Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **98**, 425–435, 2008 (for 2007)

Gyrothyris williamsi sp. nov. and inter-relationships of some taxa from waters around New Zealand and the southern oceans (Rhynchonelliformea: Terebratelloidea)

Maria Aleksandra Bitner[1], Bernard L. Cohen[2], Sarah. L. Long[3], Bertrand Richer de Forges[4] and Michiko Saito[5]

[1] Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00–818 Warsaw, Poland
E-mail: bitner@twarda.pan.pl

[2] University of Glasgow, IBLS Division of Molecular Genetics, Pontecorvo Building, 56 Dumbarton Road, Glasgow, G11 6NU, Scotland, UK
E-mail: b.l.cohen@bio.gla.ac.uk

[3] Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD
E-mail: sll@nhm.ac.uk

[4] IRD, Centre de Nouméa, BP A5 Nouméa, New Caledonia, France
E-mail: richer@ird.noumea.nc

[5] Marine Biosystems Research Centre, Chiba University, c/o Dr. T. Yamaguchi, Dept. of Earth Sciences, Faculty of Science, Chiba University, 1–33 Yayoi-cho, Inage, Chiba 263–8522, Japan
E-mail: michiko_saito2001@yahoo.co.jp

ABSTRACT: This paper describes a terebratelloid articulate brachiopod, *Gyrothyris williamsi* sp. nov., based on 95 specimens from seamounts on the Lord Howe Rise, Coral Sea, SW Pacific Ocean. The new species is attributed to *Gyrothyris* on the basis of (a) morphological and growth trajectory similarities; (b) phylogenetic analyses of an alignment of DNA sequence (~2900-sites) obtained from nuclear-encoded small- and large-subunit ribosomal RNA genes (*SSU* and *LSU*); and (c) the presence of a distinctive, two-part deletion in the *LSU* gene. It is distinguished morphologically from *Gyrothyris mawsoni* and its subspecies by both internal and external morphology and by its isolated geographical distribution, which extends the patchy, known range of this genus to an area some 2000 km north of its previous northern limit around New Zealand. Phylogenetic analyses of the rDNAs and of mitochondrial *cox1* gene sequences (663 sites) confirm previous indications that the New Zealand endemic terebratelloid genera form a clade (*Neothyris* (*Calloria*, *Gyrothyris*, *Terebratella*), but the position of *Terebratella* with respect to *Calloria* and *Gyrothyris* remains weakly established. These sequences disagree inexplicably about the closeness of the relationship between *Neothyris parva* and *N. lenticularis*. Analyses of the first sequences from *Calloria variegata*, a species restricted to the Hauraki Gulf, New Zealand, are consistent with the possibility that it originated locally, and recently, from *C. inconspicua*. *Magellania venosa* from S. America/Falklands joins with Antarctic *Magellania fragilis* and *M. joubini* to form an rDNA clade that excludes *Terebratalia* as the putative sister-group of the New Zealand terebratelloid clade. The *cox1* (but not the rDNA) sequences of the New Zealand clade pass a test for clock-like rates of evolution, and maximum likelihood pairwise distances suggest that if genetic isolation between the ancestor of Antarctic *Magellania* and the last common ancestor of the New Zealand terebratelloid clade was initiated by separation of the Antarctic and New Zealand plates ~90 Mya, isolation from *M. venosa* was initiated earlier, perhaps ~145 Mya. However, in the simple phylogenetic reconstruction presented here from *cox1* sequences, S. American and Antarctic *Magellania* spp. do not yield a well-supported clade, perhaps because of differences in base composition.

KEY WORDS: DNA sequence, geographical distribution, *Gyrothyris*, molecular systematics, morphological systematics, rDNA, *Terebratella*

The subject of this report is a large sample of a new brachiopod found among a collection from the SW Pacific (Coral Sea) shortly before contributions to this commemorative volume were invited. From external morphology the new brachiopod was clearly a member of the Terebratelloidea, but it could be distinguished from *Terebratella* by its internal anatomy and colour. It was most similar to *Gyrothyris* (Thomson 1918, 1927; Foster 1974), the known range of which lies far to the

 doi:10.1017/S1755691008075142

south of the area from which the new specimens were collected. Attribution to *Gyrothyris* was confirmed by the discovery of a (double) deletion in one nuclear gene; which provided an unambiguous synapomorphy with *G. mawsoni* and distinguished the new form from all other candidate genera. Because the external and internal anatomy of the new form was distinguishable from all previously-described species and subspecies of *Gyrothyris*, it is described as *Gyrothyris williamsi* sp. nov., in commemoration of Alwyn Williams and in appreciation of his early support for work in Glasgow on brachiopod molecular systematics.

The morphological and DNA sequence-based analyses reported here were conducted as independent, parallel investigations so that both contributed to taxonomic decision-making. It is believed that this is the first time that both approaches have thus participated in the allocation of a new brachiopod to an established taxon, although not the first time that sequence data have been included in a description (Motchurova-Dekova *et al.* 2002). It is also thought to be the first time that the colour of a newly described brachiopod has been defined in terms of international colour standards.

Nuclear-encoded rDNA sequences were also obtained from other members of the terebratelloid clade endemic to New Zealand (NZ) and adjacent waters (*Calloria inconspicua* and *C. variegata*, *Neothyris lenticularis* and *N. parva*, *Terebratella sanguinea*), and from outgroups from elsewhere in the Pacific and Southern Oceans, and further afield. Mitochondrial *cox1* sequences were also obtained from all these taxa except the new *Gyrothyris*. These data are used to explore the molecular phylogeny of the NZ terebratelloid clade.

1. Materials and methods

1.1. Specimens

The new specimens were collected by Waren dredge (DW) and beam-trawl (CP), and preserved in alcohol during a cruise (Ebisco1, October 2005) by the RV *Alis* (IRD, Nouméa, New Caledonia) to the Lord Howe Rise, Coral Sea, where the new form was found at stations DW2495, CP2505, DW2577, DW2578 and DW2606. See station list at http://www.tropicaldeepseabenthos.org. Substrates at these sites were respectively limestone; silicates with sponges; stones with lithistid sponges, stylasterids and scleractinians; and limestone plates. This cruise continued a little-known campaign of deep-sea exploration in the Indo-West-Pacific (originally under the leadership of Alain Crosnier) by French research institutions in the course of which, since 1976, about 50 cruises staffed by a small scientific group have surveyed many of the major archipelagoes, sampling in the bathymetric range of 100 to 1500 m. The huge resulting collections are curated at the Muséum national d'Histoire naturelle (MNHN) in Paris, and are being studied by ~200 taxonomists from 24 countries. Many of the results have been published (e.g. Laurin 1992, 1997; Richer de Forges *et al.* 2000; Marshall & Richer de Forges 2004; Bitner 2006a, b) in a series that is already more extensive than the Challenger Reports. Since ca. 1993, BLC has been the fortunate recipient of many of the brachiopods collected, while MAB has more recently been studying their morphology. Details of the specimens used for morphology and sequencing are given in Table 1 and in section 2.1. Growth parameter comparisons with *Terebratella sanguinea* were made using typically alate specimens of the latter (Aldridge 1981), collected by SCUBA divers in 1990. Details of these specimens are given in the caption to Figure 4.

1.2. Morphological methods

For the new collection, external dimensions were measured to the nearest 0·1 mm using digital calipers. Sulcus width was measured at the commissure. To expose the loop, soft tissue was removed by soaking in hypochlorite bleach followed by a water wash, and this was repeated as necessary. For the study of shell ultrastructure, selected specimens were embedded in Araldite 2020 resin, cut and polished, then etched with 5% HCl before coating with platinum for observation under a Philips XL-20 scanning electron microscope (MAB, Fig. 3) or imaged without coating using a LEO 1455VP model (SLL, Fig. 2). The specimens of *Terebratella sanguinea* were measured (in 1990) to the nearest 0·2 mm by Dr D. E. Lee, using vernier calipers. Shell colour was measured with a calibrated camera system (DigiEye, Leicester, UK) under D65 illumination with a standard observer function and averaged over the surface of a single, clean shell.

1.3. Molecular methods, genes sequenced, and related analyses

Molecular methods were standard and have been previously described (e.g. Saito *et al.* 2000; Cohen *et al.* 2004). The genomic segments sequenced for this study were:

a. The quasi-complete cytoplasmic small subunit ribosomal RNA gene (*SSU rDNA*). This sequence of ~1800 nucleotides has been very widely used in metazoan phylogenetics. Most of it evolves slowly, but there are some short regions which change more rapidly, probably by processes other than simple base substitution.
b. A selected, informative segment (~1100 nucleotides, see Cohen & Weydmann 2005) of the gene coding for the cytoplasmic large subunit ribosomal RNA (*LSU rDNA*). Although shorter than the *SSU* gene, this slowly-evolving sequence contains a higher proportion and larger number of informative sites.

