl. 2, figs. 1-6.

1997 *Neoancistrocrania norfolki* - Laurin, pp. 417-418, fig. 41A-E.

2009 *Neoancistrocrania norfolki* - Bitner, p. 6, fig. 2A-F.

2010 *Neoancistrocrania norfolki* - Zezina, p. 1179.

2014a *Neoancistrocrania norfolki* - Robinson, fig. 3A-H.

2014b *Neoancistrocrania norfolki* - Robinson, p. 542, fig. 2A-E.

2015 *Neoancistrocrania norfolki* - Bitner, p. 35, fig. 2A-B.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1535, one dorsal valve (MNHN IB-2013-678); stn DW 1602, one dorsal valve (MNHN IB-2013-679); stn DW 1605, one ventral valve, broken (MNHN IB-2013-680).

**Depth range:** 263-441 m.

**Measurements:** Max. length 14.8 mm, width 20.8 mm.

**Remarks.** *Neoancistrocrania norfolki* is very rare in the studied material, found in only 3 stations. Morphologically this species is readily distinguished from *Novocrania* Lee & Brunton, 2001 by its massive, mineralized ventral valve and two erect divergent processes on the dorsal valve interior (Laurin 1992, 1997; Bitner 2009, 2015) and by unique features of the soft tissues (Robinson 2014a, 2014b). However, molecular analysis shows that "*Neoancistrocrania* is no more distantly related to the Northern clade of *Novocrania* than are other *Novocrania* clades" (Cohen et al. 2014: 145) suggesting generic synonymy of *Neoancistrocrania* under *Novocrania*. Such conflict between the morpho-classification and molecular systematics is observed in other brachiopod groups as well (Cohen & Bitner 2013; Bitner & Cohen 2015).

Previously *N. norfolki* had been found only in the West Pacific (Laurin 1997; Bitner 2009, 2015; Cohen et al. 2008, 2014). The present finding extends its geographical range eastward.

Subphylum **RHYNCHONELLIFORMEA**  
 Williams, Carlson, Brunton, Holmer & Popov, 1996  
 Class **RHYNCHONELLATA** Williams, Carlson,  
 Brunton, Holmer & Popov, 1996

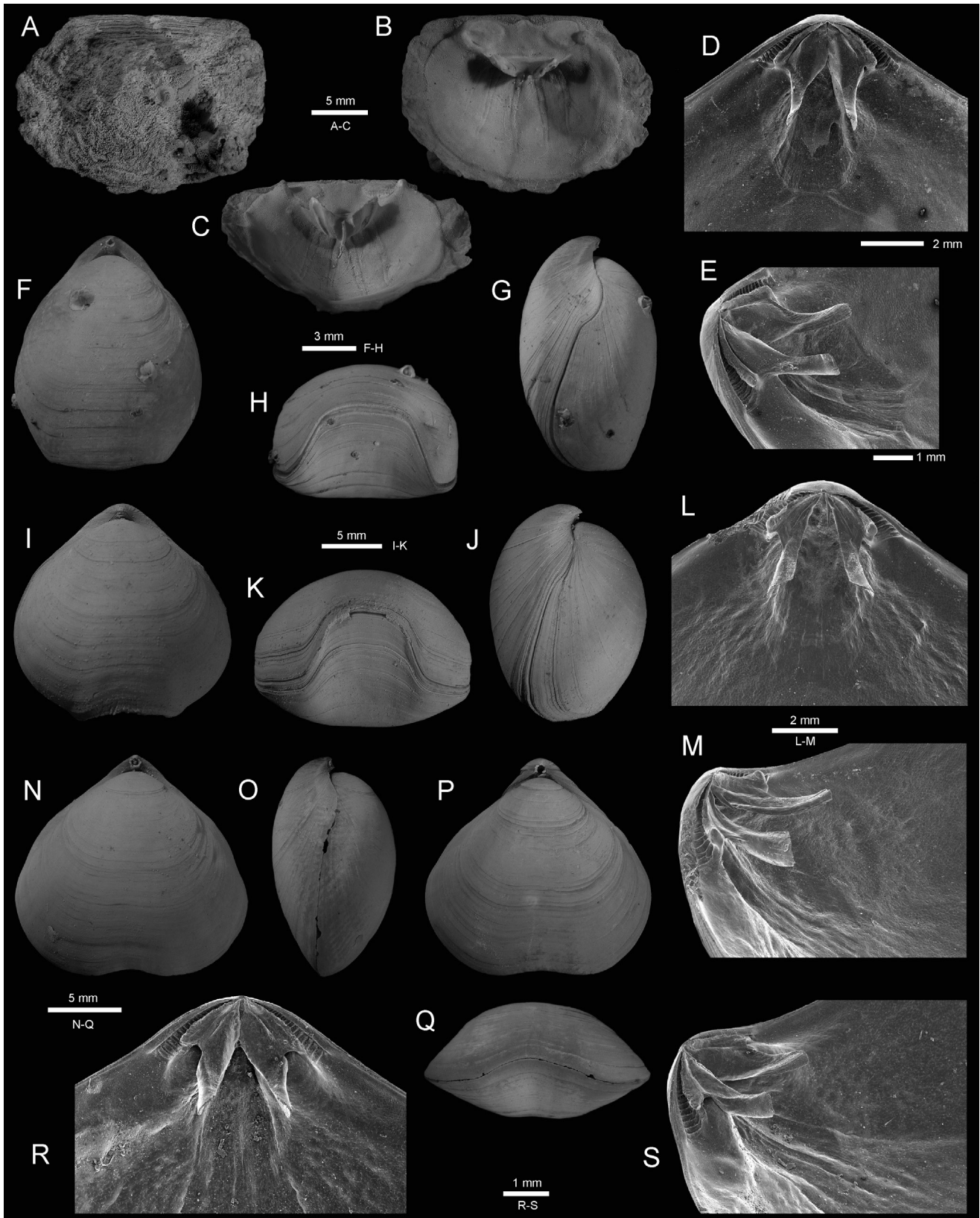


Fig. 2 - A-C - *Neoancistrocrania norfolki* Laurin, 1992, Tonga, BORDAU 2, stn DW 1602, 263-320 m, outer, inner and tilted views of dorsal valve, MNHN IB-2013-679. D-H - *Basiliola lucida* (Gould, 1862); (D-E) inner and oblique views of posterior part of dorsal valve, MNHN IB-2013-700, SEM, stn DW 1635, 320-323 m; (F-H) dorsal, lateral and anterior views of articulated specimen, MNHN IB-2013-699, stn DW 1587, 309-400 m. I-M - *Basiliola beecheri* (Dall, 1895), BORDAU 2; (I-K) dorsal, lateral and anterior views of articulated specimen, MNHN IB-2013-694, stn DW 1619, 591-593 m; (L-M) inner and oblique views of posterior part of dorsal valve, MNHN IB-2013-683, SEM, stn CP 1545, 444-447 m. N-S - *Basiliolella colurnus* (Hedley, 1905), BORDAU 2; (N-Q) dorsal, lateral views and dorsal, anterior views of two articulated specimens, MNHN IB-2013-706, stn CP 1545, 444-447 m; (R-S) inner and oblique views of posterior part of dorsal valve, MNHN IB-2013-703, SEM, stn DW 1536, 320-323 m.

Order Rhynchonellida Kuhn, 1949  
 Superfamily Pugnacoidea Rzhonsnitskaya, 1956  
 Family Basiliolidae Cooper, 1959  
 Genus *Basiliola* Dall, 1908

Type species - *Hemithyris beecheri* Dall, 1895, by original designation of  
 Dall (1908: 442)

***Basiliola lucida*** (Gould, 1862)

Fig. 2D-H

1862 *Rhynchonella lucida* Gould, p. 120.  
 2008 *Basiliola lucida* - Bitner, p. 427, fig. 5A-G (*cum syn.*).  
 2009 *Basiliola lucida* - Bitner, p. 7, fig. 3A-C.  
 2010 *Basiliola lucida* - Zezina, p. 1179.  
 2015 *Basiliola lucida* - Bitner, p. 36, fig. 2C-D.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1516, 4 articulated specimens (MNHN IB-2013-695); stn DW 1518, one articulated specimen (MNHN IB-2009-554); stn DW 1523, one articulated specimen (MNHN IB-2009-552); stn DW 1532, 19 articulated specimens, 3 ventral and one dorsal valves (MNHN IB-2009-558); stn CP 1533, 19 articulated specimens, one ventral and 2 dorsal valves (MNHN IB-2009-549); stn DW 1534, 2 articulated specimens (MNHN IB-2013-696); stn DW 1535, 2 articulated specimens (MNHN IB-2009-557); stn DW 1536, 13 articulated specimens (MNHN IB-2013-697); stn DW 1537, 2 articulated specimens (MNHN IB-2009-553); stn CP 1541, one articulated specimen (MNHN IB-2009-559); stn DW 1583, 4 articulated specimens (MNHN IB-2013-698); stn DW 1587, 9 articulated specimens (MNHN IB-2009-546, IB-2013-699); stn DW 1589, 5 articulated specimens (MNHN IB-2009-556); stn DW 1604, 7 articulated specimens (MNHN IB-2009-547); stn DW 1614, one articulated specimen (MNHN IB-2009-560); stn DW 1630, one ventral valve (MNHN IB-2009-562); stn DW 1634, 11 articulated specimens (MNHN IB-2009-548); stn DW 1635, 10 articulated specimens (MNHN IB-2009-551, IB-2013-700); stn DW 1636, 6 articulated specimens and one dorsal valve (MNHN IB-2009-555).

**Depth range:** 227-549 m.

**Measurements:** Max. length 13.9 mm, width 11.9 mm, thickness 9.3 mm.

**Remarks.** *Basiliola lucida* is the second most common species (more than 120 specimens) in this collection. Its shell is smooth with only growth lines, dorsibiconvex and strongly uniplicate. It can be easily distinguished from *B. beecheri* by its small size, elongate outline and narrower outer hinge plates (Hatai 1940; Cooper 1959; Laurin 1997; Bitner 2008, 2009, 2015).

*Basiliola lucida* is reported for the first time from the Tonga Islands although it was already identified in the nearby Fiji region (Bitner 2008). This species was originally described from off Japan (Gould 1862) and also occurs in the New Caledonian region (Laurin 1997; Bitner 2009, 2015).

