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Permian non-marine bivalves of the Falkland Islands and their palaeoenvironmental significance

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We describe the occurrence of non-marine bivalves in exposures of the Middle Permian (Capitanian) Brenton Loch Formation on the southern shore of Choiseul Sound, East Falklands. The bivalves are associated with ichnofossils and were collected from a bed in the upper part of the formation, within a 25 cm thick interval of dark siltstones and mudstones with planar lamination, overlain by massive sandstones. The shells are articulated, with the valves either splayed open or closed. At the top of the succession, mudstone beds nearly 1.5 m above the bivalve-bearing layers yielded well-preserved *Glossopteris* sp. cf. *G. communis* leaf fossils. The closed articulated condition of some shells indicates preservation under high sedimentation rates with low residence time of bioclasts at the sediment/water interface. However, the presence of specimens with splayed shells is usually correlated to the slow decay of the shell ligament in oxygen-deficient bottom waters. The presence of complete carbonized leaves of *Glossopteris* associated with the bivalve-bearing levels also suggests a possibly dysoxic-anoxic bottom environment. Overall, our data suggest that the bivalves were preserved by abrupt burial, possibly by distal sediment flows into a Brenton Loch lake, and may represent autochthonous to parautochthonous fossil accumulations. The shells resemble those of anthracosiids and are herein assigned to *Palaeanodonta* sp. aff. *P. dubia*, a species also found in the Permian succession of the Karoo Basin, South Africa. Our results confirm that (a) the true distributions in space and time of all Permian non-marine (freshwater) bivalves are not yet well known, and (b) there is no evidence for marine conditions in the upper part of the Brenton Loch Formation.

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Key words: Bivalvia, Anthracosiidae, Permian, non-marine, Brenton Loch Formation, Falkland Islands, Gondwana.

DURING the Permian, the Falkland Islands microplate was located to the south-southeast of the African continent (Adie 1952) and would have undergone flooding episodes after the '*Eurydesma* transgression'. Palaeogeographic reconstructions of the southern Panthalassic margin of Gondwana (Veevers *et al*. 1994, López-Gamundí & Rossello 1998) suggest that an intracontinental epeiric sea extended across most portions of the Paraná and Karoo basins. Similarities in stratigraphical, palaeontological and palaeomagnetic data corroborate this hypothesis (Mitchell *et al*. 1986, Marshall 1994, Johnston 2000), which is also reinforced by the correlation of the Permo-Carboniferous units of the Falkland Islands with the Dwyka and Ecca Groups and part of the Beaufort Group of the Karoo Basin in Africa, and with units of the Paraná Basin in Brazil (Trewin *et al*. 2002). As noted by González & Saravia (2010), the '*Eurydesma* sea' flooded both the Sauce Grande Basin, Argentina, and the Kalahari–Karoo basins of Namibia and South Africa. The Karoo Basin was probably closed to the east (McLachlan & Anderson 1973), a condition endorsed by the rapid decrease in faunal diversity in that direction (see González 1985, González & Saravia 2010). González & Saravia (2010) also suggested that the Sauce Grande–Karoo basins were probably connected with Western Australia by means of a 'proto-Atlantic' arm of the sea extending between South Africa and the Falkland Islands. According to González & Saravia (2010), the '*Eurydesma* sea' would not have been connected to western Argentina since the 'Central Cratogen' closed the Sauce Grande Basin to the west. However, the disconnection of the '*Eurydesma* sea' and central Patagonia might have been caused by the plate tectonic history of the region (e.g., the allochthonous origin of Patagonia), during the late Palaeozoic

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(see Rapalini 2005, Pankhurst *et al.* 2006, Ramos 2008, M.A. Pagani personal communication 2012).

In order to further investigate the possible occurrence of marine bivalves of the '*Eurydesma* fauna' in the Falkland Islands, an extensive survey for bivalve shells in the Permian succession of the Lafonia Group was conducted. Although the presence of Permian bivalves in the Brenton Loch Formation had been previously noted (Stone & Rushton 2003, Stone *et al.* 2005), those specimens were not formally assigned to a taxonomic group. Hence, we systematically describe the bivalve molluscs from the Permian (Capitanian) Brenton Loch Formation, Saladero Member, East Falkland. The palaeogeographic and palaeoenvironmental significance of the data gathered is also discussed.

Geological setting

In the Falkland Islands, the Permian succession crops out mainly in the southern part of East Falkland, where the Lafonia Group comprises the Bluff Cove, Fitzroy Tillite, Port Sussex, Brenton Loch and Bay of Harbours formations (Aldiss & Edwards 1998, 1999; Fig. 1).

The complete succession is up to 8 km thick (Trewin *et al.* 2002) and unconformably overlies marine deposits of the Devonian Port Stanley Formation, the highest unit of the West Falkland Group (Fig. 2). The sandstones and glacial tillites of the Bluff Cove Formation and Fitzroy Tillite Formation grade up into shales of the Port Sussex Formation (Trewin *et al.* 2002), which were deposited in deep-water conditions. Above the Port Sussex Formation, rhythmic claystones and sandstones of the Terra Motas, Cantera and Saladero Members of the Brenton Loch Formation are found. The presence of rhythmites composed of sand/mud couplets together with pelitic deposits suggest deposition in quiet waters, alternating with episodic deposition of prodeltaic hyperpycnal flows. Conformably succeeding the Brenton Loch Formation, the Bay of Harbours Formation encompasses the Praltos and Egg Harbour members and is characterized by an upwards increase in the recurrence and thickeness of sandstone beds, which suggests progradational deposition of river-mouth bars and distributary channels of a delta front and plain.

The presence of an ichnofauna indicative of freshwater lacustrine environments (Aceñolaza & Buatois 1993), coupled with the characteristic facies of the Lafonia Group, points to sedimentation in a constrained, internal basin in southern Gondwana. The progradational tendency seen in the upper beds of the Lafonia Group might be correlated to contemporaneous, regional Permo-Triassic units such as those found at the top of the Passa Dois Group in the Paraná Basin, Brazil, the Beaufort Group of the Karoo Basin, South Africa, and possibly the Las Tunas Formation of the Sauce Grande-Colorado Basin, Argentina (M.A. Pagani, personal communication 2012; Fig. 3).