   Because they evolve slowly overall, and show little saturation due to multiple substitutions at the same site, the two *rDNA* genes together generally yield well-supported resolution of phylogenetic relationships from genus to phylum levels, but are minimally informative below the genus, and generally invariant among conspecifics. In the present taxon-set these *rDNA* sequences exhibited only minimal length variation and could therefore be fully aligned, without ambiguity.
c. A 663 nucleotide segment of the mitochondrial gene, *cox1*, coding for 221 amino acids of the protein, cytochrome oxidase subunit-1. Compared with *rDNA*, this is a fast-evolving sequence, although it is the slowest-evolving mitochondrial protein-coding gene. This gene generally provides resolution at species and genus levels, but becomes saturated with substitutions and loses resolution at higher taxonomic levels and/or divergence-times much greater than ~100 My (Saito *et al.* 2000, 2001; Saito & Endo 2001). Unfortunately, authentic *cox1* sequence could not be amplified from the samples of *Gyrothyris williamsi*. Thus, the gene that should have been most informative for the discrimination of the new species, actually made no contribution to this question. A similar amplification problem affected *Calloria variegata*, from which the 5′-most ~200 nucleotides were not obtained.

The three gene sequences (data partitions) were concatenated manually, after addition of single 3′ boundary markers (N). The final alignment comprised the *SSU* data partition (sites 1–1777), the *LSU* partition (sites 1778–2869) and the *cox1* partition (sites 2870–3532). Details, including GenBank accession numbers, are given in Table 1.

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

Given the narrow taxonomic range of the specimens and the relatively low divergence levels involved, all sequences were aligned manually, without ambiguity. Because genes encoded in the nucleus and the mitochondrion are inherited under distinct laws, and because one critical *cox1* sequence was missing, separate analyses were performed on *rDNA* and *cox1* partitions. Thus, the *cox1* results can best be used as a partial congruence test of the phylogenetic hypotheses arising from *rDNA*. Maximum likelihood (ML) models for each data partition were selected under the Aikake information criterion (AIC, Posada & Buckley 2004) using Modeltest 3.06 (Posada & Crandall 1998). Alignment parameters were investigated and phylogenetic analyses were performed with PAUP*4b11 (Swofford 2000). Whether the sequences diverge in a roughly clock-like manner was established with a likelihood ratio test (Huelsenbeck & Rannala 1997) of the difference between optimal ML trees constructed with and without the clock enforced.

For *rDNA*, incongruence of the *SSU* and *LSU* partitions was investigated with the partition homogeneity test in PAUP*4 using branch-and-bound searches of 1000 replicates with constant and uninformative characters excluded. The PTP test for data non-randomness used heuristic search on 1000 randomisations of the ingroup sequences. Phylogenetic reconstructions are shown only from parsimony analyses, in which branch-and-bound (B&B) searches with TBR branch exchange and the MULPARS option found a single most parsimonious tree. Maximum likelihood (ML) analyses with heuristic search, ten random additions and TBR branch exchange gave essentially identical results and are not shown. Bootstrap 50% consensus trees were obtained from 500 pseudoreplicates under identical search and branch exchange conditions.

For *cox1*, analyses were performed using maximum parsimony and ML on both nucleotide (all codon positions, 1st plus 2nd, and 3rd codon positions separately) and inferred amino-acid sequences. Because the results differed in support level but not topology, only the ML (all nucleotides) bootstrap consensus tree is shown. To avoid the highest levels of saturation, the analyses shown were restricted to the nodes involving the NZ taxa plus *Magellania* spp., with *Terebratalia* spp. as outgroup, i.e. except in preliminary analyses other terebratelloid taxa and *Terebratulina* were excluded.

2. Results

Initial analyses of morphology and molecules were performed 'blind' and exchanged between the respective investigators (MAB and BLC) only after each had independently arrived at a preliminary conclusion that the new form should be assigned to *Gyrothyris*. Thus, both morphology and molecules were taxonomically informative.

2.1. Description of *Gyrothyris williamsi* sp. nov.

Superfamily Terebratelloidea King, 1850
Family Terebratellidae King, 1850
Subfamily Terebratellinae King, 1850
Genus *Gyrothyris* Thomson, 1918

Type species. *Gyrothyris mawsoni* Thomson, 1918 by original designation (Thomson 1918).

Gyrothyris williamsi sp. nov.
(Figs 1–3)

Diagnosis. Medium size terebratellide, multicostate with strongly expressed growth lines, anterior commissure strongly unisulcate, deltidial plates conjunct to nearly conjunct, cardinalia slightly thickened, cardinal process of kidney shape, median septum uniting posteriorly with inner hinge plates to form a septalium, loop trabecular with very broad ascending branches and broad transverse band with posterior indentation.

Etymology. In commemoration of the late doyen of brachiopod studies, Professor Sir Alwyn Williams, FRS FRSE.

Holotype. The specimen illustrated in Figure 1j–m, MNHN BRA-3036, collected at station CP2505; paratypes MNHN BRA-3037–3041.

Type locality. EBISCO1, station CP2505, Capela seamount, 24°46.63′S–159°41.61′E, 328–463 m.

Material examined. EBISCO1, station CP2505, Capela seamount: two complete specimens; station DW2578, Nord Bellona seamount, 20°20.55′S–158°39.7′E, 440–505 m, 25 complete specimens.

Depth range. 328–602 m.

Dimensions (mm). Measurements of the holotype and paratypes are given in Table 2. Graphs based on measurements of all 95 available articulated shells from stations DW2495, CP2505, DW2577, DW2578 and DW2606 are shown in Figure 4 and the measurements are given in Supplementary File 1.

Exterior (Fig. 1a–f, j–m). Shell (periostracum) colour a creamy, greyish yellow (Lab system: L*=77·32, a*=7·21, b*=22·24; Munsell nearest equivalent=Hue 10YR, Value 7·5, Chroma 4), ventribiconvex, medium size, up to 21 mm long, generally as wide as long (Fig. 4), subpentagonal in outline and with maximum width at about midvalve. Lateral commissure dorsally curved, anteriorly strongly unisulcate with a wide sulcus originating at the umbo. Beak short, suberect to erect, with weakly defined ridges. Pedicle foramen relatively large, circular, and permesothyrid, pedicle very short, massive, not terminally divided. Small conjunct to nearly conjunct deltidial plates. Valves ornamented by numerous ribs interrupted by strongly marked, concentric growth lines.

Interior (Figs 1g–i, 2). Pedicle valve with narrow, sessile pedicle collar. Teeth prominent, short and wide with weakly defined swollen bases. Muscle scars weakly impressed, elongate oval in outline. Brachial valve interior with slightly thickened cardinalia, with a prominent, ridged, kidney-shaped, cardinal process. The inner socket ridges are narrow, sharply pointed and curved, extending anteriorly beyond the sockets. Small outer hinge plates; inner hinge plates fused to the median septum to form a septalium. Median septum high posteriorly, continuing anteriorly as a low ridge for about two thirds of the valve length. Trabecular loop extending from short, parallel crura with small crural processes. Descending branches extending subparallel to the median septum and attached to it by short lateral connecting bands; ascending branches and transverse band very broad; transverse band with a regular, rectangular indentation, resulting in posteriorly pointed 'corners'. Lophophore plectolophous.

Shell ultrastructure (Fig. 3). In a transverse section of the centre part of the pedicle valve, the shell is 343–445 μm thick. There is a primary layer of acicular calcitic crystallites which are twice as thick (103–107 μm) under the costae as in the grooves between them (54–59 μm). The secondary layer is 289–331 μm thick; composed of fibres with an anvil-like cross-section. Close to the posterior margin, approximately mid way between the median septum and the edge of the valve, the puncta density in one shell was approximately 277 per mm^2, higher than any value recorded for *Gyrothyris* or *Terebratella* (Foster 1974, 1989). However, densities of endopunctae within

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

Table 1 Specimens, collection localities and sequences.