***Basiliola beecheri*** (Dall, 1895)

Fig. 2I-M

1895 *Hemithyris beecheri* Dall, p. 717, pl. 31, figs. 1-4.  
 2008 *Basiliola beecheri* - Bitner, pp. 427-428, fig. 5H-L (*cum syn.*).  
 2009 *Basiliola beecheri* - Bitner, p. 6-7, fig. 3D, E.  
 2010 *Basiliola beecheri* - Zezina, p. 1179.  
 2015 *Basiliola beecheri* - Bitner, pp. 35-36, fig. 2G-H.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1509, one articulated specimen (MNHN IB-2009-544); stn CP 1510, 7 articulated specimens (MNHN IB-2013-681); stn DW 1538, 2 articulated specimens (MNHN IB-2009-545); stn CP 1539, 2 articulated specimens (MNHN IB-2009-542); stn DW 1543, one articulated specimen (MNHN IB-2013-682); stn DW 1544, one articulated specimen (MNHN IB-2009-540); stn CP 1545, 15 articulated specimens, one ventral and one dorsal valves (MNHN IB-2009-538, IB-2013-683); stn CP 1546, 2 articulated specimens and one dorsal valve (MNHN IB-2009-541); stn DW 1548, one articulated specimen (MNHN IB-2013-684); stn DW 1554, one articulated specimen (MNHN IB-2013-685); stn DW 1555, one articulated specimen (MNHN IB-2013-686); stn CH 1557, one articulated specimen (MNHN IB-2013-687); stn DW 1569, one articulated specimen (MNHN IB-2013-688); stn CP 1593, one articulated specimen (MNHN IB-2013-689); stn DW 1597, one articulated specimen (MNHN IB-2013-690); stn DW 1614, 2 articulated specimens (IB-2009-543); stn DW 1615, one articulated specimen (IB-2009-539); stn DW 1617, 4 articulated specimens (MNHN IB-2013-691); stn DW 1618, one articulated specimen (MNHN IB-2013-692); stn DW 1619, 2 articulated specimens and 2 ventral valves (MNHN IB-2013-693-694).

**Depth range:** 427-656 m.

**Measurements:** Max. length 18.9 mm, width 17.1 mm, thickness, 12.5 mm.

**Remarks.** *Basiliola beecheri* is relatively common (more than 50 specimens) in the material collected from the Tonga Islands. It is a medium-sized rhynchonellide characterized by a smooth except for concentric growth lines, dorsibiconvex, strongly uniplicate shell, and internally by wide hinge plates, subfalciform crura and lack of cardinal process. Although widely distributed in the Pacific from New Caledonia to Fiji and Hawaii (Dall 1895; Laurin 1997; Logan 2007; Bitner 2006b, 2008, 2009, 2015), this is the first record from Tonga.

Genus *Basiliolella* d'Hondt, 1987

Type species - *Basiliolella ferox* d'Hondt, 1987 by original designation  
 of d'Hondt (1987: 39)

***Basiliolella colurnus*** (Hedley, 1905)

Fig. 2N-S

1905 *Hemithyris colurnus* Hedley, pp. 44-45, figs. 7-8.  
 1920 *Hemithyris colurnus* - Dall, p. 288.  
 1959 *Eohemithyris colurnus* - Cooper, p. 32, pl. 15, figs. 15-26.  
 1981a *Eohemithyris colurnus* - Zezina, p. 11.  
 2010 *Eohemithyris colurnus* - Zezina, p. 1180.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1516, 2 articulated specimens (MNHN IB-2013-701); stn DW 1532,

4 articulated specimens (MNHN IB-2013-702); stn DW 1534, 2 articulated specimens (MNHN IB-2009-550); stn DW 1536, 2 articulated specimens (MNHN IB-2013-703); stn DW 1543, 2 articulated specimens (MNHN IB-2013-704); stn CP 1545, 7 articulated specimens and one ventral valve (MNHN IB-2013-705-706); stn DW 1589, one articulated specimen (MNHN IB-2013-707); stn 1604, one articulated specimen (MNHN IB-2013-708); stn DW 1606, one articulated specimen (MNHN IB-2013-709); stn DW 1612, one articulated specimen (MNHN IB-2009-561); stn DW 1634, one articulated specimen (MNHN IB-2013-710).

**Depth range:** 227-447 m.

**Measurements:** Max. length 14.6 mm, width 15.2 mm, thickness 8.5 mm.

**Remarks.** *Basiliolella colurnus* is the third rhychonellide brachiopod recognized in the material under study. This is a medium-sized species with smooth with numerous distinct growth lines, nearly equally convex shell subpentagonal in outline. The anterior commissure is uniplicate with a broad, gentle fold. The dorsal interior with a low median ridge and thickened crural bases. In size and outline *B. colurnus* is similar to *B. beecheri* but it differs in being nearly equally convex, weakly uniplicate and having thickened crural bases, whereas *B. beecheri* has unequal valves and strongly folded anterior commissure.

*B. colurnus* is known from off the eastern coast of Australia (Cooper 1959; Zezina 1981a; Logan 2007). Zezina (2010) also reported this species from the southern Sea of Japan, but without description or illustration. This is its first record from Tonga.

#### Order Terebratulida Waagen, 1883

##### Suborder Terebratulidina Waagen, 1883

##### Superfamily Dyscolioidea Fischer & Ehlert, 1891

##### Family Dyscolidae Fischer & Ehlert, 1891

##### Subfamily Dyscolinae Fischer & Ehlert, 1891

##### Genus *Dyscolia* Fischer & Ehlert, 1890

Type species - *Terebratulina nyvillei* Davidson, 1878 by original designation by Fischer & Ehlert (1890: 70)

#### *Dyscolia johannisdavisi* (Alcock, 1894)

1894 *Terebratulina johannisdavisi* Alcock, p. 139.

1940 *Dyscolia johannis-davisi* - Helmcke, p. 261, figs. 22, 25, 25b.

1959 *Dyscolia johannisdavisi* - Muir-Wood, pp. 300-302, pl. 1, figs. 1, 3, 4.

1986 *Dyscolia* cf. *johannisdavisi* - Hiller, pp. 106-110, figs. 4, 5.

1994 *Dyscolia johannisdavisi* - Zezina, pp. 46-48, fig. 2.

1997 *Dyscolia johannisdavisi* - Laurin, pp. 429-430, fig. 43J-L.

2009 *Dyscolia johannisdavisi* - Bitner, p. 11, fig. 6E, F.

**Material examined:** Tonga Islands, BORDAU 2 cruise, stn DW 1617, one dorsal valve, broken (MNHN IB-2013-711).

**Depth range:** 483-531 m.

**Remarks.** Although the material is very limited and poorly preserved, a very large size (observed width 42.7 mm) and smooth marked by concentric growth lines, thick shell with incurved valve margins make *Dyscolia johannisdavisi* one of the most easily recognizable species among living brachiopods. This species was long considered to be restricted to the Indian Ocean (Helmcke 1940; Muir-Wood 1959; Cooper 1983; Hiller 1986; Zezina 1994) until it was discovered in material from the New Caledonian region (Laurin 1997; Bitner 2009). This is its second occurrence in the Pacific and the first from Tonga.

#### Subfamily Aenigmathyridinae Cooper, 1983

##### Genus *Abyssothyris* Thomson, 1927

Type species - *Terebratulina nyvillei* Davidson, 1878 by original designation (Thomson 1927: 170)

#### *Abyssothyris wyvillei* (Davidson, 1878)

1878 *Terebratulina Wyvillei* Davidson, p. 436.

2008 *Abyssothyris wyvillei* - Bitner, p. 429, fig. 6I-L (*cum syn.*).

2010 *Abyssothyris wyvillei* - Zezina, p. 1185.

**Material examined:** Tonga, BORDAU 2 cruise, stn CP 1625, one articulated specimen, strongly broken (MNHN IB-2013-712), stn DW 1630, one immature articulated specimen (MNHN IB-2013-790).

**Depth range:** 360-824 m.

**Measurements:** Max. length 8.2 mm, width 8.0 mm and thickness, 5.1 mm.

**Remarks.** This short-looped species is very rare and poorly preserved in the material from Tonga. It is characterized by a small, smooth, except for growth lines, and thin shell with a deeply unisulcate anterior commissure. The lack of dorsal median septum makes it readily distinguishable from the externally very similar genus *Nipponithyris* Yabe & Hatai, 1934 (see Bitner 2008).

Like most species described here, this is the first record of *A. wyvillei* from Tonga, but it is known from many localities in the Pacific Ocean and has a circumpolar distribution in the South Ocean (Cooper 1982, 1983; Foster 1989; Laurin 1997; Bitner 2006b, 2008; Logan 2007; MacFarlan et al. 2009).

#### Genus *Xenobrochus* Cooper, 1981

Type species - *Gryphus africanus* Cooper, 1973 by original designation (Cooper 1981: 19)

***Xenobrochus rotundus* Bitner, 2008**

Fig. 3A-E

2008 *Xenobrochus rotundus* Bitner, pp. 429-431, fig. 6A-H.  
 2010 *Xenobrochus rotundus* - Zezina, p. 1185.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1534, one immature articulated specimen (MNHN IB-2013-713); stn DW 1537, 14 articulated specimens, 9 ventral and 2 dorsal valves (MNHN IB-2013-714); stn DW 1544, one articulated specimen (MNHN IB-2013-715); stn DW 1552, one articulated specimen (MNHN IB-2013-716).

**Depth range:** 302-500 m

**Measurements:** Max. length 9.0 mm, width 6.5 mm, thickness 7.0.

**Remarks.** *Xenobrochus rotundus* was originally described from the Fiji and Wallis and Futuna Islands (Bitner 2008); Tonga is another occurrence of this species. The shell is small, smooth with poorly marked growth lines, strongly biconvex with recti-marginate anterior commissure. Its beak is suberect with a small, circular foramen. The deltidial plates form a wholly visible symphytium. The cardinalia include a distinct, semi-elliptical cardinal process and very narrow hinge plates. The loop is short, and its transverse band has a weak fold. The specimens from Tonga differ from those from Fiji in being more elongate.