We focused our survey on exposures of the Permian (Capitanian) Saladero Member, Brenton Loch Formation, at Rory's Creek, a locality 8 km NW of Walker Creek Farm, on the southern shore of Choiseul Sound, East Falkland (Fig. 1); there, the presence of bivalves had already been established (Stone & Rushton 2003, Stone *et al.* 2005). Locally, the Brenton Loch Formation is up to 70 m thick and is characterized by the interbedding of very fine sandstones, claystones and laminated siltstones (Fig. 2). Generally, the succession is marked by the upward decrease in the proportion of sandstone beds and an upward increase in the abundance and thickness of rhythmite units, composed of intercalations of sandstone, siltstone and mudstone. The increase in the proportion of fine-grained suspension deposits relative to turbidite beds in the upper portions of the Saladero Member indicates that sedimentation was progressively more distal and in deeper water (Aldiss & Edwards 1999).

All specimens were collected from a single bed located 1 m above the base of the section composed of laminated dark-grey siltstone intercalated with mudstones and thin massive sandstones (Fig. 2). The shells are dispersed, typically preserved as splayed articulated valves commonly in a convex-up attitude and lying concordantly to the bedding and, more rarely, as closed articulated pairs (see following section). The bivalve specimens comprise complete silicified shells, and internal and external moulds, without any sign of abrasion and/or bioerosion. Elsewhere in the fossiliferous unit, dark claystone contains sparse fossils of complete carbonized leaves of *Glossopteris* sp. cf. *G. communis* Feistmantel, 1879 (Fig. 4A, B).

The sandstone interbeds are massive or rarely upward-fining and cross-laminated. The millimetre-scale intercalation between laminated claystone and sandstone gives the rock a rhythmic appearance, indicative of deposition alternatively by suspension and traction. It is noteworthy that the sandstone facies are commonly bioturbated and feature small loading structures at the contact with pelitic facies. Locally, these can obliterate original sedimentary structures. Sinuous, simple and unbranched horizontal tubes, of <1.5 mm thickness, filled with similar material to the rock matrix are also common at the top of some beds. Such traces are assigned to the ichnogenus *Paleophycus* (Fig. 4D) and are interpreted as feeding ichnites, produced by sedimentary infilling of burrows after the activity of predatory or suspension-feeding animals (Pemberton & Frey 1982). Other forms include continuous to discontinuous (0.8 mm to 1.2 mm thick), curved to meandering burrows, with undulating and small discontinuous semi-cylindrical ridges, and characterized by millimetre-spaced constrictions. These are assigned to the ichnogenus *Vagorichnus* (Fig. 4E, F),

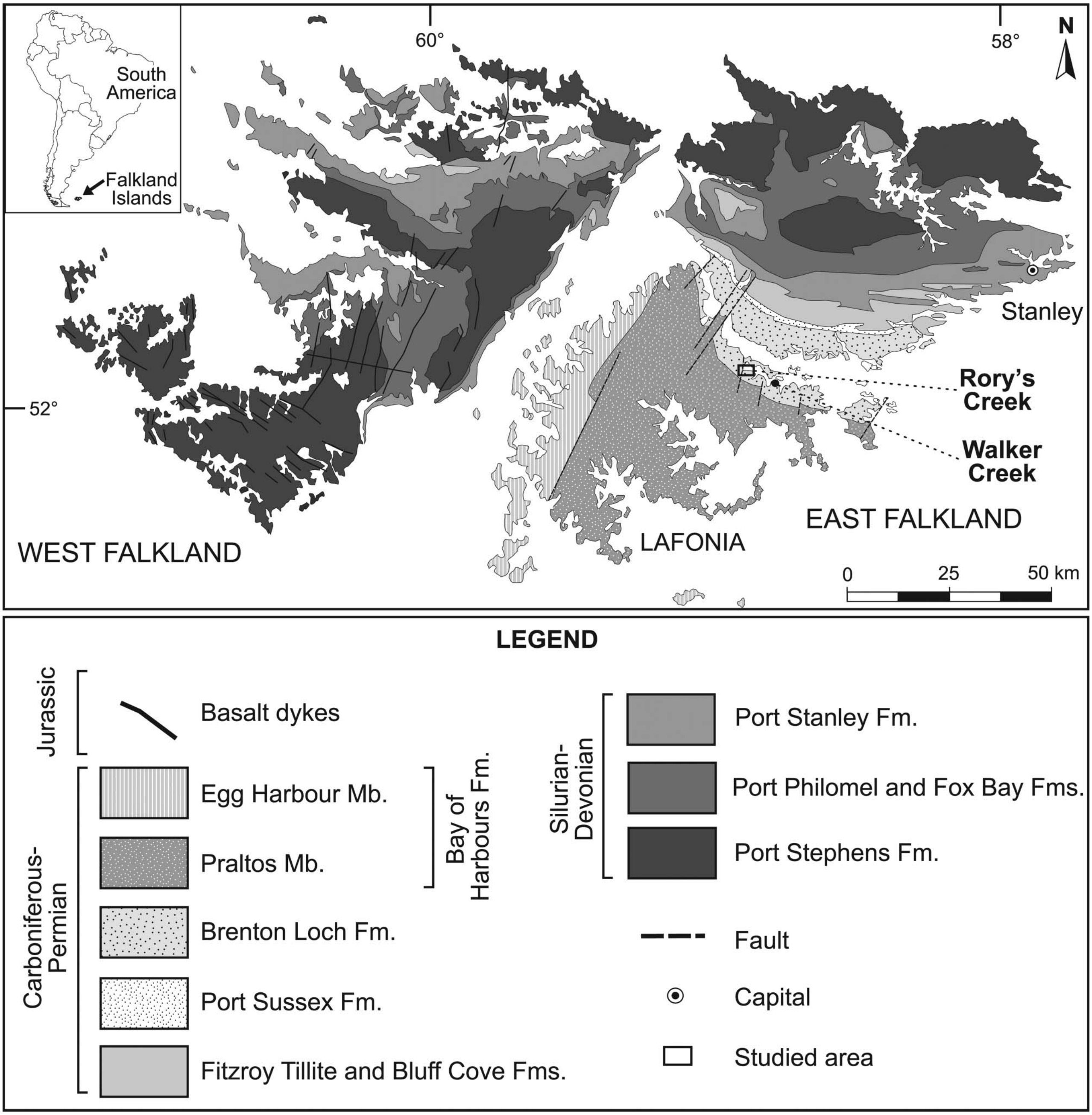

Fig. 1. Location of the Falkland Islands relative to South America and a geological map of the islands showing the outcrop of the Brenton Loch Formation and the location of the Rory's Creek study area, East Falkland (based on Aldiss & Edwards 1998).