	Taxon	Collection locality and collector (identified by)	Glasgow DNA (D or DNZ prefix) and GenBank accession numbers. New sequences marked*			Reference to previously published sequences and museum vouchers
			SSU	*LSU*	*cox1*	
Ingroup						
	Calloria inconspicua	DNZ378: Matakana, Leigh, North Island, 36°24′S, 174°45′E, SCUBA, I. Stringer (BLC) D1313: Tasman Bay, Gt. King Is., 34°09′S 172°08′E, G. Loh (BLC)	DNZ378 AF025938	DNZ378* DQ871292	D1313* DQ871278	*SSU* (Cohen *et al.* 1998)
	Calloria variegata	Crayfish Rock, Little Barrier Island, 36°13′S 175°03′E, 5 m, G. Loh (D. E. Lee)	D1667* DQ871287	D1667* DQ871293	Cav1* DQ871279	This paper
	Gyrothyris mawsoni	DNZ45, D1319, D1320: Off Tiaroa Head, Otago, 45°41′S, 171°05′E, ~60 m. RV Munida (BLC, DEL)	DNZ45 AF025941	D1320* DQ871294	DNZ45* DQ871280	*SSU* (Cohen *et al.* 1998)
	Gyrothyris williamsi	D1647: Ebisco1, DW2495, Capela seamount, 24°44.11′S, 159°42.9′E, 350–357 m, BRdeF (MAB) Gw1, Gw2: Ebisco1, DW2578, Nord Bellona, 20°19.8′S, 158°39.7E, 440–505 m, (BLC)	D1647* DQ871288	D1647* DQ871295	Gw1, Gw2 (no sequence)	This paper Glasgow University Hunterian Museum accession GLAHM 126475
	Neothyris parva	Off Tiaroa Head, Otago, 45°41′S, 171°05′E, RV Munida, ~60 m (BLC, DEL)	DNZ53 AF025944	DNZ53* DQ871299	DNZ53* DQ871284	*SSU* (Cohen *et al.* 1998)
	Neothyris lenticularis	DNZ361 & 364: Queen Charlotte Sound, North Island, 41°13′S 174°06′E, 20–30 m, C. Duffy (CD, BLC) D1315: Iwirua Pt., Grove Arm, Q. Charlotte Sd., 41°16′S 174°00′E, C. Duffy (CD, BLC)	DNZ361* DQ871290	D1315* DQ8871298	DNZ361* DQ871283	This paper
	Terebratella sanguinea	DNZ137: Off Tiaroa Head, Otago, 45°41′S, 171°05′E, ~60 m, RV Munida (BLC, D. E. Lee) DNZ150: The Neck, Paterson Inlet, Stewart Is., 46°58′S 168°09′E, 5–15 m, C. Thayer (CT, DEL) DNZ264: Shark Bay, Wellington Harbour, 41°06.5′S 174°47′E, 9 m, W. A. Hoverd (WAH, BLC)	DNZ264* DQ871291	DNZ137* DQ871300	DNZ 150* DQ871286	This paper
Outgroups						
	Magellania fragilis	ANT/XV3, Weddell Sea, 73°4′S 2°1′W, ~300 m, T. Brey (BLC, CHCB)	D1296 AF202110	D1296* DQ871296	D1296* DQ871281	*SSU* (Cohen 2000)
	Magellania joubini	As *M. fragilis*	(not reported)	(not reported)	D1295* (not reported)	This paper
	Magellania venosa	D1390: Falkland Islands, 52°39′S 58°36′W, depth 130–190 m, J. Pompert (BLC) D1432: Bahia Grigorio, Magellan Strait, 54°S 73°W, 25 m, E. Mutchke Orellana (BLC)	D1390* DQ871289	D1390* DQ871297	Same site as D1390* DQ871282	This paper
	Terebratalia transversa	D1055: Point George, Puget Sound, 47°15′N 123°30′W, C. Thayer (CT)	AF342802		D1055* DQ871285	*SSU*, *LSU* (Mallatt & Winchell 2002)
	Terebratulina retusa	Firth of Lorne, Scotland, 56°20′N 05°40′W, 5–15 m, A. S. G. Curtis (BLC)	U08324	AY839244	AJ245743	*SSU* (Cohen *et al.* 1998) *LSU* (Cohen & Weydmann 2005) *cox1* (Stechmann & Schlegel 1999)

Table 2 Measurements of type specimens (mm).

Specimen number	Length	Width	Depth	Sulcus width
MNHN BRA-3036 (holotype)	20·9	20·8	13·8	10·2
MNHN BRA-3037 (paratype)	15·5	15·0	10·1	9·0
MNHN BRA-3038 (paratype)	16·6	17·1	10·7	11·6

the shell of living species are variable and seem not to be taxonomically very useful (see also Foster 1974, p. 113).

Remarks on morphology. Because of limitations inherent in dredge sampling, the specimens of *Gyrothyris williamsi* sp. nov. available for study included none shorter than 8·7 mm. There were also none longer than 21 mm. The maximum size to which *G. williamsi* grows is unknown, but the closely spaced growth lines, anterior shell steepness and trabecular loop of the larger *G. williamsi* (Fig. 1) suggest that these specimens may be near-adult or adult. The mean length of *G. mawsoni* shells is slightly greater than the largest available *G. williamsi* (Fig. 4a) and the longest *G. mawsoni* can reach 35 mm (Foster 1974, 1989), so that between-species comparisons well-matched for size could not be made; all specimens figured by Foster (1974) are longer than 21 mm. However, if the larger *G. williamsi* are near-adult or adult, the comparisons that follow may nevertheless be between animals of similar developmental stages. All comparisons between different species and populations, of course, may also be distorted by potential differences in the relative growth-rates of loops and other structures. The comparisons should be interpreted with this in mind.

In external appearance, the specimens of *Gyrothyris williamsi* sp. nov. are most similar to *G. mawsoni* Thomson, 1918 and (excluding colour) *Terebratella sanguinea* (Leach, 1814). The growth trajectories of width and depth relative to length are very similar to those of *G. mawsoni*, but differ from those of *T. sanguinea* (Fig. 4). Externally, the new specimens differ from *Terebratella* in colour, shape, convexity and strength of ornament. *Gyrothyris williamsi* sp. nov. also differs externally from the type species by having stronger ornamentation and being more deeply sulcate. In *G. williamsi* numerous, distinct ribs are observed, even in specimens about 8 mm long, and the ribs are interrupted by strongly marked growth lines. The ribs in *G. mawsoni* are less numerous, less distinctly defined and not interrupted by strongly marked growth lines (Foster 1974, 1989). The shell of *G. mawsoni* is weakly unisulcate and a shallow sulcus becomes marked only near the anterior margin, whilst in *G. williamsi* the sulcus originates at the umbo and is sharply defined on the whole shell.

Internally, *G. williamsi* has a narrower loop but a much broader transverse band and ascending branches than *G. mawsoni*, and its crural processes are shorter and less pointed. The new species also differs internally from *Terebratella*. The cardinalia of *Terebratella* are extremely variable and the inner hinge plates may or may not unite with the median septum (Foster 1974, pl. 22). This contrasts with the small kidney-shaped cardinal process, and broad, elongate septalium of the specimens described here, which show similarities to *Gyrothyris mawsoni* in the way that they are calcified and in the form of the cardinal process, but which differ in the loop. Although the trabecular loop of the specimen of *G. mawsoni* illustrated by Thomson (1918, 1927) was broken, it clearly shows lateral connecting bands and it is also apparent that the ascending branches and transverse band are more delicate than those of the trabecular loop of the specimens illustrated here. In turn, the ascending branches and the transverse band of *G. mawsoni* illustrated by Foster (1974, pl. 18, fig. 19, pl. 19, figs 1, 2) are very delicate and narrow, not resembling the very broad ascending branches and transverse band observed in the specimens from the Coral Sea. In the pedicle valve of *G. mawsoni* the teeth are strong, projecting, with swollen bases (Foster 1974) while in the material described here the teeth are short but wide, and swollen bases are weakly defined. Foster (1974) distinguished the three subspecies of *Gyrothyris*, all of which are variable in shape and external ornamentation between moderate ribbing to absent (Foster 1989). But it was also noted that 'More detailed collecting may show them . . . to intergrade to such a degree that sub-specific names are unwarranted', i.e. the differences in outline and ornament by which they were defined may be attributable to inadequately documented intraspecific variability. There are marked similarities in the cardinalia, but the loops of both Foster's subspecies (*G. mawsoni antipodesensis* and *G. mawsoni aucklandensis*) are long and delicate, and in larger specimens often in teloform phase. The loops in the specimens of *G. williamsi* examined by the present authors were in the development phase from late bilacunar to trabecular. SEM study of these specimens clearly shows the lateral connecting bands forming from the median septum. The secondary shell fibres of the median septum can be seen to be growing over the remnants of the resorbed descending branches (which have well defined growth lines) as illustrated by MacKinnon (1993). The development of lateral connecting bands, which are continuous with the median septum rather than remnants of the descending loop branches that have not completely resorbed, is a key feature in the diagnosis of the Terebratellinae (MacKinnon *et al*. 1993). This contrasts with Foster's (1974) description of the connecting bands as reduced and the loop as teloform in many larger specimens of *G. mawsoni*. Foster (1974) observed specimens of *G. mawsoni* in which connecting bands were still joined to the septum but not united with the loop, but this has not been seen in *G. williamsi*. Overall, the morphological differences between *G. mawsoni* and the new material in ornamentation, sulcation and character of the loop suggest that the new brachiopod is sufficiently divergent to justify its designation as a new species of *Gyrothyris*.