## Superfamily Cancellothyridoidea Thomson, 1926

## Family Cancellothyrididae Thomson, 1926

## Subfamily Cancellothyridinae Thomson, 1926

Genus *Terebratulina* d'Orbigny, 1847

Type species - *Anomia retusa* Linnaeus, 1758, by subsequent designation of Brunton et al. (1967: 176)

***Terebratulina reevei* Dall, 1920**

Fig. 3F-G

1920 *Terebratulina reevei* Dall, pp. 305-306.  
 2008 *Terebratulina reevei* - Bitner, p. 434, fig. 8A-G (*cum syn.*).  
 2009 *Terebratulina reevei* - Bitner, p. 13, fig. 7B.  
 2010 *Terebratulina reevei* - Zezina, p. 1186.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1516, 2 articulated specimens (MNHN IB-2013-749); stn DW 1523, 3 articulated specimens (MNHN IB-2013-750); stn DW 1567, 13 articulated specimens and one ventral valve (MNHN IB-2013-751); stn DW 1632, one articulated specimen (MNHN IB-2013-752).

**Depth range:** 229-618 m.

**Measurements:** Max. length 8.8 mm, width 6.2 mm, thickness 3.6 mm.

**Remarks.** *Terebratulina reevei* is one of the three *Terebratulina* species recognized in the Tonga

collection. This species differs from those described below in its smaller size and coarsely ribbed ornamentation. The ribs are also less numerous. First described from off the Philippines (Dall 1920), *T. reevei* is known also from the New Caledonian and Fijian regions (Laurin 1997; Bitner 2006b, 2008, 2009). The specimens from off Celebes and Borneo assigned to *T. reevei* by Zezina (1981a) are much larger. This attribution remains unclear because neither illustrations and nor detailed description were provided.

***Terebratulina japonica* (G.B. Sowerby, 1846)**

Fig. 3H-K

1846 *Terebratulina japonica* G.B. Sowerby, p. 91.  
 2008 *Terebratulina japonica* - Bitner, p. 433, fig. 7A-D (*cum syn.*).  
 2010 *Terebratulina japonica* - Zezina, p. 1185.  
 2017 *Terebratulina japonica* - Bitner & Romanin, p. 287, fig. 1A-B.  
 2018 *Terebratulina japonica* - Bitner & Romanin, p. 556, fig. 6C-D.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1509, one articulated specimen (MNHN IB-2009-537); stn DW 1516, 5 articulated specimens (MNHN IB-2013-725-726); stn DW 1523, 7 articulated specimens (MNHN IB-2013-727); stn DW 1524, 3 articulated specimens (MNHN IB-2013-728); stn DW 1548, 2 articulated specimens (MNHN IB-2013-729); stn DW 1554, one articulated specimen (MNHN IB-2013-730); stn DW 1555, 3 articulated specimens (IB-2013-731); stn CH 1557, 14 articulated specimens (MNHN IB-2013-732); stn DW 1569, one articulated specimen (MNHN IB-2013-733); stn DW 1570, one articulated specimen (MNHN IB-2013-734); stn CP 1582, one articulated specimen (MNHN IB-2013-735); stn DW 1584, 2 articulated specimens (MNHN IB-2013-736); stn DW 1585, one articulated specimen (MNHN IB-2013-737); stn DW 1597, one articulated specimen (MNHN IB-2013-738); stn DW 1604, one articulated specimen (MNHN IB-2013-739); stn DW 1615, one articulated specimen (MNHN IB-2013-740); stn DW 1616, one articulated specimen (MNHN IB-2013-741); stn DW 1617, one articulated specimen (MNHN IB-2013-742); stn DW 1618, 3 articulated specimens (MNHN IB-2013-743); stn DW 1619, 6 articulated specimens and one ventral valve (MNHN IB-2013-744-745); stn CP 1620, one articulated specimen (MNHN IB-2013-746); stn CH 1621, 5 articulated specimens (MNHN IB-2009-536); stn CP 1640, one articulated specimen (MNHN IB-2013-747).

**Depth range:** 79-781 m.

**Measurements:** Max. length 13.5 mm, width 10.9 mm, thickness 6.3 mm.

**Remarks.** The second *Terebratulina* species in the material under study is *T. japonica*. It is relatively common, with more than 60 specimens. This species can be easily differentiated from *T. reevei* by its ornamentation of numerous, fine ribs and from *T. australis* by its elongate oval outline and large foramen. The anterior commissure in adult *T. japonica* is weakly and broadly uniplicate. Originally described from off Japan (G.B. Sowerby 1846; Hatai 1940;

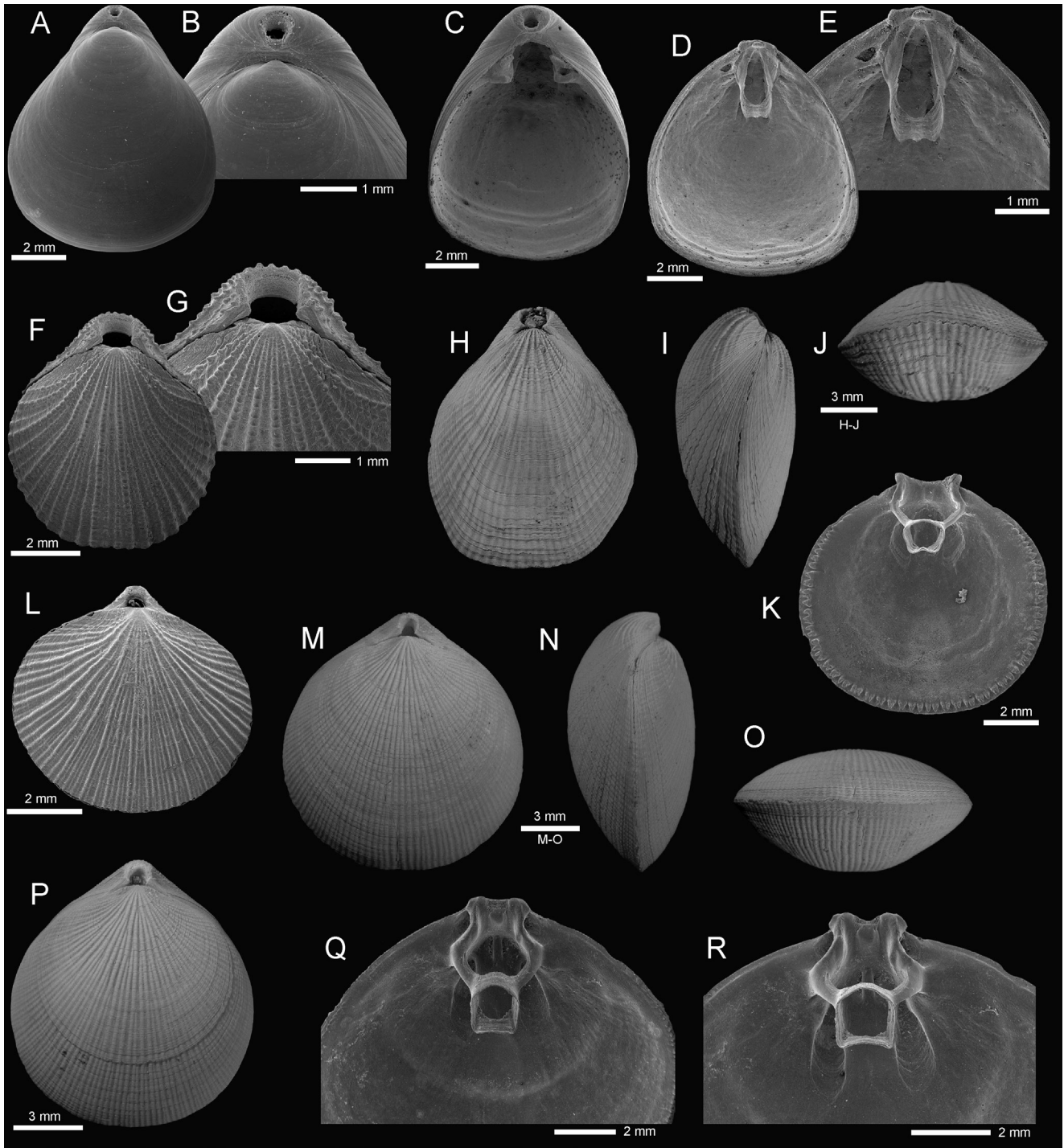


Fig. 3 - A-E - *Xenobrochus rotundus* Bitner, 2008, Tonga, BORDAU 2, SEM, A-B dorsal view of articulated specimen, and enlargement of posterior part to show details of the beak, MNHN IB-2013-714, stn DW 1537, 391-421 m; C-E inner views of disarticulated specimen, MNHN IB-2013-716, stn DW 1552, 491-500 m, (C) ventral valve, (D-E) dorsal valve, and enlargement (E) of posterior part to show details of brachial skeleton. F-G - *Terebratulina reevei* Dall, 1920, BORDAU 2, MNHN IB-2013-750, SEM, stn DW 1523, 300-302 m, dorsal view of articulated specimen, and enlargement (G) of posterior part. H-K - *Terebratulina japonica* (G.B. Sowerby, 1846), BORDAU 2, H-J dorsal, lateral and anterior views of articulated specimen, MNHN IB-2013-725, stn DW 1516, 229-246 m; K inner view of dorsal valve, MNHN IB-2013-745, SEM, stn DW 1619, 591-593 m. L-S - *Terebratulina australis* Bitner, 2006, BORDAU 2, L dorsal view of young specimen, MNHN IB-2013-748, SEM, stn DW 1631, 407-443 m; M-O dorsal, lateral and anterior views of articulated specimen, MNHN IB-2013-722, stn DW 1628, 400-416 m; P dorsal view of articulated specimen, MNHN IB-2013-724, stn DW 1634, 321-322 m; Q-R inner and tilted views of dorsal valve, MNHN IB-2013-718, SEM, stn CP 1510, 461-497 m.