a deep-lake ichnofossil produced by mobile deposit-feeders and commonly found in turbidite context (Buatois *et al.* 1998). The Falkland examples are preserved in medium relief, commonly along sand-mud interfaces. At the same level, elongate (20.3 mm long by 4.8 mm wide), bilobate furrows preserved in epirelief show herringbone-like ridges with a characteristic V pattern. This trace has affinities with the *Cruziana* ichnogenus (Fig. 4G), commonly regarded as the trails and shallow burrows produced by arthropods. Finally, horizontal to sub-horizontal (0.72–0.83 mm thick) simple tubes, filled with sand were found in mudstone and laminated siltstone facies intercalated with the bioturbated sandstones. These feeding burrows were probably produced by worm-like invertebrates and can be assigned to the ichnogenus *Planolites* (Fig. 4C).

Systematic palaeontology

(by F. Quaglio, M.G. Simões, L.E. Anelli and L. Warren)

Bivalve remains are rare and have been recovered from the Saladero Member, Brenton Loch Formation, at only one locality. Despite exhaustive searches, only 11 specimens have been found. Some were collected by P. Stone in November, 2001, and in February, 2004, and are housed in the British

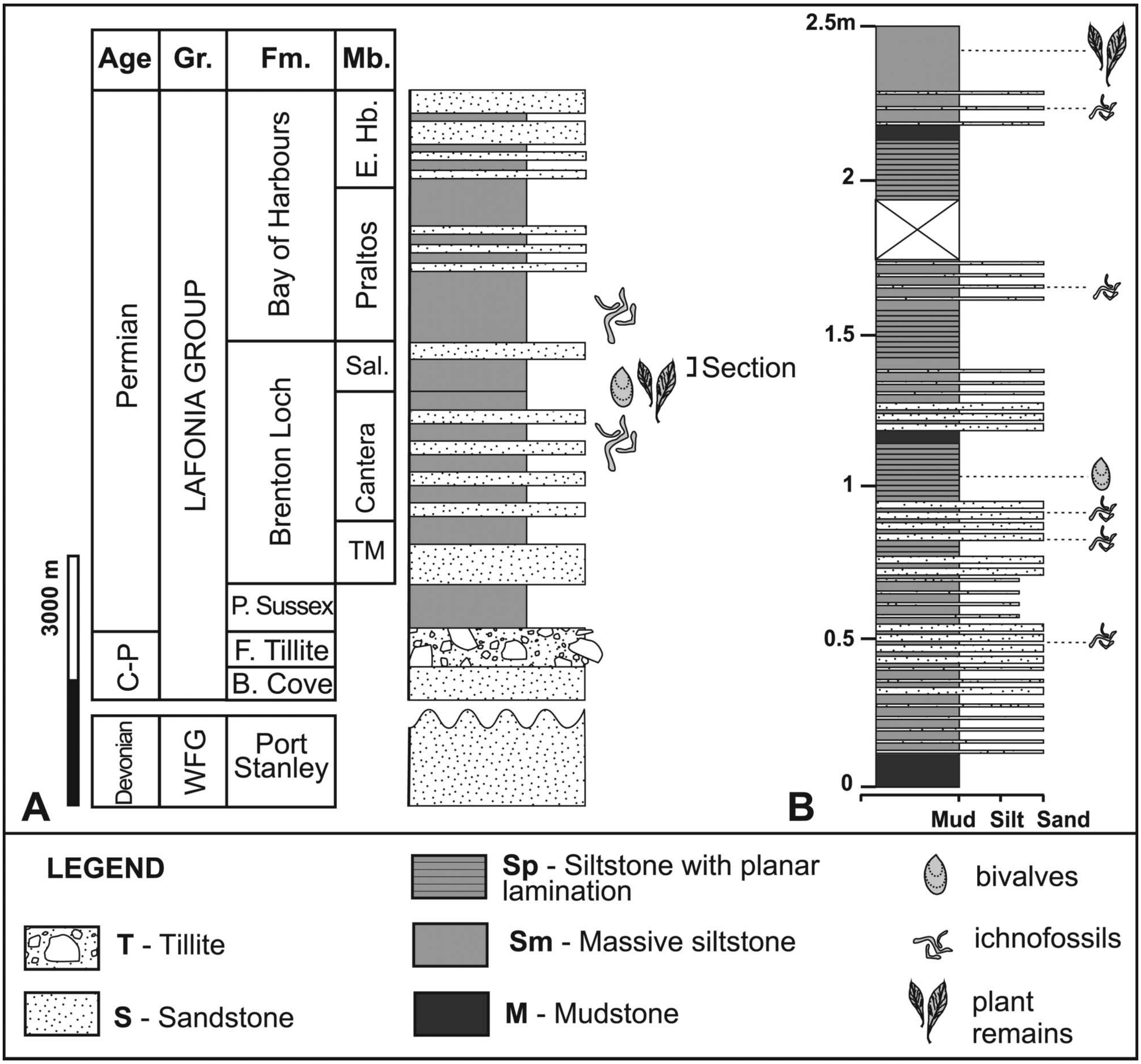

Fig. 2. Lithostratigraphic division of the Lafonia Group in East Falkland, Falkland Islands (based on Trewin *et al.* 2002). **A**, Generalized stratigraphic section of the Lafonia Group. **B**, Stratigraphic section of the Brenton Loch Formation at Rory's Creek. C-P, Carboniferous–Permian. Units: B. Cove, Bluff Cove; E. Hb., Egg Harbour; F. Tillite; Fitzroy Tillite; P. Sussex, Port Sussex; Sal., Saladero; TM, Terra Motas; WFG, West Falkland Group.