DNA sequences. The *SSU* and *LSU rDNA* sequences obtained from *Gyrothyris williamsi* are specified in Table 1. These and the synapomorphic deletions illustrated in Figure 5b form part of the description and strongly support allocation of the new specimens to the genus *Gyrothyris*. No information on between-individual variability is currently available.

2.2. Gene trees of *Gyrothyris* and other terebratelloids

2.2.1. rDNA. With the *Terebratulina* outgroup sequence either included or excluded, the rDNA sequences showed no base composition heterogeneity (P>0·9) and ILD tests showed no significant heterogeneity between the *SSU* and *LSU* partitions (0·25>P>0·18). In a PTP test, the shortest tree (L=435) was much shorter than all trees from permuted data (P=0·001). With *Terebratulina* included, there was substantial saturation of transitions and transversions, but this reduced to slight saturation when *Terebratulina* was omitted (not shown). These details suggest that the rDNA sequences are likely to yield valid reconstructions of relationships among ingroup taxa that differ at enough sites. Figure 5a shows the maximum parsimony phylogram and bootstrap support (%) resulting from analysis of the rDNA sequence partition, which comprised 2869 characters of which 106 were parsimony-informative and 213 variable but uninformative. Limited resolution (for whatever reason) is indicated by the presence of two nodes with bootstrap proportions <50%, but the topology recovered is generally informative and, with one exception, consistent with expectations based on traditional systematics. The unexpected feature is the failure of *Neothyris parva* and

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

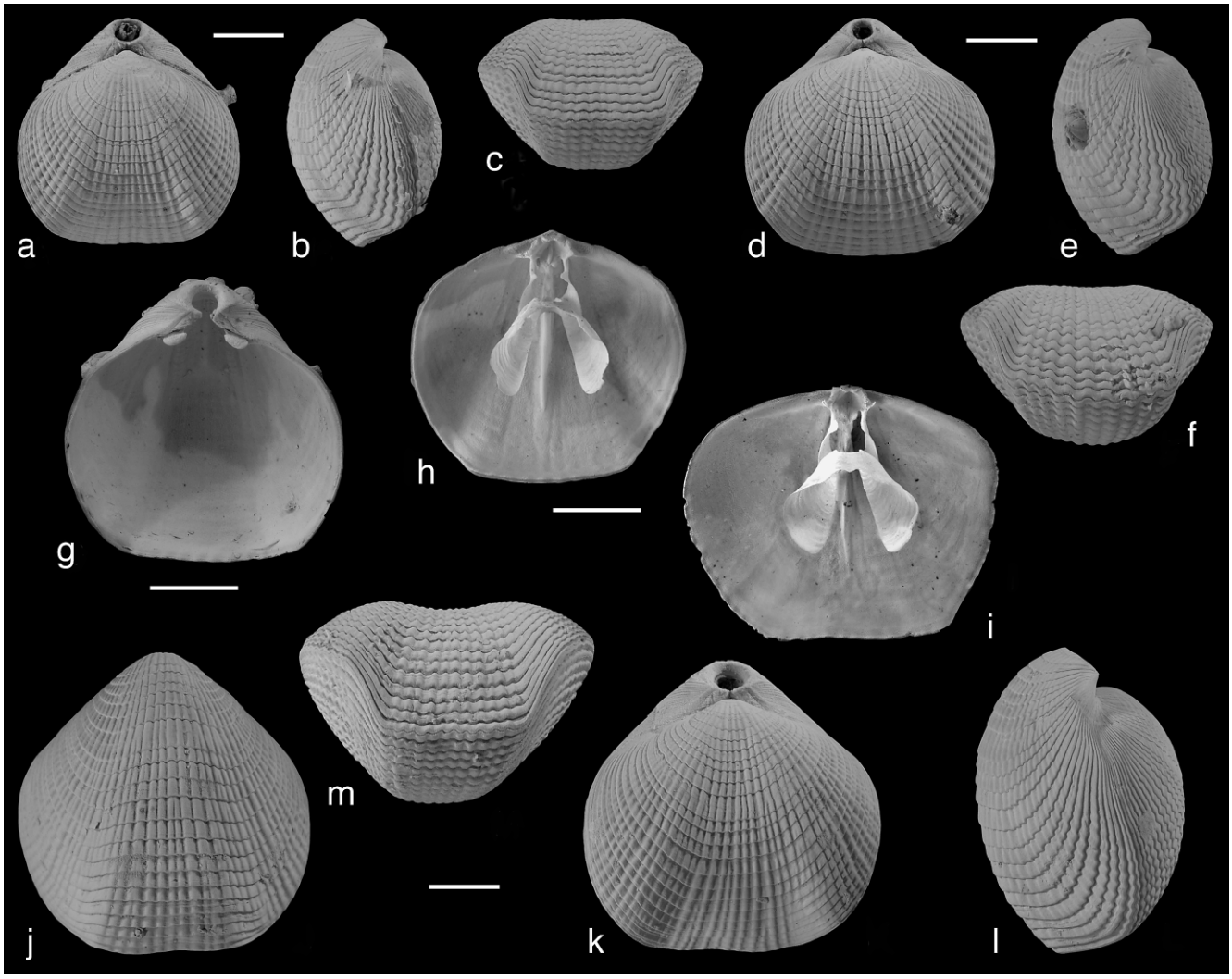

Figure 1 *Gyrothyris williamsi* sp. nov., Lord Howe Rise, Coral Sea: (a–f) dorsal, lateral and anterior views of complete paratype specimens, Ebisco, DW 2578, MNHN BRA-3037, MNHN BRA-3038; (g) inner view of ventral valve, paratype, Ebisco, DW 2578, MNHN BRA-3039; (h–i) inner views of dorsal valves, paratypes, Ebisco, DW 2578, MNHN BRA-3040–3041; (j–m) ventral, dorsal, lateral and anterior views of complete specimen, holotype, Ebisco, DW 2505, MHNH BRA-3036. Scale bar = 0·5 cm.

N. lenticularis to form a well-supported clade; the relatively basal position of *N. parva* receives even stronger bootstrap support in both ML and minimum evolution distance trees (the latter based on both ML and Kimura 2-parameter distances, not shown). The maximum likelihood and ML bootstrap consensus trees were identical in topology and very similar in support values to Figure 5a. Point estimates of rDNA divergence between species pairs (ML pairwise distances) were: *Calloria* and *Gyrothyris* spp., two comparisons both = 0·0022; *Magellania venosa*/*fragilis* = 0·026, and *Neothyris* spp. = 0·122, showing the unexpectedly large apparent distance between the *Neothyris* species. Exploratory analyses revealed that when *SSU* and *cox1* are analysed either separately or together (see below for *cox1*), a well-supported *Neothyris* clade is found; its absence is due only to the *LSU* sequence, within which the divergent phylogenetic signal is widely distributed. No certain explanation can be offered for the apparently discordant behaviour of *LSU* in this respect. The possibility that it characterises the particular *Neothyris* populations from which this gene was sampled will require additional study.

As expected, both *Calloria* and *Gyrothyris* form strongly-supported clades, with *Terebratella* the (weakly supported) sister-group of *Calloria*. *Gyrothyris williamsi* sp. nov. is an unambiguous sister-taxon of *G. mawsoni* and this is strongly supported by the shared presence of a two-part presumed deletion in *LSU*, not known from any other taxon examined, including several additional Terebratelloidea (not shown). The deleted sites correspond to nucleotides 4573–4579 and 4586–4588 in the *LSU* of *Xenopus*, Genbank accession X59734, where they lie in a short variable region flanked by conserved blocks, as indicated in Figure 5b. In addition, the rDNA analyses confirm that *Magellania* is the sister-group of the NZ taxa and that the Antarctic species, *M. fragilis*, is the closer sister-taxon (ML mean ± SE distances for seven pairwise comparisons: *M. fragilis*/NZ = 0·029 ± 0·0014; *M. venosa*/NZ = 0·050 ± 0·002).