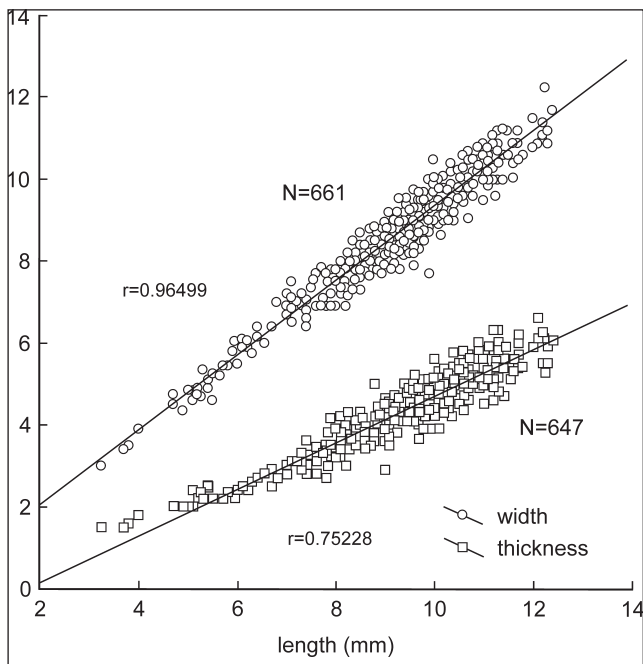


Fig. 4 - Intraspecific variation in *Terebratulina australis* Bitner, 2006. Scatter diagram plotting length to width and thickness. N number of specimens.

Logan 2007) it was also found in the South China Sea (Bitner & Romanin 2017, 2018) and Fiji (Bitner 2006b, 2008).

### *Terebratulina australis* Bitner, 2006

Figs. 3L-R, 4

2006b *Terebratulina australis* Bitner, pp. 25-27, fig. 5D-J.

2008 *Terebratulina australis* - Bitner, p. 434, fig. 7E-I.

2010 *Terebratulina australis* - Zezina, p. 1186.

**Material examined:** Tonga, BORDAU 2 cruise, stn CP 1510, 3 articulated specimens (MNHN IB-2013-717-718); stn DW 1517, one articulated specimen (MNHN IB-2009-534); stn DW 1518, 4 articulated specimens (MNHN IB-2013-719); stn DW 1520, one articulated specimen (MNHN IB-2013-720); stn DW 1523, 5 articulated specimens (MNHN IB-2009-525); stn DW 1524, 3 articulated specimens (MNHN IB-2009-533); stn CP 1525, 3 articulated specimens (MNHN IB-2009-524); stn DW 1532, 90 articulated specimens, 25 ventral and 20 dorsal valves (MNHN IB-2009-528); stn CP 1533, 2 articulated specimens and 2 dorsal valves (MNHN IB-2009-526); stn DW 1534, 12 articulated specimens (MNHN IB-2009-523); stn DW 1536, 35 articulated specimens and one ventral valve (MNHN IB-2009-530); stn DW 1537, 49 articulated specimens, one ventral and one dorsal valves (MNHN IB-2009-521); stn DW 1540, 13 articulated specimens (MNHN IB-2009-535); stn CP 1541, 2 articulated specimens (MNHN IB-2009-531); stn DW 1606, 4 articulated specimens (MNHN IB-2013-721); stn DW 1611, 2 articulated specimens (MNHN IB-2009-522); stn DW 1612, 8 articulated specimens (MNHN IB-2009-532); stn DW 1614, 3 articulated specimens (MNHN IB-2009-527); stn DW 1628, 147 articulated specimens, 3 ventral and 3 dorsal valves (MNHN IB-2009-520, IB-2013-722); stn DW 1630, 55 articulated specimens (MNHN IB-2009-516); stn DW 1631, 99 articulated specimens, 2 ventral and 12 dorsal valves

(MNHN IB-2009-529, IB-2013-748); stn DW 1632, one articulated specimen (MNHN IB-2013-723); stn DW 1634, 42 articulated specimens and one ventral valve (MNHN IB-2009-519, IB-2013-724); stn DW 1635, 42 articulated specimens and one dorsal valve (MNHN IB-2009-517); stn DW 1636, 20 articulated specimens (MNHN IB-2009-518).

**Depth range:** 300-618 m.

**Measurements:** Max length 12.4 mm, width 11.7 mm, thickness 6.1 mm (see also Fig. 4).

**Remarks.** *Terebratulina australis* is the most common species (more than 700 specimens) in this collection. It was originally described from off the Fiji Islands (Bitner 2006b, 2008) where it is rare. The shell is thickened posteriorly. The inner socket ridges are narrow but massive, the ring is broad and subsquare. By its rounded outline, shell surface covered with numerous, fine but distinct ribs and a very small foramen this species differs from other *Terebratulina* species.

This species, although not described yet, was also recognized in the material from New Zealand (J.H. Robinson, personal communication).

### Suborder *Terebratellidina* Muir-Wood, 1955

Superfamily Laqueoidea Thomson, 1927

Family Frenulinidae Hatai, 1938

Subfamily Frenulininae Hatai, 1938

Genus *Frenulina* Dall, 1895

Type species - *Anomia sanguinolenta* Gmelin, 1791 by original designation of Dall (1895: 724)

### *Frenulina sanguinolenta* (Gmelin, 1791)

Fig. 5A-B

1791 *Anomia sanguinolenta* Gmelin, p. 3347.

2014 *Frenulina sanguinolenta* - Bitner, pp. 250, 252-253, 255, fig. 8A-E (*cum syn.*).

2015 *Frenulina sanguinolenta* - Bitner, p. 41, fig. 4F-G.

2016 *Frenulina sanguinolenta* - Bitner & Logan, p. 24, fig. 13A.

2016 *Frenulina sanguinolenta* - Álvarez, pp. 63-65, pls. 25K-BB, 26A-O.

2018 *Frenulina sanguinolenta* - Bitner & Romanin, pp. 558-559, fig. 6O-P.

**Material examined:** Tonga, BORDAU 2 cruise, Stn DW 1569, one articulated specimen (MNHN IB-2013-756).

**Measurements:** Length 6.3 mm, width 6.1 mm, thickness 3.6 mm.

**Depth range:** 433 m.

**Remarks.** This species, although already reported from the Tonga region (Thomson 1927; Saito & Endo 2001; Logan 2007; Zezina 2010), is represented by only one specimen in the studied material. By its red colour pattern and a small, sulcate shell *Frenulina sanguinolenta* is easily distinguishable among



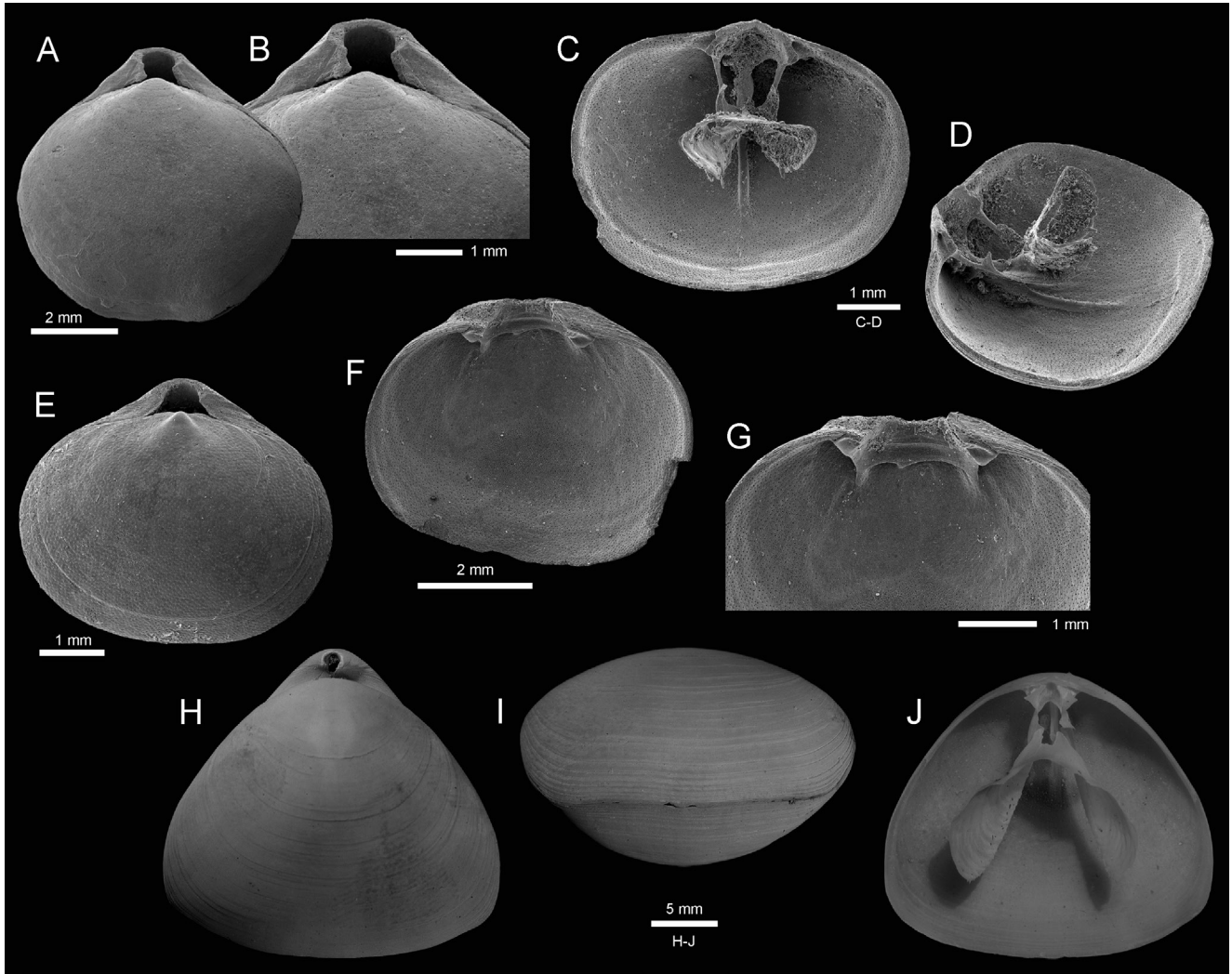


Fig. 5 - A-B - *Frenulina sanguinolenta* (Gmelin, 1791), BORDAU 2, MNHN IB-2013-756, stn DW 1569, 433 m, dorsal view of articulated specimen, and enlargement (B) of posterior part, SEM. C-G - *Septicollarina zezinae* Bitner, 2009, Tonga, BORDAU 2, MNHN IB-2013-755, stn DW 1523, 300-302 m, SEM; (C-D) inner and oblique views of dorsal valve; (E) dorsal view of articulated specimen; (F-G) inner and tilted views of ventral valve to show dental plates and pedicle collar supported by a septum. H-J - *Fallax neocaledonensis* Laurin, 1997, MNHN IB-2013-753, BORDAU 2, stn DW 1617, 483-531 m; (H-I) dorsal and anterior views of articulated specimen; (J) inner view of dorsal valve of the same disarticulated specimen.

brachiopods. It is one of the most widely distributed species in the West Pacific, known from Japan, Australia and New Caledonia to French Polynesia and Hawaii (Hatai 1940; Emig 1987; Saito 1996; Laurin 1997; Logan 2007; Bitner 2006a, 2006b, 2008, 2009, 2010, 2014, 2015; Simon & Hoffmann 2013; Bitner & Romanin 2018; Álvarez 2016; Simon et al. 2016, 2018). Recently it has also been recognized in the Madagascar area (Bitner & Logan 2016).