Geological Survey Palaeontology Collection, Nottingham, UK, under the code LX1010. Specimens collected subsequently by M.G. Simões, F. Quaglio and L.V. Warren in March, 2011, are housed in the collection of the Laboratório de Paleontologia e Sistemática of the Institute of Geosciences, University of São Paulo, Brazil, under the prefix GP. The specimens are preserved as internal and external moulds. In the laboratory they were mechanically prepared following standard palaeontological techniques described by Feldmann *et al.* (1989); detailed features were studied after the preparation of plasticine casts. The suprageneric systematics is based on Bieler *et al.* (2010) and the elongation and obesity indices are described according to Stanley (1970). However, caution is necessary when using these biometric indices, since the specimens are deformed due to the strain (see below).

The alpha taxonomy of many Carboniferous to Permian bivalve species seems excessively subdivided (Lucas *et al.* 2006) because most morphological variations are also linked to the mode of life of these bivalves (ecomorphophenotypic variations) and are not necessarily interspecific in origin (see Lucas *et al.* 2006).

During the study of the Brenton Loch Formation bivalves we noticed that morphological variation can also be produced by taphonomy and tectonic factors (e.g., strain), and in this way they are *taphotaxa* (= morphological variants defined by taphonomic artefacts). Lucas (2001) introduced this term to refer to fossil species and genera erected on the basis of

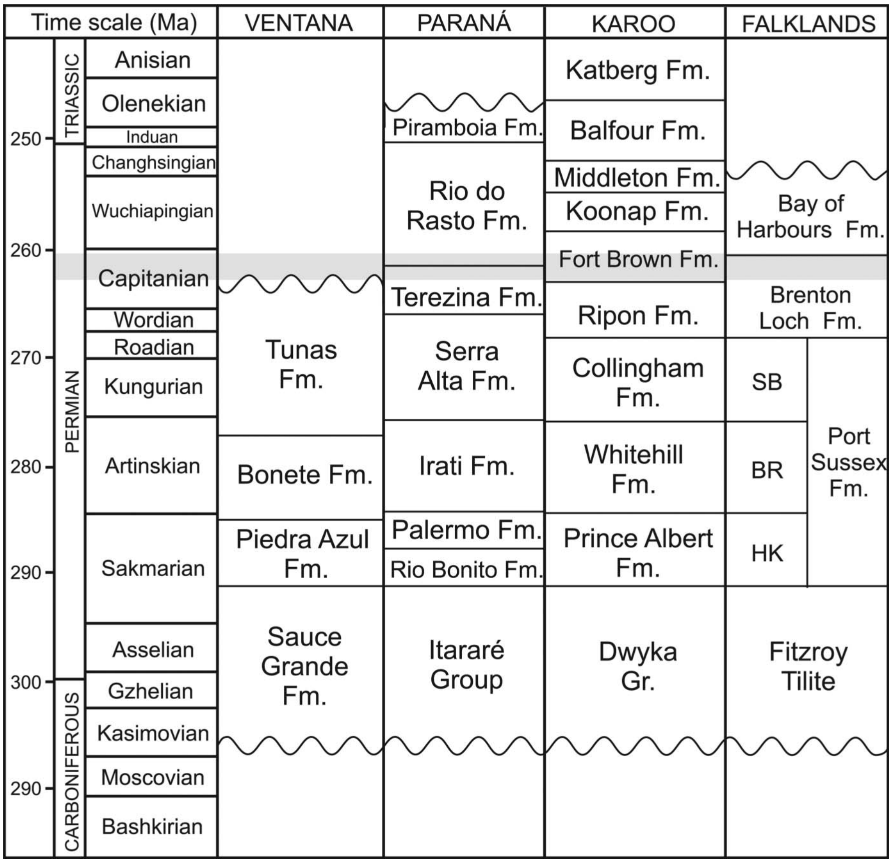

Fig. 3. Stratigraphic correlation for the late Palaeozoic and early Mesozoic units of Ventana, Paraná and Karoo basins and Falkland Islands. The grey band corresponds to the time interval studied (based on the time-scale of Walker & Geissman, 2009, with data from Veevers *et al.* 1994, Aldiss & Edwards 1998, López-Gamundí & Rossello 1998, Aldiss & Edwards 1999, Trewin *et al.* 2002, Milani 2004, Catuneanu *et al.* 2005, López-Gamundí 2006, Santos *et al.* 2006).

characters that have been modified by taphonomic processes. Taphotaxa are invalid because the characters employed to diagnose them are artefacts of preservation.

The bivalve specimens from the Brenton Loch Formation are typically preserved with the valves splayed open, although some are closed and articulated (see Fig. 5). The shells of the specimens with valves splayed open are deformed by compression. In these specimens, the commissural planes of both valves are not precisely parallel to the bedding. This is because the commissural planes of articulated open valves tend to form an acute angle to the bedding. One of the shells of a given single specimen tends to lie parallel to the bedding, whereas the other valve does not. Hence, valves of the same specimen are not equally deformed. Generally, the right valve is more elongated than the left valve (see Fig. 5 and measurements in Table 1). Therefore, most of the morphological variations in those shells are produced by taphonomic and tectonic factors (e.g., strain). The specimens are compressed in the oblique or anterior–posterior plane of the valves, or even laterally. Specimens compressed anterior–posteriorly are deformed in such a manner that they have exaggerated width (obesity).

East Falkland was subject to Permo-Triassic south-verging folding, striking east–west to west/northwest–east/southeast (Curtis & Hyam 1988), which implies a general north–south-trending compression. Deformation of the bivalves should have been influenced by such compression, with the resulting shapes arising from their individual positions in relation to the orientation of tectonic stress.

In this way, the bivalve shells of the Brenton Loch Formation provide good examples of how morphology can be modified by factors other than biology. Hence, caution must be exercised when comparing the shell shape of the studied bivalves with the morphology of other Permian, non-marine bivalve species.