2.2.2. ***cox1***. Because it represents a mitochondrial protein-coding gene, the *cox1* partition is likely to exhibit a more heterogeneous evolutionary history than rDNA; first, second and third codon positions evolve under different selective regimes and rearrangements of mitochondrial gene order leading to strand exchange result in different strand-specific mutational biases. Chi-squared tests for base composition heterogeneity revealed that at least two such complications do exist in the present data:

(a) Overall base composition of the NZ endemic genera (*Calloria*, *Gyrothyris*, *Neothyris*, *Terebratella*) is homogeneous (P = 0·68), as it is in the same group plus *Magellania venosa* (P = 0·78), but the NZ genera plus *M. fragilis* and *M. joubini* are less homogeneous (P = 0·16) and, consistent with

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

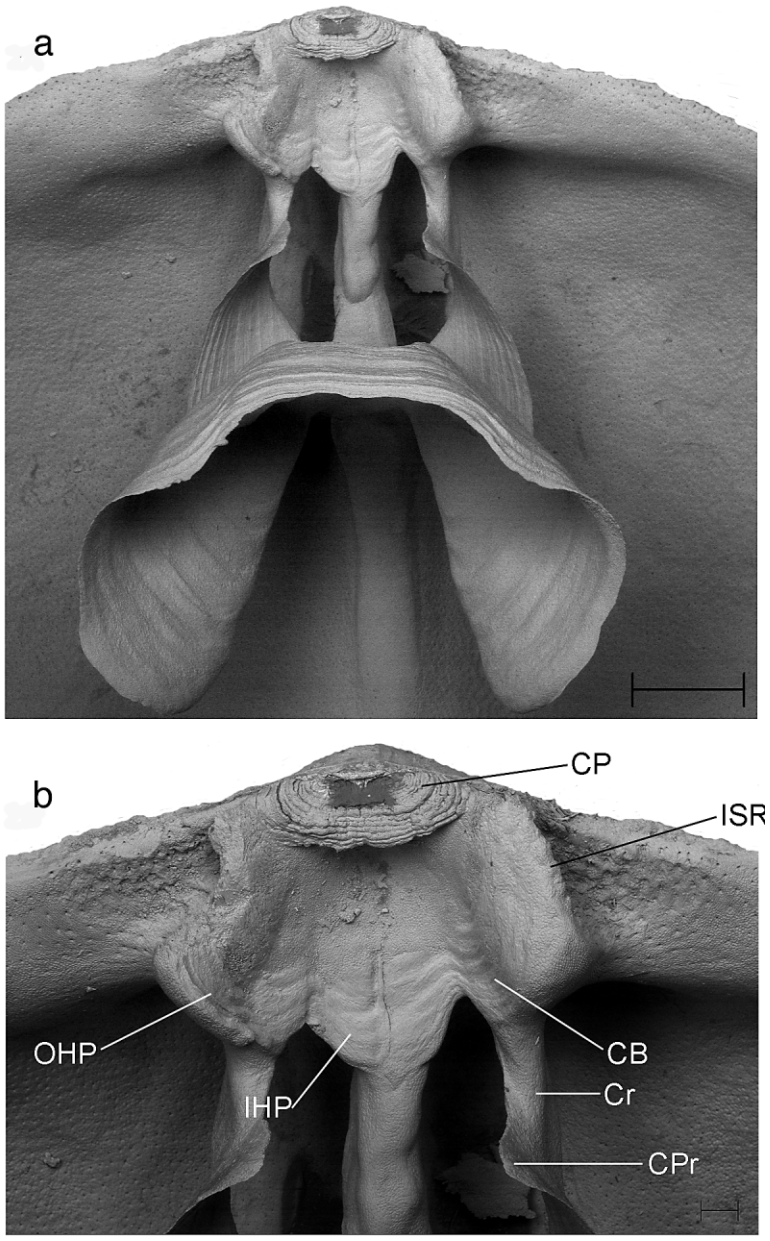

Figure 2 *Gyrothyris williamsi* sp. nov., Lord Howe Rise, Coral Sea, EBISCO, DW 2577, MNHN BRA-3042. SEM images of the dorsal valve interior, (a) showing the loop and cardinalia. Scale bar=1 mm; (b) detail of cardinalia of the same specimen showing the cardinal process (CP), inner socket ridges (ISR – note these are broken), crural bases (CB), crural process (CPr), crura (Cr), inner hinge plates (IHP) and outer hinge plates (OHP). Scale bar=2 mm.

this, the two groups of *Magellania* are significantly different (P=0·002). Because phylogenetic reconstructions can falsely cluster taxa with similar base composition, the relative positions in *cox1* trees of the *Magellania* taxa, especially *M. fragilis* and *M. joubini*, must be treated with caution.

(b) Various biases are known to differentially affect the evolution of nucleotides in first, second and third codon positions. For example the *cox1* base composition over all taxa and positions shows significant heterogeneity (P=0·04), but over first and second positions combined there are no significant differences (P=1·00), while third positions show significant heterogeneity (P<0·001 reflecting, for example, differences in mean G+C composition such as *Calloria*= 0·21, *Neothyris*=0·12, *M. venosa*=0·17, *M. fragilis* and *M. joubini*=0·21). Marked variations in brachiopod *cox1* base composition similar to those noted here have been reported previously (Saito *et al.* 2000).

In addition to these complications, the entire *cox1* sequence of *Gyrothyris williamsi* and about one third of that of *Calloria variegata* were not obtained, so that only limited conclusions are available. Figure 6 therefore shows the outcome of a relatively simple analysis: the bootstrap consensus tree resulting from maximum likelihood reconstruction with the simplest model that fits all *cox1* nucleotide sites of the included taxa. While it agrees with the rDNA analyses in placing *Magellania* spp. as the sister-group of the remaining taxa, the failure to resolve a *Magellania* clade probably can be attributed to the base composition difference noted above. Another difference from the rDNA tree is the position of *Terebratella sanguinea*, but in both rDNA and *cox1* trees this has weak bootstrap support, indicating that a definitive resolution of the relationship between *Terebratella*, *Calloria* and *Gyrothyris* requires additional evidence. However, *cox1* agrees with rRNA in finding that *Neothyris* is the sister-group of (*Terebratella*, *Calloria*, *Gyrothyris*). The *cox1* ML phylogram (not shown)