Superfamily Kingenoidea Elliott, 1948

Family Aulacothyropsidae Dagens, 1972

Subfamily Babukellinae MacKinnon, Smirnova & Lee, 2006

### Genus *Septicollarina* Zezina, 1981

Type species - *Septicollarina bemiechinata* Zezina, 1981 by original designation of Zezina (1981a: 16)

### *Septicollarina zezinae* Bitner, 2009

Fig. 5C-G

- 2008 *Septicollarina* sp. - Bitner, pp. 437-439, fig. 16A.
- 2009 *Septicollarina zezinae* Bitner, pp. 14, 24-25, fig. 8A-N.
- 2010 *Septicollarina* sp. - Zezina, p. 1189.
- 2014 *Septicollarina zezinae* - Bitner, p. 250, figs. 6A-I, 7A-H.
- 2015 *Septicollarina zezinae* - Bitner, p. 41, fig. 4H-I.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1516, one articulated specimen (MNHN IB-2013-754); stn DW 1523, 4 articulated specimens (MNHN IB-2013-755).

**Depth range:** 229-302 m.

**Measurements:** Max. length 4.6 mm, width 5.9 mm, thickness 3.4 mm.

**Remarks.** This species is rare in the Tonga material, and is represented only by immature specimens. Its shell is transversely subpentagonal with the surface covered with delicate radial lines and rare pustules. The ventral valve interior has distinct dental plates and a wide pedicle collar supported by a short median septum. The cardinalia are without a cardinal process and with inner hinge plates attached to the median septum, forming a septalium. The loop has broad ascending branches and transverse band and is weakly spinose anteriorly.

Although widely distributed in the SW Pacific, occurring from New Caledonia, Fiji to French Polynesia (Bitner 2008, 2009, 2014, 2015), this is the first record of *S. zezinae* from Tonga.

#### Genus *Fallax* Atkins, 1960

Type species - *Fallax dalliniformis* Atkins, 1960, by original designation (Atkins 1960: 72)

#### *Fallax neocaledonensis* Laurin, 1997

Fig. 5H-J

- 1997 *Fallax neocaledonensis* Laurin, pp. 444-448, figs. 31-34, 46a-o.  
 2006b *Fallax neocaledonensis* - Bitner, p. 27, fig. 5a-c.  
 2008 *Fallax neocaledonensis* - Bitner, p. 437, fig. 10H-J.  
 2009 *Fallax neocaledonensis* - Bitner, p. 13, fig. 7I-L.  
 2015 *Fallax neocaledonensis* - Bitner, p. 41, fig. 4J-K.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1554, one articulated specimen (MNHN IB-2013-789); stn DW 1617, one articulated specimen (MNHN IB-2013-753).

**Depth range:** 482-531 m.

**Measurements:** Max. length 21.6 mm, width 23.0 mm, thickness 15.9 mm.

**Remarks.** *Fallax neocaledonensis* is characterized by a smooth, with numerous growth lines shell, widely triangular in outline and the presence of well-developed dental plates. Its loop is of diploform type with broad ascending branches. In the material under study this species is very rare. In the New Caledonia region from where it was originally described, *F. neocaledonensis* is one of the most common species (Laurin 1997; Bitner 2009, 2015). It was also identified in the material from Fiji (Bitner 2006b, 2008).

#### Superfamily Platidioidea Thomson, 1927

##### Family Platidiidae Thomson, 1927

##### Subfamily Platidiinae Thomson, 1927

#### Genus *Amphithyris* Thomson, 1918

Type species - *Amphithyris buckmani* Thomson, 1918 by original designation of Thomson (1918: 20)

#### *Amphithyris buckmani* Thomson, 1918

Fig. 6A-F

- 1918 *Amphithyris buckmani* Thomson, p. 22, pl. 15, fig. 9, pl. 16, fig. 35.  
 2006b *Amphithyris buckmani* - Bitner, pp. 28-30, fig. 6a-f.  
 2008 *Amphithyris buckmani* - Bitner, pp. 440-442, fig. 11A-L.  
 2008 *Amphithyris buckmani* - MacKinnon et al., p. 329, fig. 1A-D.  
 2010 *Amphithyris buckmani* - Zezina, p. 1192.  
 2014 *Amphithyris buckmani* - Nauendorf et al., pp. 224-225.

**Material examined:** Tonga, BORDAU 2 cruise, stn CP 1560, 5 articulated specimens (MNHN IB-2013-757); stn CP 1562, 32 articulated specimens and one dorsal valve (MNHN IB-2013-758-759); stn CP 1578, 2 articulated specimens (MNHN IB-2013-760); stn DW 1612, 2 articulated specimens (MNHN IB-2013-761); stn DW 1628, 5 articulated specimens (MNHN IB-2013-762); stn DW 1630, one articulated specimen (MNHN IB-2013-763); stn DW 1631, 6 articulated specimens (MNHN IB-2013-764).

**Depth range:** 327-443 m.

**Measurements:** Max. length 4.0 mm, width 4.3 mm, thickness 1.3 mm.

**Remarks.** With more than 50 specimens *Amphithyris buckmani* is a relatively common species in the Tonga material but this is its first record from the area. Originally this species was described from the waters of New Zealand (Thomson 1918; MacKinnon et al. 2008; Nauendorf et al. 2014), later being also found in the Fiji region where it is the commonest species (Bitner 2006b, 2008).

This micromorphic species has a convex ventral valve with radial lines and a smooth, flat dorsal valve. Its foramen is very large, amphithyrid, subcircular to oval in outline. The internal morphology is very simple with a few characters only. The socket ridges are short, projecting slightly beyond the margin. The median septum is short and low. Crura and loop are not developed. The specimens from Tonga are smaller than those described from New Zealand and Fiji where *A. buckmani* can reach more than 5 mm in length (Bitner 2008; MacKinnon et al. 2008).

#### Genus *Annuloplatidia* Zezina, 1981

Type species - *Annuloplatidia indopacifica* Zezina, 1981 by original designation of Zezina (1981b: 144)

#### *Annuloplatidia curiosa* Bitner, 2014

Fig. 6G-M

- 2014 *Annuloplatidia curiosa* Bitner, pp. 255-258, figs. 9A-H, 10A-F (*cum syn.*).  
 2015 *Annuloplatidia curiosa* - Bitner, p. 42, fig. 5K-L.  
 2018 *Annuloplatidia curiosa* - Bitner & Romanin, pp. 559-561, fig. 7H-M.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1521, 2 articulated specimens (MNHN IB-2013-765); stn DW 1605, 7 ar-