Subclass AUTOBRANCHIA Grobben, 1894
Superorder HETEROCONCHIA Hertwig, 1895
Clade HETERODONTA Neumayr, 1884
Order UNCERTAIN
Superfamily ANTHRACOSIODEA Amalitsky, 1892
Family ANTHRACOSIIDAE Amalitsky, 1892

Palaeanodonta Amalitsky, 1895

Palaeanodonta sp. aff. **P. dubia** (Amalitsky) (Table 1, Fig. 5)

Material. Splayed valves with the internal portion retained in the rock matrix (LX1010-2B, –3, –6; GP/1T/2275); external moulds of splayed valves (LX1010-1, –2A; GP/1T/2276, 2279); internal mould of the

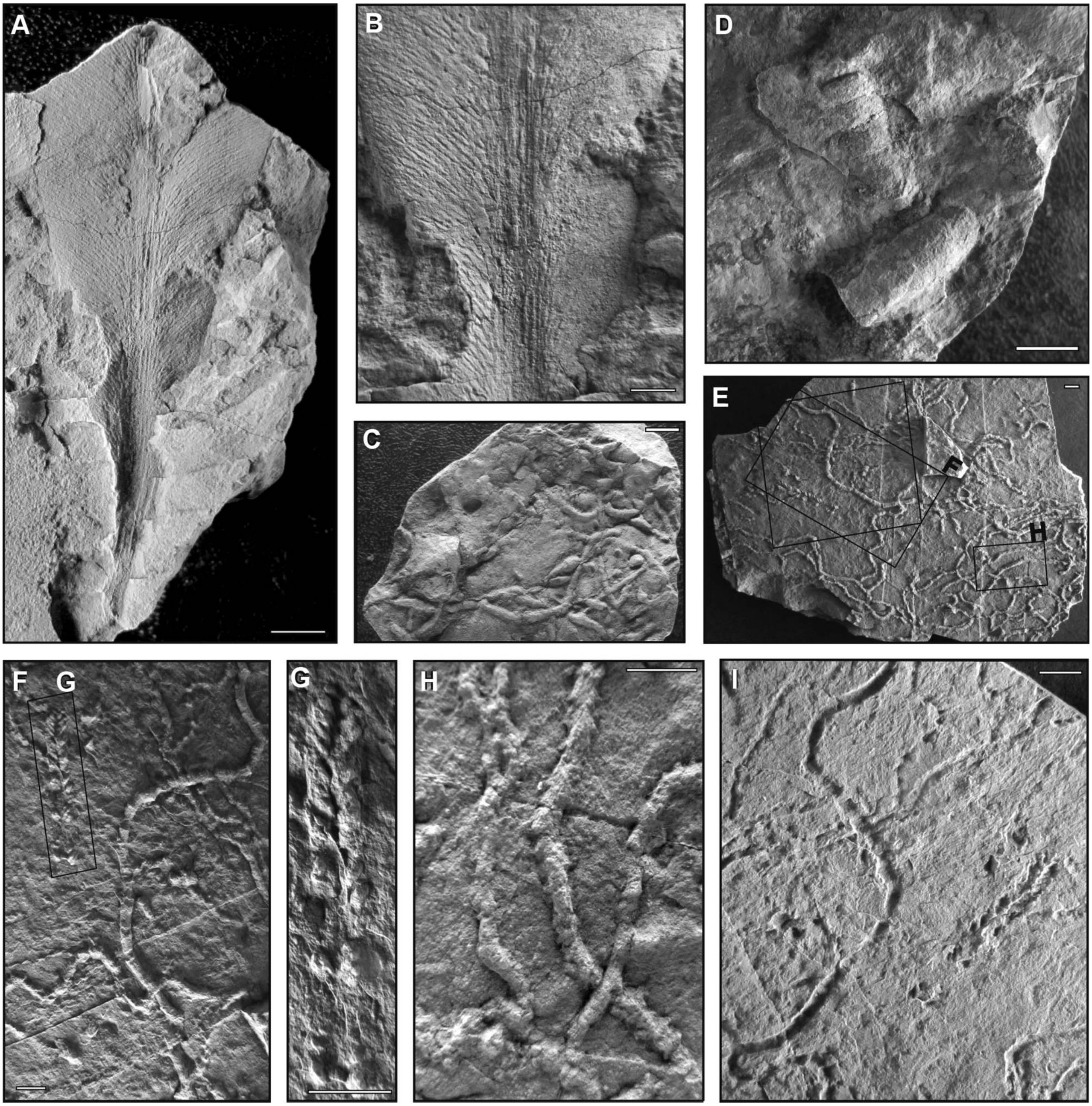

Fig. 4. Plant and ichnofossils from the Saladero Member of the Brenton Loch Formation at Rory's Creek, East Falkland. **A** and **B**, GP/3T/2439, *Glossopteris* sp. cf. *G. communis*; **A**, whole specimen; **B**, detail of leaf base. **C**–**I**, ichnofossils; **C**, GP/7T/34, *Planolites* sp.; **D**, GP/7T/35, *Paleophycus* sp.; **E**–**H**, part, in positive relief; **E**, whole sample with guides to the following images; **F**, *Vagorichnus* sp., showing *Cruziana* sp. in upper left. **G**, detail of *Cruziana* sp.; **H**, detail of *Vagorichnus* sp.; **I**, counterpart of E. Scale bars = 5 mm.

dorsal portion of an articulated pair (LX1010-5A); external moulds of the anterior region of an articulated pair (LX1010-5B; GP/1T/2277, 2278a).

Description. Shell ovate, equivalved, inequilateral, elongate to moderately elongate (L/H = 0.94–1.98), with height around two-thirds of the length. Umbo low and broad, faintly projecting above dorsal line, located anteriorly at one-third of the length, with beaks slightly prosogyrous and divergent in internal moulds (LX1010-5A, GP/1T/2278a); posterior umbonal carina rounded, faintly marked. Lunule small, rounded; escutcheon absent. External surface of shell ornamented with growth lines of varying width, irregularly spaced and superimposed by commarginal rugae; inner layer of shell composed of antimarginal ridgelets as shown in internal mould (GP/1T/2277). Anterior dorsal margin short and straight, anterior extremity rounded; ventral margin convex, posterior extremity with ill-defined respiratory margin; posterior dorsal margin straight to faintly curved. A very slim line runs close to the posterior dorsal margin, which may represent a narrow external ligament. Commissure line of posterior dorsal region straight and faint. Internal features unknown.