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

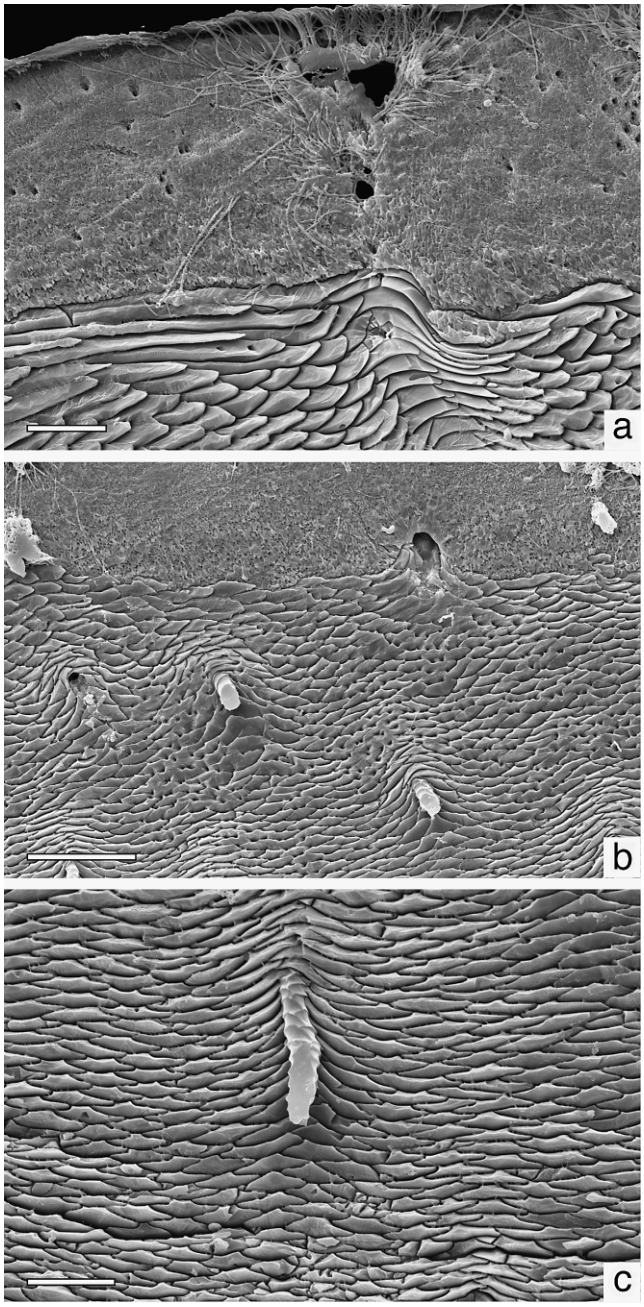

Figure 3 *Gyrothyris williamsi* sp. nov., transverse sections of the pedicle valve, Ebisco, DW 2578, MNHN BRA-3041, SEM micrographs: (a) detail showing primary/secondary layer boundary, visible perforation and a radiating brush; (b) section of the shell showing the boundary of the acicular primary and fibrous secondary layer; (c) secondary fibrous layer, showing modification of fibres near a punctum. Scale bars=(a) (c) 20 μm; (b) 50 μm.

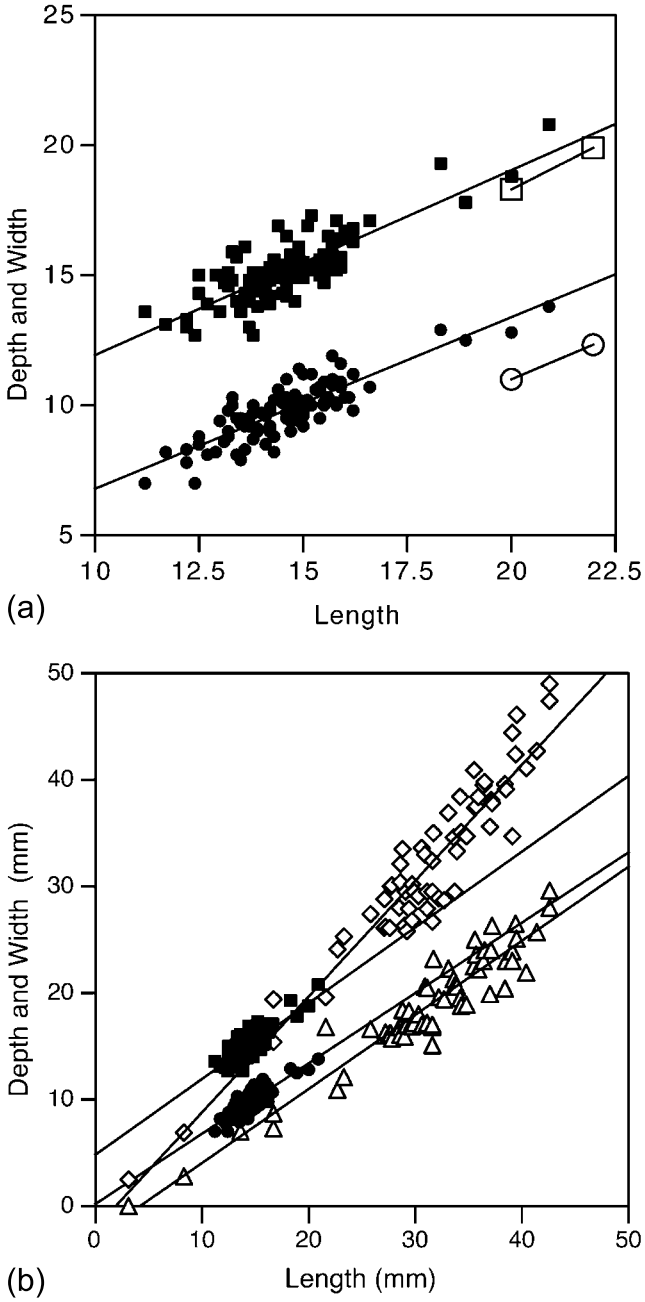

Figure 4 (a) Length versus width (filled squares) and depth (filled circles) of 95 articulated shells of *Gyrothyris williamsi* compared with mean length, width (open square) and depth (open circle) of 55 shells of *G. mawsoni* (data for site USC1417 from Tables A7 and A8, Foster 1974). The length=20 mm data-points from Foster (1974) were estimated in his reduced major axis regression analysis whereas the upper length data-points are his actual means. (b) Comparison of *Gyrothyris* and *Terebratella* shell sizes: length versus width (L/W, filled squares) and length versus depth (L/D, filled circles) of 95 articulated shells of *Gyrothyris williamsi* compared with L/W (open diamonds) and L/D (open triangles) of 63 articulated shells of *Terebratella sanguinea*. Because the size data for *G. williamsi* and *T. sanguinea* are not normally distributed, the least-squares regression lines shown are only rough guides. The equations of the regression lines are: *Gyrothyris* L/W, linear, $y=0{\cdot}711 \times +4{\cdot}824$, $r^2=0{\cdot}672$; *Gyrothyris* L/D, linear, $y=0{\cdot}660 \times +0{\cdot}189$, $r^2=0{\cdot}730$; *Terebratella* L/W, power, $y=0{\cdot}755 \times^{1{\cdot}087}$, $r^2=0{\cdot}962$; *Terebratella* L/D, linear, $y=0{\cdot}695 \times -2{\cdot}898$, $r^2=0{\cdot}901$. For *Terebratella* L/W, the linear equation $y=1{\cdot}089 \times -2{\cdot}074$, $r^2=0{\cdot}901$ explained less of the variability than the almost-linear power curve shown.

places *N. parva* much closer to *N. lenticularis* than does the rDNA analysis (Fig. 5a).

2.2.3. Molecular clock analyses. The rDNA partition failed likelihood ratio tests for clock-like divergence ($P<0{\cdot}05$ for all combinations of taxa tested). The *cox1* partition passed the test ($P\sim0{\cdot}3$), but only when reduced to the NZ taxa plus *Magellania venosa*. On a *cox1* ultrametric ML tree (not shown) the branch-length from the root to *M. venosa* was 0·257, whilst that from the root divergence of the NZ taxa was 0·161. Assuming that radiation of the NZ taxa started soon after the vicariance that separated Antarctica and New Zealand ~90 Mya, separation of the NZ clade from the S. American/Falklands *Magellania* is implied to have begun earlier, perhaps ~144 MYa (0·257/0·161 × ~90=~144). This very rough estimate is compatible with genetic isolation resulting from either earlier plate movements during the breakup of Gondwana or later reinforcement following the opening of the Drake Passage and establishment of a circum-Antarctic current.

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

(a)

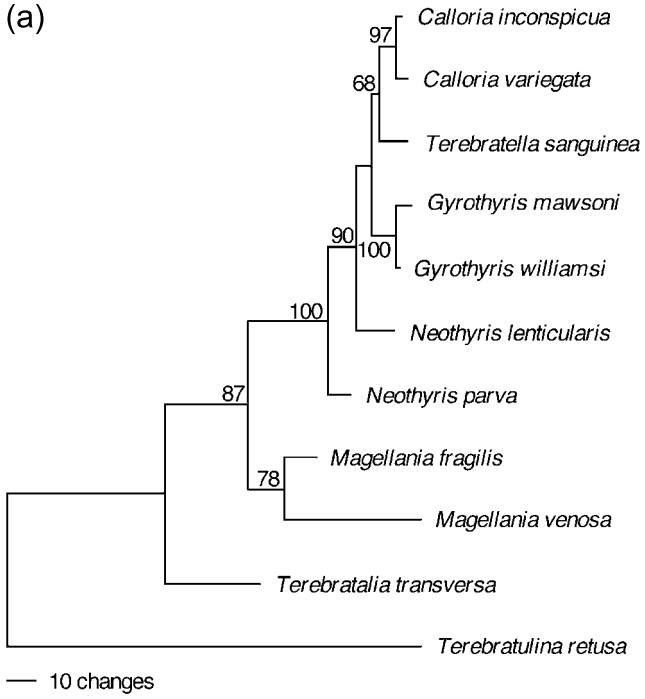

Figure 5 rDNA sequence results. (a) Branch-and-bound parsimony phylogram (L=435, CI=0·85, RI=0·67) with added bootstrap frequencies (>50%) from B&B search of 1000 pseudoreplicates. The distal node without a bootstrap label may be considered as collapsed, resulting in the trichotomy (*Neothyris lenticularis*) (*Gyrothyris* spp.) (*Terebratella* (*Calloria* spp.)). Branch lengths are proportional to inferred amount of sequence change. (b) Presumed deletion(s) in a region of the *LSU* gene. As aligned here, the deleted nucleotides correspond to sites 4573–4579 and 4586–4588 in the *LSU* of *Xenopus*, Genbank accession X59734. Relatively conserved sites are marked 'c' and variable ones, 'v'.