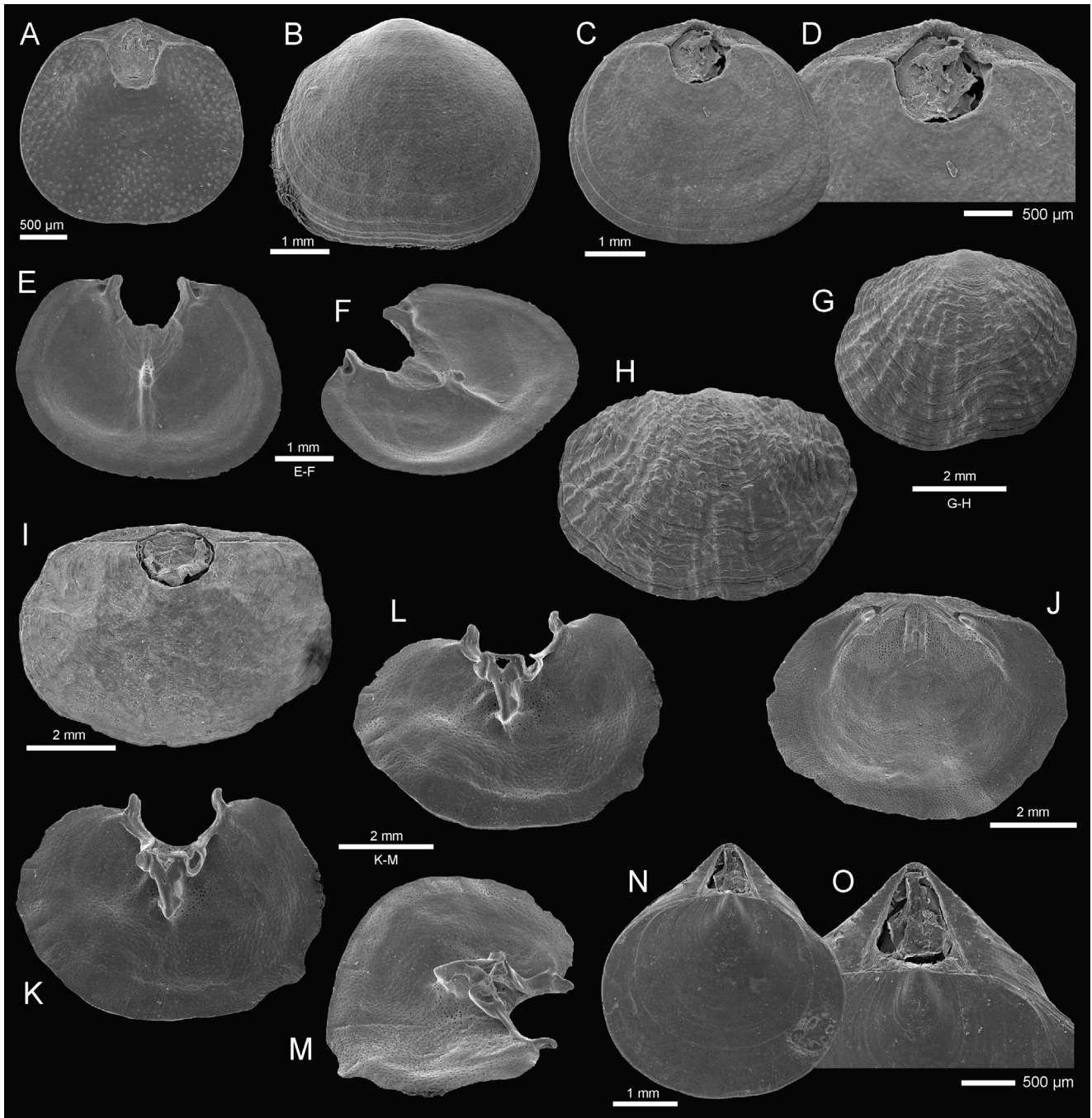


Fig. 6 - A-F - *Amphithyris buckmani* Thomson, 1918, Tonga, BORDAU 2; (A) dorsal view of young articulated specimen, MNHN IB-2013-759, stn CP 1562, 417-424 m; (B) ventral view of articulated specimen, MNHN IB-2013-760, stn CP 1578, 329-331 m; (C-D) dorsal view of articulated specimen, and enlargement (D) of posterior part to show details of the beak, MNHN IB-2013-759, stn CP 1562; (E-F) inner and oblique views of dorsal valve, MNHN IB-2013-759, stn CP 1562. G-M - *Annuloplatidia curiosa* Bitner, 2014, BORDAU 2; (G-H) ventral views of two articulated specimens, MNHN IB-2013-766, stn DW 1605, 441 m; (I) dorsal view of complete specimen, MNHN IB-2013-767, stn DW 1615, 482-504 m; (J-M) inner views of disarticulated specimen, MNHN IB-2013-768, stn DW 1616, 664-781 m, (J) ventral valve, (K-M) inner, tilted and oblique views of dorsal valve. N-O - *Leptothyrella fijiensis* Bitner, 2008, dorsal view of articulated specimen, and enlargement (O) of posterior part, MNHN IB-2013-769, stn DW 1566, 530-531 m. All SEM.

articulated specimens (MNHN IB-2013-766); stn DW 1615, 7 articulated specimens (MNHN IB-2013-767); stn DW 1616, 11 articulated specimens (MNHN IB-2013-768).

**Depth range:** 225-781 m.

**Measurements:** Max. length 5.2 mm, width 7.4 mm, thickness 2.2 mm.

**Remarks.** *Annuloplatidia curiosa* is relatively rare in the investigated material; it was found in only 4 stations. This species is large for the genus, being readily distinguishable from other *Annuloplatidia* species by ribbed ornamentation of the ventral

valve. Its dorsal valve surface is rough and irregular with poorly marked growth lines. Internally it is characterized by a loop with descending branches attached to ascending branches that diverge from the septum and the ascending branches are connected by a transverse band.

This species is widely distributed in the SW Pacific, being recorded from New Caledonia, New Zealand, Wallis and Futuna Islands and French Polynesia (Bitner 2007, 2008, 2014, 2015). Recently it was also identified in the material from the South China Sea, constituting the first occurrence in the northern hemisphere waters (Bitner & Romanin 2018).

Subfamily Phaneroporinae Zezina, 1981

Genus *Leptothyrella* Muir-Wood, 1965

Type species - *Leptothyris ignota* Muir-Wood, 1959 by original designation of Muir-Wood (1959: 308)

***Leptothyrella fijiensis*** Bitner, 2008

Fig. 6N-O

2008 *Leptothyrella fijiensis* Bitner, p. 442-444, fig. 13A-L.

2010 *Leptothyrella fijiensis* - Zezina, p. 1193.

**Material examined:** Tonga, BORDAU 2 cruise, stn CP 1566, 2 articulated specimens (MNHN IB-2013-769).

**Depth range:** 530-531 m.

**Measurements:** Max. length 4.0 mm, width 3.6 mm, thickness 1.2 mm.

**Remarks.** This species is very rare in the collection from Tonga, found in only one station. Previously *L. fijiensis* has been known only from Fiji, its type locality (Bitner 2008). Its shell is small, smooth with poorly defined concentric growth lines, weakly biconvex with a large, triangular hypothyril foramen. The beak ridges are sharp with two rows of small tubercles. The specimens from Tonga are more rounded than those from Fiji.

Superfamily Terebratelloidea King, 1850

Family Dallinidae Beecher, 1893

Subfamily Dallininae Beecher, 1893

Genus *Dallina* Beecher, 1893

Type species - *Terebratula septigera* Lovén, 1846 by original designation of Beecher (1893: 383)

***Dallina triangularis*** Yabe & Hatai, 1934

Fig. 7N

1934 *Dallina triangularis* Yabe & Hatai, p. 662, figs. 31-35.

1940 *Dallina triangularis* - Hatai, p. 320, pl. 7, figs. 22-27.

2008 *Dallina triangularis* - Bitner, pp. 444-446, fig. 16B-G.

2010 *Dallina triangularis* - Zezina, p. 1195.

2018 *Dallina triangularis* - Bitner & Romanin, p. 559, fig. 7A-B.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1607, one articulated specimen, partly broken (MNHN IB-2009-1198).

**Depth range:** 356-367 m.

**Remarks.** This species is very rare in the investigated material, represented by one partly broken specimen. It is characterized by a medium-sized (length 32.5 mm), smooth, ornamented only by weakly defined growth lines shell with a paraplicate anterior commissure and a large, circular permeothyrid foramen. Internally the characteristic features are a lack of dental plates and a long loop not attached to the septum.

*Dallina triangularis* was established based on the material from off Japan (Yabe & Hatai 1934; Hatai 1940). It is also known from Fiji (Bitner 2008) and recently recognized in the South China Sea (Bitner & Romanin 2018).

Subfamily Nipponithyridinae Hatai, 1938

Genus *Campages* Hedley, 1905

Type species - *Campages furcifera* Hedley, 1905 by original designation of Hedley (1905: 43)

***Campages ovalis*** Bitner, 2008

Fig. 7F-M

2008 *Campages ovalis* Bitner, pp. 449-451, fig. 18A-J.

2010 *Campages ovalis* - Zezina, p. 1196.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1517, one articulated specimen (MNHN IB-2009-1240); stn DW 1523, 3 articulated specimens (MNHN IB-2013-770); stn CP 1525, one articulated specimen and one ventral valve (MNHN IB-2013-771); stn DW 1532, 14 articulated specimens, 2 ventral and 2 dorsal valves (MNHN IB-2013-772); stn DW 1535, one articulated specimen and one ventral valve (MNHN IB-2013-773); stn DW 1536, 4 articulated specimens (MNHN IB-2013-774); stn DW 1537, 3 articulated specimens (MNHN IB-2013-775); stn DW 1540, one articulated specimen (MNHN IB-2013-776); stn DW 1583, 4 articulated specimens (MNHN IB-2013-777); stn DW 1587, 2 articulated specimens (MNHN IB-2013-778); stn DW 1604, one articulated specimen (MNHN IB-2013-779); stn DW 1606, one articulated specimen (MNHN IB-2013-780); stn DW 1612, one articulated specimen (MNHN IB-2013-781); stn DW 1628, 4 articulated specimens (MNHN IB-2013-782); stn DW 1634, 5 articulated specimens (MNHN IB-2013-783); stn DW 1635, 2 articulated specimens (MNHN IB-2013-784); stn DW 1636, 5 articulated specimens (MNHN IB-2013-785).