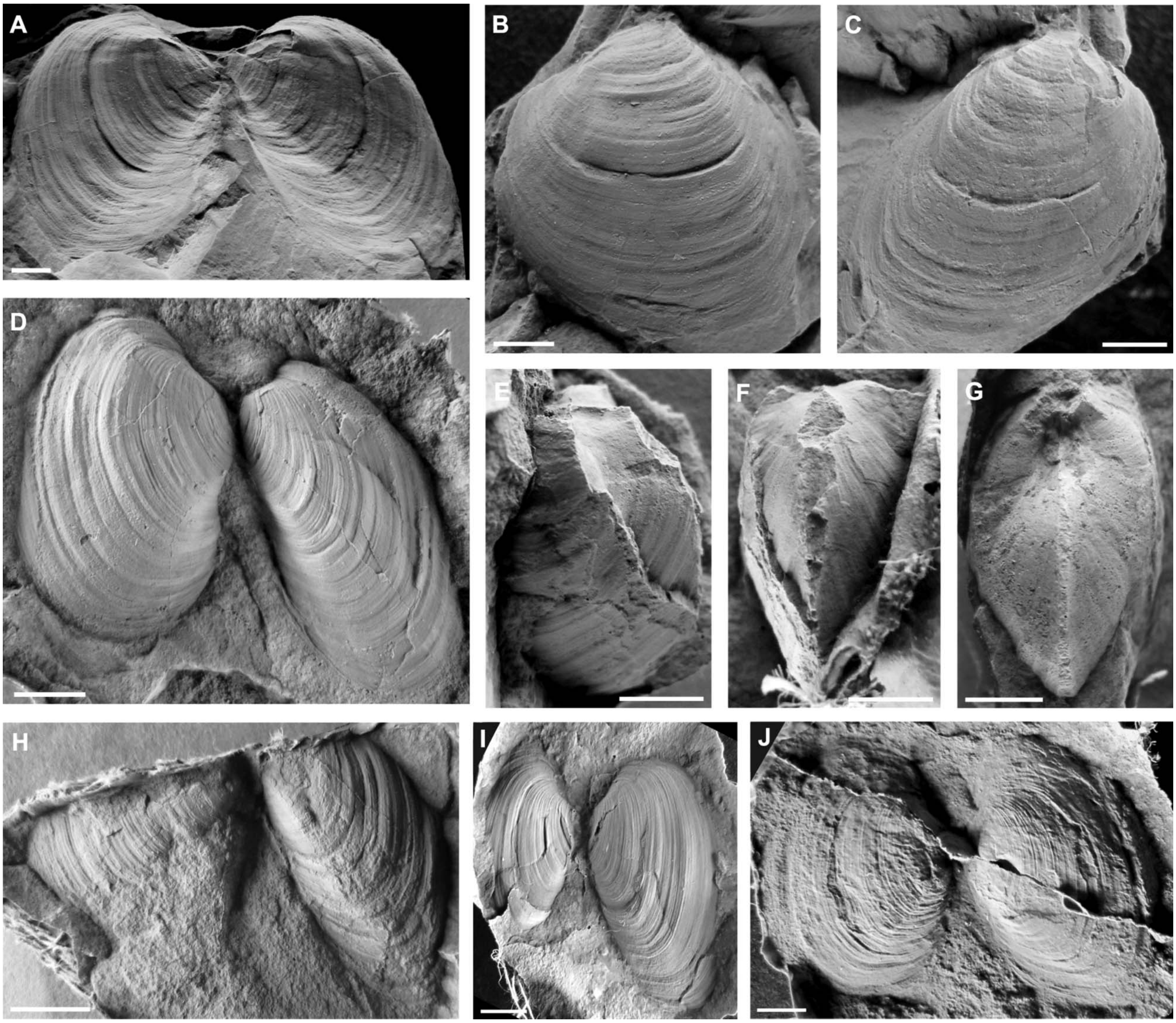

Fig. 5. Palaeanodonta sp. aff. *P. dubia* from Saladero Member of Brenton Loch Formation at Rory's Creek, East Falkland. **A**–**C**, GP/1T/2275; **A**, both valves butterflied; **B**, left valve; **C**, right valve; **D**, latex cast of GP/1T/2276; **E**–**F**, latex cast of GP/1T/2278a; **E**, anterior-right view; **F**, anterior view; **G**, latex cast of GP/1T/2277, anterior view; **H**, latex cast of GP/1T/2279; **I**, latex cast of LX1010-2A; **J**, latex cast of LX1010-1. Scale bars = 5 mm.

Remarks. The sedimentology of the Brenton Loch Formation strongly suggests that the preserved bivalves were freshwater forms (see below). During the late Palaeozoic, non-marine bivalves (e.g., anthracosiids, palaeomutelids, myaliniids) had a cosmopolitan distribution. Well-known records are from southern Africa and Madagascar, Antarctica, southwestern and eastern United States, the Oka-Volga River Basin, Russia, southern Asia and South America (Hind 1894–1896, Amalitsky 1895, Schmidt 1910, Cox 1932, Eagar & Weir 1971, Bradshaw 1984, Eagar & Peirce 1993, Eagar & Belt 2003, Rinehart *et al*. 2003, Díaz-Saravia 2009, Rinehart & Lucas 2010).

The presence of a lunule and a perceptible, narrow, external ligament in our specimens exclude the possibility of them being part of Unionacea Fleming, 1828. Rather, these features point to Anthracosiacea Amalitsky, 1892, a representative of late Palaeozoic non-marine faunas. In the studied shells, the straight and faint commissural line of the posterior dorsal region suggests the presence of undeveloped teeth or even their absence. Those features, added to the general shape (including expected variations due to tectonic deformation), point to affiliation with *Palaeanodonta* Amalitsky, 1895. *Palaeanodonta* specimens have been described from Russia, Poland, Africa and Antarctica (Amalitsky 1895, Cox 1935, Bradshaw 1984, Karwowski & Klapcinski 1986) and were recorded, although not described or illustrated, in China (e.g., Zhu *et al*. 2005), where the genus is used as a Permian biostratigraphic proxy.