(b)

Variability	c c c c c c c c c c c c c c c c c c c c v v v v v v v v v v v v v v v v v v v v v c c c c c c c c c c c c c
Calloria inconspicua	GGCGCAATGAAAGTGAAGGGCC-AGGCGTCT-GGTCCGAGGTGGGATCCC
Calloria variegata	GGCGCAATGAAAGTGAAGGGCC-AGGCGTCT-GGTCCGAGGTGGGATCCC
Gyrothyris mawsoni	GGCGCAATGAAAGTGAAG-------CGTCC-G---CGAGGCGGGATCCC
Gyrothyris williamsi	GGCGCAATGAAAGTGAAG-------CGTCC-G---CGAGGCGGGATCCC
Magellania fragilis	GGCGCAATGAAAGTGAAGGGCC-AGGCTTCT-GGTCCGAGGTGGGATCCC
Magellania venosa	GGCGCAATGAAAGTGAAGGGCC-AGGCTTCT-GGTCCGAGGTGGGATCCC
Neothyris lenticularis	GGCGCAATGAAAGTGAAGGGCC-AGGCGTCT-GGTCCGAGGTGGGATCCC
Neothyris parva	GGCGCAATGAAAGTGAAGGGCC-AGGCGTCT-GGTCCGAGGTGGGATCCC
Terebratalia transversa	GGCGCAATGAAAGTGAAGGGCC-AGGTCGCT-GGCCCGAGGTGGGATCCC
Terebratella sanguinea	GGCGCAATGAAAGTGAAGGGCC-AGGCATCT-GGTCCGAGGTGGGATCCC
Terebratulina retusa	GGCACAATGAAGGTGAAGGGCT-AGGCAGCT-GGTCCGAGGTGGGATCCC
Xenopus X59734	GGCGCAATGAAGGTGA-GGGCCGGGGCGCCCCGGCT-GAGGTGGGATCCC

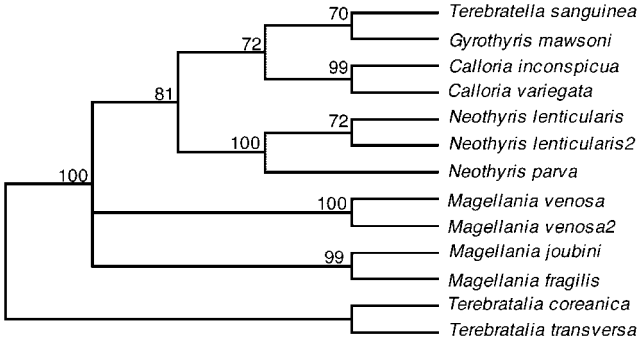

Figure 6 *cox1* sequence results. The bootstrap 50% majority rule consensus tree from ML reconstructions based on branch-and-bound searches with TBR branch exchange on 500 pseudoreplicates of the *cox1* alignment using the AIC-optimal all-sites model (HKY+gamma, number of rates=2; transition:transversion ratio=3·1188; gamma distribution shape parameter=0·2477; proportion of invariant sites=0; base composition=empirical). Bootstrap values are given as %. Branch lengths have no meaning.

2.3. Remarks on biogeography of *Gyrothyris*

The genus *Gyrothyris* has no fossil record and has been represented so far by only one extant species, *G. mawsoni*, known from the waters around NZ and the Antipodes and Macquarie Islands (Thomson 1918; Foster 1974; Richardson 1994; Lüter 2008), more than 2000 km south and slightly east of the new locality on the Lord Howe Rise. The present collection extends the range of the genus, but we know that it does not have an undetected, wider distribution because it has not been found at many brachiopod-yielding stations in the SW Pacific, including the Norfolk Ridge seamounts that lie between the reported localities on the Lord Howe Rise and those around and S of New Zealand (Richer de Forges, Bitner & Cohen, unpublished data, 2001–2007). *Gyrothyris* populations on the Lord Howe rise are likely to be genetically isolated from previously-reported populations because the latter all lie S of the subtropical front that divides warmer, northern waters from temperate to cold, sub-antarctic waters around southern New Zealand, the Antipodes and Macquarie islands (Nelson & Cooke 2001). This, and other oceanic fronts (Budillon & Rintoul 2003) inhibit the exchange of larvae between water bodies, and probably have done so for ~30 My.

3. Discussion

Here, we believe for the first time, the ascription of a new brachiopod to an existing taxon involves both morphological description and evidence from DNA sequence. Morphology alone shows that the new form can be excluded from all candidate genera except *Gyrothyris*, with which it forms a well-supported rDNA clade and shares an unusual gene deletion. Thus, attribution to *Gyrothyris* is supported by

https://doi.org/10.1017/S1755691008075142 Published online by Cambridge University Press

complementary and synergistic evidence. The decision to describe it as a new species was based on a combination of morphological difference and genetical isolation, inferred from a biogeographical distribution disjunct from previously described *Gyrothyris* populations. Evidence that most brachiopods have limited dispersal potential is provided by their long history of regional endemism and by studies of larval settlement in living forms (Richardson 1997). Even taxa with long-lived, planktotrophic, stages may show some regional endemism (Endo *et al*. 2001). It is therefore reasonable to assume effective reproductive isolation and to consider as distinct species morphologically distinguishable populations separated by thousands of kilometres of ocean and water-body boundaries such as the sub-antarctic front. In principle, molecular analyses could further guide a decision on species status by revealing consistent levels of divergence and/or reciprocal monophyly, but it proved impossible to sequence the target mitochondrial gene, *cox1*, of *Gyrothyris williamsi* in the limited time available for this study. On the other hand, this failure itself distinguishes *G. williamsi* from *G. mawsoni* because it implies divergence at one or more amplification priming sites, which typically are very conserved sequences.

In addition to the primary focus of this report, the results presented bear on several other issues, two of which will be briefly noted:

1. The first sequences are reported from the NZ endemic form, *Calloria variegata* (Cooper & Doherty 1993), which is known only from the Hauraki Gulf on the east coast of North Island, where it preferentially occupies more exposed situations than *C. inconspicua*. Morphology, geography and molecular phylogeny agree that *C. variegata* and *C. inconspicua* are close sisters, suggesting that *C. variegata* may be a local variant that originated relatively recently from *C. inconspicua*, and it would be interesting to know more about the differences between these species and whether they can interbreed. They are more accessible than the only other southern hemisphere example of sympatric brachiopod species, the Antarctic sisters, *Magellania fragilis* and *M. joubini*.
2. Previous analyses based on *SSU* rDNA or on *cox1* alone disagreed whether the closest sister-group of the NZ genera is respectively *Terebratalia* or *Magellania* (e.g. Cohen 2001; Saito *et al*. 2001). Addition to *SSU* rDNA of *LSU* data confirms the *cox1* result: *Magellania* is closest. On the other hand, the two datasets now disagree whether *Magellania* spp. form a single molecular clade. Here, although rDNA clearly supports a single *Magellania* clade, *cox1* does not, but this can probably be discounted because of marked base-compositional variation. Both BLC and MS have repeatedly failed to obtain sequence from specimens of *M. flavescens* from Australian shelf waters, and it remains to be seen whether molecular evidence will eventually support a clade containing all *Magellania* species.

4. Acknowledgements

MAB is grateful to the Royal Society of Edinburgh for exceptional support under the RSE–Polish Academy of Sciences International Exchange Programme, 2005. A test version of PAUP* was kindly made available by J. Wilgenbusch, University of South Florida. We are grateful to Daphne E. Lee, University of Otago, for shell measurements, and to Judy Peterson and Roger Deacon, Southern Aqualung Divers, Invercargill, who collected the measured specimens of *Terebratella sanguinea* from George Sound. Thanks are due to Alison Gilchrist and Peter Rhodes, Department of Colour and Polymer Chemistry, University of Leeds, for determining the colour of a specimen of *Gyrothyris williamsi* in terms of internationally accepted standards. Carsten Lüter and Kazuyoshi Endo provided helpful reviews.