**Depth range:** 227-421 m.

**Measurements:** Max. length 10.4 mm, width 8.2 mm, thickness 8.0 mm.

**Remarks.** This species is moderately com-

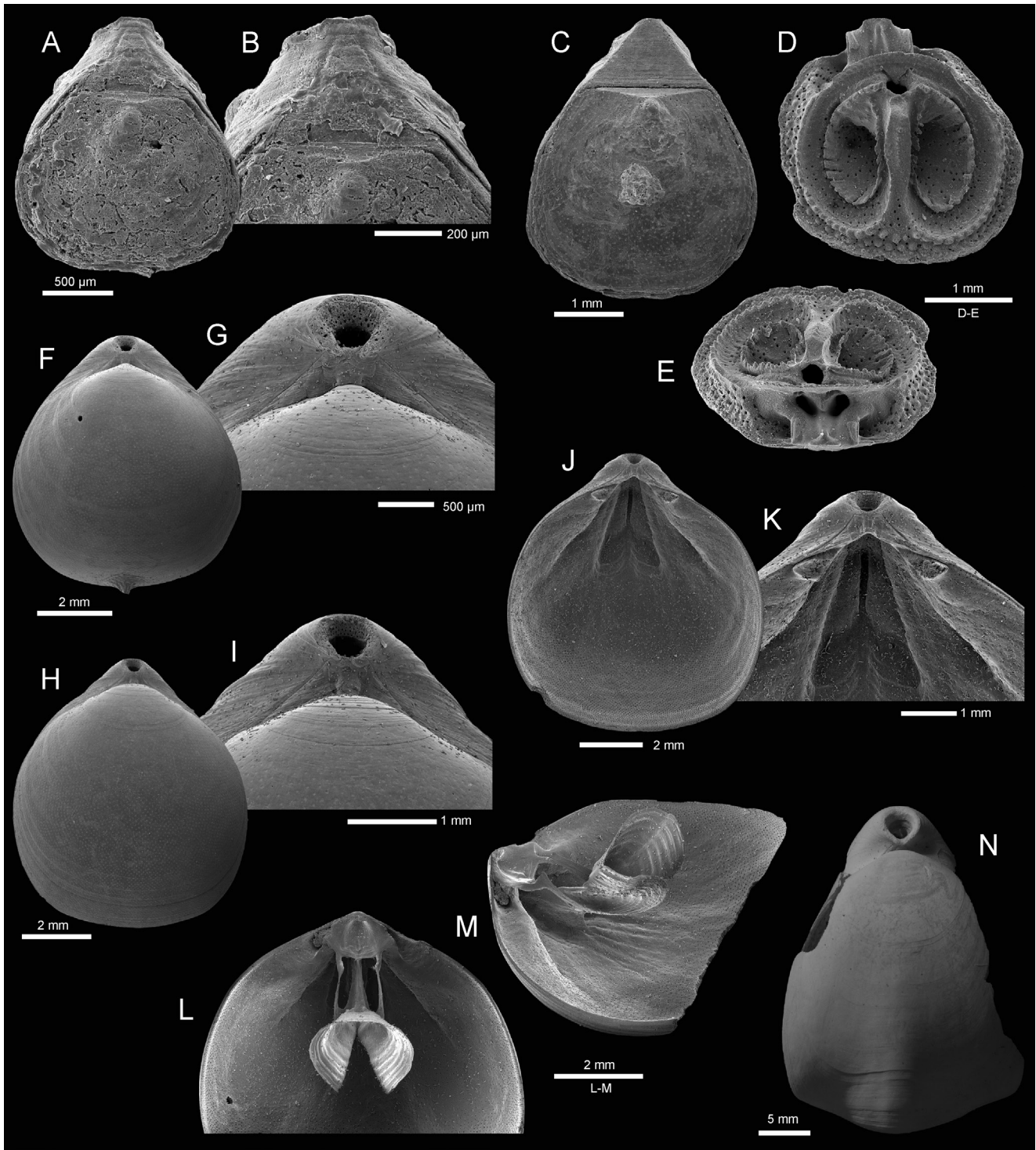


Fig. 7 - A-B - *Minutella minuta* (Cooper, 1981), Tonga, dorsal view of articulated specimen, and enlargement (B) of posterior part to show rugideltidium, MNHN IB-2013-788, BORDAU 2, stn DW 1521, 225-233 m, SEM. C-E - *Thecidellina maxilla* (Hedley, 1899), BORDAU 2, MNHN IB-2013-787, stn DW 1567, 351-356 m, SEM; (C) dorsal view of articulated specimen; (D-E) inner and posterior views of dorsal valve. F-M - *Campages ovalis* Bitner, 2008, MNHN IB-2013-772, BORDAU 2, stn DW 1532, 322 m, SEM; (F-I) dorsal views of two articulated specimens, and enlargement (G, I) of posterior part; (J-K) inner view of ventral valve and enlargement of posterior part to show delthyrial cavity; (L-M) inner and oblique views of dorsal valve. N - *Dallina triangularis* Yabe & Hatai, 1934, dorsal view of articulated specimen, partly broken, MNHN IB-2009-1198, BORDAU 2, stn DW 1607, 356-367 m.

mon (nearly 60 specimens) and widely distributed (found in 17 stations). Hitherto it has been known only from Fiji and Wallis and Futuna Islands (Bitner

2008). *C. ovalis* is a small species with a rounded to oval, strongly biconvex shell. It has a small, circular foramen and a visible symphytium. Its teeth are

small and without dental plates. The loop is typical for the genus with narrow, parallel descending branches and a broad hood. The muscle scars are strongly defined.

Order **Thecideida** Elliott, 1958

Superfamily Thecideoidea Gray, 1840

Family Thecidellinidae Elliott, 1958

Subfamily Thecidellininae Elliott, 1953

Genus *Thecidellina* Thomson, 1915

Type species - *Thecidium barretti* Davidson, 1864, by original designation of Thomson (1915: 462)

***Thecidellina maxilla*** (Hedley, 1899)

Fig. 7C-E

1899 *Thecidea maxilla* Hedley, pp. 508-510, fig. 57.

2008 *Thecidellina maxilla* - Bitner, p. 451, fig. 19A-C (*cum syn.*).

2009 *Thecidellina maxilla* - Bitner, pp. 17-18, fig. 12A-J.

2010 *Thecidellina maxilla* - Bitner, pp. 651-653, fig. 5G-J

2010 *Thecidellina maxilla* - Zezina, p. 1181.

2014 *Thecidellina maxilla* - Bitner, p. 259, fig. 11A-I.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1514, one articulated specimen (MNHN IB-2013-786); stn DW 1567, one articulated specimen and one dorsal valve (MNHN IB-2013-787).

**Depth range:** 130-356 m.

**Measurements:** Max. length 4.1 mm, width 3.2 mm, thickness 2.0 mm.

**Remarks.** *Thecidellina maxilla*, like all species attributed to this genus, is characterized by a flat interarea without pseudodeltidium, named planodeltidium by Logan & Baker (2013), and a single, straight dorsal septum (Hedley 1899; Cooper 1954; Lee & Robinson 2003). It is well-known in the South-West Pacific although determination and validity of the Pacific species of *Thecidellina* has been the subject of discussion (e.g. Lee & Robinson 2003; Hoffmann et al. 2009; Simon et al. 2018). In the opinion of Lee & Robinson (2003) morphological characters on which particular species of *Thecidellina* have been defined are minor and all Indo-Pacific forms could be variants of *Thecidellina maxilla*. In contrast other researchers (Hoffmann et al. 2009; Simon & Hoffmann 2013; Simon et al. 2018) find the differences in shell morphology to be noticeable. In their recent paper on thecideides Simon et al. (2018) discussed the taxonomic position of *T. maxilla* and concluded that several specimens attributed to the latter species by d'Hondt (1987), Laurin (1997), and Bitner (2007, 2009, 2014, 2015) represent either the species *T. congregata* Cooper, 1954 or a new species, or in some cases the specimens cannot be evaluated

because of insufficient description and illustration. It is worth mentioning that Simon et al. (2018) did not express their opinion about specimens of *T. maxilla* well illustrated and described by Lee & Robinson (2003) and Bitner (2008, 2010).

Nevertheless, all researchers (Lee & Robinson 2003; Simon & Hoffmann 2013; Simon et al. 2018) suggest that to elucidate this taxonomic problem morphological and ontogenetic studies of large populations together with molecular genetic analyses are strongly needed.

Subfamily Minutellinae Logan & Baker, 2013

Genus *Minutella* Hoffmann & Lüter, 2010

Type species: *Minutella tristani* Hoffmann & Lüter, 2010 by original designation of Hoffmann & Lüter (2010: 141)

***Minutella minuta*** (Cooper, 1981)

Fig. 7A-B

1981 *Thecidellina minuta* Cooper, p. 61, pl. 6, fig. 27-40.

2009 *Thecidellina minuta* - Bitner, p. 18, fig. 13A-I.

2010 *Thecidellina minuta* - Bitner, p. 653, fig. 5A-F.

2010 *Minutella minuta* - Hoffmann & Lüter, pp. 148, 150, pl. 2, figs. 13-18, pl. 3, figs. 13-15.

2010 *Minutella* cf. *minuta* - Hoffmann & Lüter, pp. 150, 152, pl. 3, figs. 16-24.

2013 *Minutella minuta* - Logan & Baker, p. 438, figs. 1F, 4I.

2013 *Minutella minuta* - Logan & Bitner, pp. 163-166, fig. 2A-O.

2013 *Minutella* cf. *minuta* - Simon & Hoffmann, pp. 405-412, pl. 1, figs. 1-5, pl. 2, figs. 1-8.

2018 *Minutella* cf. *minuta* - Simon et al., pp. 495-496, pl. 7, figs. 1-2.

**Material examined:** Tonga, BORDAU 2 cruise, stn DW 1521, one articulated specimen (MNHN IB-2013-788).

**Depth range:** 225-233 m.

**Measurements:** Length 1.8 mm, width 1.5 mm, thickness 0.9 mm.

**Remarks.** *Minutella minuta* is very rare in the material collected in the Tonga area. This species is characterized by a very small size and interarea with convex, triangular rugideltidium sensu Logan & Baker (2013). The present finding extends its geographical range eastward.

Recently *Minutella* is recorded from many localities in the Pacific, from Okinawa, Indonesia, Australia and New Caledonia to Palau, Fiji and Tonga (Hoffmann & Lüter 2010; Logan & Bitner 2013; Simon & Hoffmann 2013; Simon et al. 2016, 2018). Hoffmann & Lüter (2010), Simon & Hoffmann (2013) and Simon et al. (2018) stated that while all Pacific representatives of *Minutella* are nearly identical to the specimens of *M. minuta* described from Samper Bank, south-east of Madagas-

car, western Indian Ocean (the type locality of this species [Cooper 1981]) they prefer to describe them as *M. cf. minuta* because a few minor differences are present, although they do indicate that those few minor morphological differences can be affected by species variability. Logan & Bitner (2013), however, consider those minor differences as insufficient to separate distinct species and suggest that the Indo-Pacific forms are only varieties of *M. minuta*. This opinion is followed here.

As mentioned above morphological studies on large populations, combined with molecular analysis could resolve such taxonomic problems.

## DISCUSSION

Twenty brachiopod species belonging to 17 genera have been identified in the material collected during the French cruise BORDAU 2 to the Tonga Islands, SW Pacific (Fig. 1). With 14 species, terebratulide brachiopods dominate in the collection, while craniids have one representative, rhynchonellides have three, and thecideide brachiopods have two representatives. Together with *Novocrania turbinata* the total number of species documented in this region is 21. This is only a slightly lower diversity than that in the Fiji region (Bitner 2008; Hoffmann & Lüter 2010). If compared with the New Caledonian (Bitner et al. 2008; Bitner 2009, 2010, 2011, 2015; Bitner & Cohen 2015) and New Zealand regions (MacKinnon et al. 2008; MacFarlan et al. 2009; Nauendorf et al. 2014; Robinson et al. 2016) the diversity of brachiopods in Tonga is half as great, being however significantly higher than that in French Polynesia (Bitner 2006a, 2007, 2014). Thus, the diversity of brachiopods from Tonga fits well to the pattern of decrease in species number, observed in the Pacific from west to east (see also discussion in Bitner 2014).

Apart from *Frenulina sanguinolenta* the remaining species represent the first records for Tonga. The studied brachiopod fauna shows the greatest affinity to that from Fiji and New Caledonia, having 16 and 12 species in common, respectively (Laurin 1997; Bitner 2008, 2009, 2010, 2011, 2015). Most species have a wide distribution, being known from several localities in the Indo-Pacific province, however, there are also some with a very restricted dis-

tribution like *Leptothyrella fijiensis* known so far only from Fiji (Bitner 2008). Also *Xenobrochus rotundus* and *Campages ovalis* have the restricted distribution, being reported earlier from Fiji and Wallis and Futuna Islands (Bitner 2008). This collection also extends the known ranges of several forms, including *Neoancistrocrania norfolki* and *Basiliolella columnus*. The latter species has been known so far from the eastern coast of Australia (Logan 2007). Interestingly, two species, *Terebratulina japonica* and *Dallina triangularis* have a similar distribution; both species were described originally from off Japan (Hatai 1940) and have been also recognized in the South China Sea, Fiji and Tonga (Bitner 2008; Bitner & Romanin 2018; this paper).