In his original designation, Amalitsky (1895) diagnosed *Palaeanodonta* with well-defined muscle scars, features not present in specimens from the Brenton Loch Formation. The presence of a lunule was mentioned by Weir (1969) in the emended diagnosis. Previous records in the Permian deposits

Specimen	Valve	Length	Height	Elongation (L/H)	H/L
LX1010-1	R	19.4	12.6	1.54	0.65
LX1010-1	L	18.2	12.9	1.41	0.71
LX1010-2B	R	28.8	14.5	1.98	0.50
LX1010-3	R	18.3	13.5	1.35	0.74
LX1010-3	L	18.9*	10.6	1.78	0.56
LX1010-6	R	18.3	12.2	1.50	0.67
LX1010-6	L	19.5	11.4	1.71	0.58
GP/1T/2275	L	26	21	1.23	0.81
GP/1T/2275	R	26.5*	28.3*	0.94	1.07
GP/1T/2276	R	24*	16*	1.43†	0.67
GP/1T/2276	L	23.4	15	1.56	0.64

Table 1. Measurements of representative specimens of *Palaeanodonta* sp. aff. *P. dubia* from the Brenton Loch Formation, Falkland Islands. *Incomplete specimen; †calculated by extrapolation of growth lines to give a complete valve measurement.

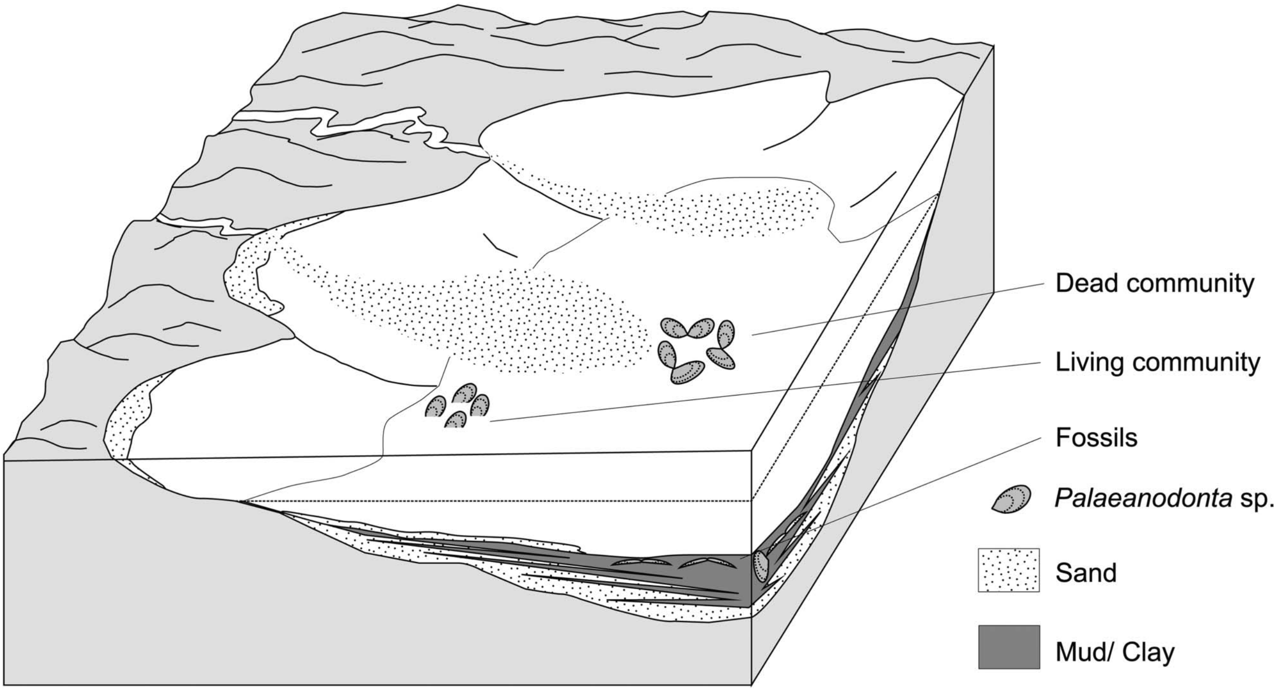

Fig. 6. Diagram of inferred depositional environments of the bivalve-bearing level of the Brenton Loch Formation showing episodic bottom influx of sand sediments by river discharge.

of South and East Africa (Weir 1969) predict the presence of the genus in the Falkland Islands during late Palaeozoic times.

Palaeanodonta sp. aff. *P. dubia* from the Brenton Loch Formation is similar to *P. fischeri* from the Ohio Range, Antarctica (Bradshaw 1984), in dorsal margin angle, posterior elongation, ornamentation and the possible presence of opisthodetic ligament, but differs in general shape. However, because the Antarctic specimens are strongly compressed and most Falkland specimens are obliquely deformed, a comparison of general shape is not appropriate for taxonomic assessment.

Specimens from the Brenton Loch Formation are similar to specimens found in Permian deposits of Germany and described by Schmidt (1910) as belonging to the *P. ernae* group. The main similarities are the great convexity of the shell surface, central positioning of the umbo and well-marked growth lines. However, *P. ernae* lacks a posterior carina, a character present in specimens from the Falkland Islands.

Falkland specimens are also similar to *P. dubia* (Amalitsky) described by Cox (1935) from the Mzombe Formation (*sensu* Dypvik *et al.* 2001), a mid- to Upper Permian unit of the Kilombero Rift Basin, Tanzania. The size, general shape and measurement ratios are strikingly similar, which could lead one to consider them to be of the same species. Further, the Tanzanian Mzombe Formation (Ruhembe Group) is correlated with the succession spanning the top of the Ecca Group (Fort Brown Formation) and the base of the Beaufort Group

(Coonap Formation) in South Africa (Dypvik *et al.* 2001). In turn, these African units are correlated with the upper part the Brenton Loch Formation and the lower part of the Bay of Harbours Formation in the Falkland Islands (Trewin *et al.* 2002). The great morphological similarities between the bivalve specimens, and the possible correlation of the Mzombe and Brenton Loch formations, would suggest their potentially close affinity. However, the fact that all described South African, Tanzanian and Falkland units are typical of freshwater conditions may instead suggest faunal convergence. Moreover, because no other comparable features were described in the African material, *Palaeanodonta* specimens from the Falkland Islands are only considered to have close affinity to *P. dubia*.