5. Note added in proof

The brachidium of a species of *Gyrothyris mawsoni* of approximately the same size as the illlustrated paratype of *G. williamsi* n. sp. is shown in Lüter 2008, figure 2M.

6. References

Aldridge, A. E. 1981. Intraspecific variation of shape and size in subtidal populations of two Recent New Zealand articulate brachiopods. *New Zealand Journal of Zoology* **8**, 169–74.

Bitner, M. A. 2006a. Recent brachiopods from the Fiji and Wallis and Futuna Islands, Southwest Pacific. *In* Justine, J. L. & Richer de Forges, B. (eds) *Tropical Deep Sea Benthos, 24. Mémoires du Muséum national d'Histoire naturelle* **193**, 15–32.

Bitner, M. A. 2006b. The first record of brachiopods from the Marquesas Islands, French Polynesia, south-central Pacific. *Pacific Science* **60**, 417–24.

Budillon, G. & Rintoul, S. R. 2003. Fronts and upper ocean thermal variability south of New Zealand. *Antarctic Science* **15**, 141–52.

Cohen, B. L. 2000. Monophyly of brachiopods and phoronids: reconciliation of molecular evidence with Linnaean classification (the subphylum Phoroniformea nov.). *Proceedings of the Royal Society, London, Series B* **267**, 225–31.

Cohen, B. L. 2001. Brachiopod molecular phylogeny advances. *In* Brunton, C. H. C., Cocks, R. & Long, S. L. (eds) *Brachiopods Past and Present*, 121–8. London: Taylor & Francis.

Cohen, B. L., Gawthrop, A. B. & Cavalier-Smith, T. 1998. Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society B* **353**, 2039–61.

Cohen, B. L., Améziane, N., Eléaume, M. & Richer de Forges, B. 2004. Crinoid phylogeny: a preliminary analysis (Echinodermata: Crinoidea). *Marine Biology* **144**, 605–17.

Cohen, B. L. & Weydmann, A. 2005. Molecular evidence that phoronids are a subtaxon of brachiopods (Brachiopoda: Phoronata) and that genetic divergence of metazoan phyla began long before the Early Cambrian. *Organisms, Diversity & Evolution* **5**, 253–73.

Cooper, G. A. & Doherty, P. J. 1993. *Calloria variegata*, a new Recent species of brachiopod (Articulata: Terebratulida) from northern New Zealand. *Journal of the Royal Society of New Zealand* **23**, 271–81.

Endo, K., Ozawa, T. & Kojima, S. 2001. Nuclear and mitochondrial gene sequences reveal unexpected genetic heterogeneity among northern Pacific populations of the brachiopod *Lingula anatina*. *Marine Biology* **139**, 105–12.

Foster, M. W. 1974. Recent Antarctic and Sub-Antarctic Brachiopods. *Antarctic Research Series* **21**, 1–181.

Foster, M. W. 1989. Brachiopods from the extreme South Pacific and adjacent waters. *Journal of Paleontology* **63**, 268–301.

Huelsenbeck, J. P. & Rannala, B. 1997. Phylogenetic methods come of age: testing hypotheses in an evolutionary context. *Science* **276**, 227–32.

Laurin, B. 1992. Découverte d'un squelette de soutien du lophophore de type 'crura' chez un brachiopode inarticulé: déscription de *Neoancistrocrania norfolki* gen. sp. nov. (Craniidae). *Comptes Rendues de l'Academie des Sciences, Paris, Life Sciences* **314**, 343–50.

Laurin, B. 1997. Brachiopoda: brachiopodes récoltés dans les eaux de la Nouvelle-Calédonie et des îles Loyauté, Matthew et Chesterfield. *In* Crosnier, A. (ed.) *Résultats des Campagnes MUSORSTOM. Mémoires du Muséum nationale d'Histoire naturelle* **176**, 411–71.

Leach, W. E. 1814. *Zoological miscellany; being descriptions of new, or interesting animals*. London: B. Millan.

Lüter, C. 2005. Brachiopods of the Deep-Sea Expedition SO 168 – diversity and biogeography. *In* Harper, D. A. T., Long, S. L. & McCorry, M. (eds) *Fifth International Brachiopod Congress. Abstracts*, p. 43. Copenhagen: Natural History Museum of Denmark, University of Copenhagen.

Lüter, C. 2008. Recent brachiopods collected during the deep-sea cruise SO 168 ZEALANDIA with the research vessel FS SONNE between Mt Spong (Tasman Sea) and the Chatham Islands

(Pacific) in 2002/2003. *In* Harper, D. A. T., Long, S. L. & Nielsen, C. (eds) *Brachiopoda: Fossil and Recent. Fossils and Strata* **54**, 311–20. Chichester: Wiley-Blackwell.

MacKinnon, D. I. 1993. Loop ontogeny and ultrastructure in brachiopods of the Family Terebratellidae. *In* Kobayashi, I., Mutvei, H. & Sahni, A. (eds) *Structure, formation and evolution of fossil hard tissues*, 31–40. Tokyo: Tokai University Press.

MacKinnon, D. I., Beus, S. S. & Lee, D. E. 1993. Brachiopod fauna of the Kokoamu Greensand (Oligocene), New Zealand. *New Zealand Journal of Geology and Geophysics* **36**, 327–47.

Mallatt, J. & Winchell, C. J. 2002. Testing the new animal phylogeny: first use of combined large-subunit and small-subunit rRNA gene sequences to classify the protosomes. *Molecular Biology and Evolution* **19**, 289–301.

Marshall, B. A. & Richer De Forges, B. (eds) 2004. *Tropical Deep Sea Benthos, Volume 23. Mémoires du Muséum national d'Histoire naturelle* **191**, 1–640.

Motchurova-Dekova, N., Saito, M. & Endo, K. 2002. The Recent rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa, Japan. *Paleontological Research* **6**, 299–319.

Nelson, C. S. & Cooke, P. J. 2001. History of oceanic front development in the New Zealand sector of the Southern Ocean during the Cenozoic – a synthesis. *New Zealand Journal of Geology and Geophysics* **44**, 535–53.

Posada, D. & Crandall, K. P. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14**, 817–18.

Posada, D. & Buckley, T. R. 2004. Model selection and model averaging in phylogenetics: advantages of Aikake information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**, 793–808.

Richardson, J. 1994. Origins and dispersal of a brachiopod family – the systematics, biogeography and evolution of the family Terebratellidae. *Proceedings of the Royal Society of Victoria* **106**, 17–29.

Richardson, J. R. 1997. Biogeography of articulated brachiopods. *In* Williams, A. (ed.) *Treatise on Invertebrate Palaeontology, Part H. Brachiopoda, Revised*, 463–72. Boulder, Colorado and Lawrence, Kansas: Geological Society of America and the University of Kansas.

Richer de Forges, B., Koslow, J. A. & Poore, G. C. B. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* **405**, 944–7.

Saito, M., Kojima, S. & Endo, K. 2000. Mitochondrial COI sequences of brachiopods: genetic code shared with protostomes; limits of utility for phylogenetic reconstruction. *Molecular Phylogenetics and Evolution* **15**, 331–44.

Saito, M. & Endo, K. 2001. Molecular phylogeny and morphological evolution of laqueoid brachiopods. *Paleontological Research* **5**, 87–100.

Saito, M., Endo, K. & Cohen, B. L. 2001. Molecular phylogenetics and evolution of long-looped brachiopods. *In* Brunton, C. H. C., Cocks, R. & Long, S. L. (eds) *Brachiopods Past and Present*, 129–37. London: Taylor and Francis.

Stechmann, A. & Schlegel, M. 1999. Analysis of the complete mitochondrial DNA sequence of the brachiopod *Terebratulina retusa* places Brachiopoda within the protostomes. *Proceedings of the Royal Society, London, Series B* **266**, 2043–52.

Swofford, D. L. 2000. *Phylogenetic Analysis Using Parsimony* (*and *Other Methods*). Sunderland, MA: Sinauer Associates.

Thomson, J. A. 1918. Brachiopoda. *Scientific Reports (series C), Australasian Antarctic Expedition, 1911–1914* **4**, 1–76.

Thomson, J. A. 1927. *Brachiopod morphology and genera (Recent and Tertiary)*, Manual 7: New Zealand Board of Science and Art.

MS received 29 June 2006. Accepted for publication 24 September 2007.