Although low affinity is observed with the fauna from New Zealand, sharing 6 species (MacFarlan et al. 2009; Bitner 2014), two species, *Terebratulina australis* and *Amphithyris buckmani* occur only in New Zealand, Fiji and Tonga. *T. australis* was originally described from Fiji where it is rare, but in the Tonga collection it is predominant, constituting nearly 60% of the material. Similarly, *A. buckmani* was originally described based on one specimen from the New Zealand waters by Thomson (1918) and for 90 years it had been considered as endemic to New Zealand until it was discovered in the Fiji region where it is the most common species (Bitner 2008). The finding in Tonga extends the geographical range of both species.

*Acknowledgements:* My sincere thanks are to Philippe Bouchet for the opportunity to study the material and to Pierre Lozouet and Jérôme Mainguy (all Muséum national d'Histoire naturelle, Paris) for providing facilities during the visit at the Museum. Jeffrey H. Robinson (University of Otago, Dunedin) is thanked for the helpful discussion on craniid brachiopods. The macrophotographs were taken by Grażyna Dziewińska (Institute of Paleobiology, Warszawa) to whom I am grateful. I thank the Editor, Gaia Crippa and two reviewers, Fernando Álvarez (University of Oviedo, Oviedo) and J.H. Robinson for their helpful suggestions. J. Robinson also improved English.

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## APPENDIX - Station list

Station	Location	Depth	Species
<b>Tonga Islands</b>			
<b>BORDAU 2</b>			
DW 1509	21°05'S, 175°22'W	456-510 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
CP 1510	21°05'S, 175°23'W	461-497 m	<i>Basiliola beecheri</i> <i>Terebratulina australis</i>
DW 1514	21°18'S, 175°05'W	130-133 m	<i>Thecidellina maxilla</i>
DW 1516	21°21'S, 175°02'W	229-246 m	<i>Basiliola lucida</i> <i>Basiliolella colurnus</i> <i>Terebratulina japonica</i> <i>Terebratulina reevei</i> <i>Septicollarina zezinae</i>
DW 1517	21°21'S, 175°07'W	342 m	<i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1518	21°21'S, 175°07'W	336-347 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i>
DW 1520	21°25'S, 175°03'W	447-450 m	<i>Terebratulina australis</i>
DW 1521	21°19'S, 175°01'W	225-233 m	<i>Annuloplatidia curiosa</i> <i>Minutella minuta</i>
DW 1523	21°18'S, 175°00'W	300-302 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i> <i>Terebratulina japonica</i> <i>Terebratulina reevei</i> <i>Septicollarina zezinae</i> <i>Campages ovalis</i>
DW 1524	21°17'S, 175°00'W	351-354 m	<i>Terebratulina australis</i> <i>Terebratulina japonica</i>
CP 1525	21°17'S, 174°59'W	349-351 m	<i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1532	21°44'S, 175°20'W	322 m	<i>Basiliola lucida</i> <i>Basiliolella colurnus</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
CP 1533	21°44'S, 175°20'W	322-329 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i>
DW 1534	21°43'S, 175°19'W	302-327 m	<i>Basiliola lucida</i> <i>Basiliolella colurnus</i> <i>Xenobrochus rotundus</i> <i>Terebratulina australis</i>
DW 1535	21°43'S, 175°18'W	268 m	<i>Neoancistrocrania norfolki</i> <i>Basiliola lucida</i> <i>Campages ovalis</i>
DW 1536	21°45'S, 175°21'W	320-323 m	<i>Basiliola lucida</i> <i>Basiliolella colurnus</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>

Station	Location	Depth	Species
DW 1537	21°41'S, 175°19'W	391-421 m	<i>Basiliola lucida</i> <i>Xenobrochus rotundus</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1538	21°39'S, 175°19'W	471-508 m	<i>Basiliola beecheri</i>
CP 1539	21°37'S, 175°19'W	558-586 m	<i>Basiliola beecheri</i>
DW 1540	21°15'S, 175°14'W	317-329 m	<i>Terebratulina australis</i> <i>Campages ovalis</i>
CP 1541	21°15'S, 175°14'W	319-333 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i>
DW 1543	21°16'S, 175°18'W	427-436 m	<i>Basiliola beecheri</i> <i>Basiliolella colurnus</i>
DW 1544	21°18'S, 175°18'W	441-443 m	<i>Basiliola beecheri</i> <i>Xenobrochus rotundus</i>
CP 1545	21°17'S, 175°17'W	444-447 m	<i>Basiliola beecheri</i> <i>Basiliolella colurnus</i>
CP 1546	21°18'S, 175°18'W	430-441 m	<i>Basiliola beecheri</i>
DW 1548	20°38'S, 175°03'W	476-478 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
DW1552	20°38'S, 174°58'W	491-500 m	<i>Xenobrochus rotundus</i>
DW 1554	20°38'S, 174°58'W	482-498 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i> <i>Fallax neocaledonensis</i>
DW 1555	20°11'S, 174°45'W	591 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
CH 1557	20°10'S, 174°42'W	578 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
CP 1560	19°52'S, 174°39'W	365-372 m	<i>Amphithyris buckmani</i>
CP 1562	19°52'S, 174°42'W	417-424 m	<i>Amphithyris buckmani</i>
CP 1566	21°02'S, 175°18'W	530-531 m	<i>Leptothyrella fijiensis</i>
DW 1567	21°02'S, 175°19'W	351-356 m	<i>Terebratulina reevei</i> <i>Thecidellina maxilla</i>
DW 1569	21°02'S, 175°19'W	433 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i> <i>Frenulina sanguinolenta</i>
DW 1570	21°02'S, 175°19'W	533-578 m	<i>Terebratulina japonica</i>
CP 1578	19°42'S, 174°25'W	329-331 m	<i>Amphithyris buckmani</i>
CP 1582	18°41'S, 174°03'W	79-82 m	<i>Terebratulina japonica</i>
DW 1583	18°37'S, 174°03'W	327-360 m	<i>Basiliola lucida</i> <i>Campages ovalis</i>
DW 1584	18°36'S, 174°01'W	439 m	<i>Terebratulina japonica</i>
DW 1585	18°33'S, 173°57'W	578 m	<i>Terebratulina japonica</i>
DW 1587	18°37'S, 173°54'W	309-400 m	<i>Basiliola lucida</i> <i>Campages ovalis</i>
DW 1589	18°39'S, 173°54'W	281 m	<i>Basiliola lucida</i> <i>Basiliolella colurnus</i>

Station	Location	Depth	Species
CP 1593	19°06'S, 174°18'W	436-442 m	<i>Basiliola beecheri</i>
DW 1597	20°40'S, 174°55'W	598-610 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
DW 1602	20°49'S, 174°57'W	263-320 m	<i>Neoancistrocrania norfolki</i>
DW1604	22°16'S, 175°17'W	-350 m	<i>Basiliola lucida</i> <i>Basiliolella columnus</i> <i>Terebratulina japonica</i> <i>Campages ovalis</i>
DW 1605	22°17'S, 175°16'W	441 m	<i>Neoancistrocrania norfolki</i> <i>Annuloplatidia curiosa</i>
DW 1606	22°16'S, 175°20'W	313-316 m	<i>Basiliolella columnus</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1607	22°15'S, 175°23'W	356-367 m	<i>Dallina triangularis</i>
DW 1611	23°00'S, 175°47'W	278-323 m	<i>Terebratulina australis</i>
DW 1612	23°02'S, 175°47'W	327-342 m	<i>Basiliolella columnus</i> <i>Terebratulina australis</i> <i>Amphithyris buckmani</i> <i>Campages ovalis</i>
DW 1614	23°02'S, 175°51'	429-549 m	<i>Basiliola lucida</i> <i>Basiliola beecheri</i> <i>Terebratulina australis</i>
DW 1615	23°03'S, 175°53'W	482-504 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i> <i>Annuloplatidia curiosa</i>
DW 1616	23°04'S, 175°54'W	664-781 m	<i>Terebratulina japonica</i> <i>Annuloplatidia curiosa</i>
DW 1617	23°03'S, 175°53'W	483-531 m	<i>Basiliola beecheri</i> <i>Dyscolia johannisdavisi</i> <i>Terebratulina japonica</i> <i>Fallax neocaledonensis</i>
DW 1618	24°13'S, 176°18'W	627-656 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
DW 1619	24°16'S, 176°20'W	591-593 m	<i>Basiliola beecheri</i> <i>Terebratulina japonica</i>
CP 1620	24°18'S, 176°20'W	572 m	<i>Terebratulina japonica</i>
CH 1621	24°19'S, 176°23'W	570-573 m	<i>Terebratulina japonica</i>
CP 1625	23°28'S, 176°22'W	824 m	<i>Abyssothyris wyvillei</i>
DW 1628	23°22'S, 176°18'W	400-416 m	<i>Terebratulina australis</i> <i>Amphithyris buckmani</i> <i>Campages ovalis</i>
DW 1630	23°23'S, 176°18'W	360 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i> <i>Abyssothyris wyvillei</i> <i>Amphithyris buckmani</i>
DW 1631	23°23'S, 176°18'W	407-443 m	<i>Terebratulina australis</i> <i>Amphithyris buckmani</i>
DW 1632	23°22'S, 176°18'W	613-618 m	<i>Terebratulina australis</i> <i>Terebratulina reevei</i>

Station	Location	Depth	Species
DW 1634	21°45'S, 175°20'W	321-322 m	<i>Basiliola lucida</i> <i>Basiliolella columnus</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1635	21°44'S, 175°20'W	320-323 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1636	21°44'S, 175°20'W	321-331 m	<i>Basiliola lucida</i> <i>Terebratulina australis</i> <i>Campages ovalis</i>
DW 1640	21°09'S, 175°24'W	564-569 m	<i>Terebratulina japonica</i>