Palaeoenvironment

Palaeanodonta sp. aff. *P. dubia* was probably an active, shallow burrower that may have thrived in fine-grained, lake-bottom sediment. Most of the studied specimens from the Falkland Islands were preserved as articulated valves. Indeed, one of the main taphonomic features of the fossiliferous layers of the Brenton Loch Formation in the Rory's Creek area is the predominance of articulated specimens, commonly in a concave-down attitude relative to bedding. Generally, the specimens were preserved with the two valves splayed open on the bedding plane, the so-called 'butterfly condition' (see Allmon 1985), which develops in hours to days after death (Schäfer 1972). This is because the dead shells tend to lie at the sediment/water interface and those still articulated tend to gape. Once dead, the adductor muscles no longer pull the valves together, and both valves are opened through contraction of the ligament (see Cadée 2002). Hence, the splayed open shells of *Palaeanodonta* sp. aff. *P. dubia* were probably buried soon (in weeks) after death. All studied specimens seem to be preserved with the commissural plane parallel or oblique to the bedding. These observations indicate that live infaunal bivalves were exhumed and had experienced a subsequent short period of exposure on the sediment/water interface, during which decomposition of the adductor muscle and shell gaping took place. During the history of the Permian Falklands 'delta', sedimentation was rapid (N.H. Trewin, personal communication 2012). Hence, the 'butterflied' shells found in the Brenton Loch Formation are a good indicator of rapid (but not abrupt) burial (see also Allmon 1985, David *et al.* 2010). Further, the preservation of 'butterflied' shells in a concave-down position indicates low-energy conditions after the exhumation event, and relatively rapid subsequent reburial, inhibiting the complete disarticulation of the valves (see Cantalamessaa *et al.* 2005, David *et al.* 2010).

Finally, the butterfly condition of bivalve shells in very fine siliciclastic sediments has been commonly correlated with a lack of bioturbation and with slow decay of the ligament in oxygen-deficient waters (Plotnick 1986, Allison & Briggs 1991). Some authors consider that 'butterflied' shells are most commonly found in sedimentary facies associated with severely to extremely dysoxic bottom conditions (see Etter 1996, Schatz 2005). At Rory's Creek, the restricted layer with dispersed shells of *Palaeanodonta* sp. aff. *P. dubia* is massive and devoid of trace fossils, and may indicate a brief period of oxygen-deficient conditions within the lake bottom, in which the Brenton Loch Formation was deposited. The presence of only a few specimens, constrained to a single level at the top of the Saladero Member, also illustrates the short-lived character of the benthic bivalve community, whose mortality may be associated with time intervals in which the basin lake bed was under anoxic–dysoxic bottom conditions. Around the same stratigraphic level, beds of dark claystones containing sparse fossils of complete carbonized leaves of *Glossopteris* sp. cf. *G. communis* (Fig. 4A, B) also suggest deposition under redox conditions.

The palaeoenvironmental interpretation discussed above is also supported by the presence of trace fossils such as *Planolites* sp. and *Paleophycus* sp. (Fig. 4C, D), typical members of the *Mermia* ichnofacies (Seilacher 1967). This ichnofacies is indicative of the low-energy, subaqueous environments, commonly found in lacustrine depositional systems (Buatois & Mángano 1995, 1998). The occurrence of burrows assigned to *Vagorichnus* sp. (Fig. 4E, F, H, I), previously recorded in Jurassic strata (see Buatois *et al.* 1995), provides evidence for the presence of another ichnogenus belonging to the *Mermia* ichnofacies (Buatois *et al.* 1998) and increases the probability of deposition under freshwater conditions. Another ichnogenus found at Rory's Creek that is typical of the *Mermia* ichnofacies is *Cruziana* sp. (Fig. 4E–G, I). Virtually any arthropod with several similar pairs of legs can produce *Cruziana*-like traces (N.H. Trewin, personal communication 2012). Although many lower Palaeozoic *Cruziana* sp. traces have been assigned to trilobites (Seilacher 1985), other groups of arthropods, including aglaspids, or branchiopod crustaceans (see a summary by Aceñolaza & Milana 2005) may alternatively have been responsible. This ichnogenus has been recorded in various palaeoenvironmental settings, from shallow marine to freshwater (Seilacher 1985, Crimes 1987, Bromley & Asgaard 1979).

Sedimentologically, the association of mudstone and subordinate sandstone facies suggests a predominance of settling muds in quiet-water conditions with no significant reworking by wave or current action. The dark colour of the rocks and the presence of complete, carbonized leaves suggest predominantly reducing bottom-conditions during deposition. Mudstone sedimentation was sporadically interrupted by dense hyperpycnal flows, resulting in fine sandstone interbeds between the claystone and siltstone beds (Fig. 6).

The presence of ichnofossils in the sandstones is evidence that the input of sandy material by hyperpycnal fluxes may have contributed to the oxygenation of the bottom water, allowing colonization by bioturbators. The intercalation of deposits laid down by traction and suspension processes, producing the observed rhythmic alternation of sandstones and claystones, may have resulted from climatically controlled environmental oscillations, as previously suggested by Trewin *et al.* (2002). This sedimentary intercalation would seem to have been closely related to fluctuations in the prevalence of oxidizing or reducing bottom conditions.

Summary and conclusions

1. We found no palaeontological evidence for a marine environment in the Permian Brenton Loch Formation (see also Trewin *et al.* 2002).
2. The morphology of the studied bivalves has been modified by taphonomy and tectonic strain, and the variation evident may not reflect interspecific differences.
3. Despite the comments above, morphologically similar bivalves are found in Permian freshwater deposits of Tanzania, South Africa and the Ohio Range, Antarctica, all of which formed part of the same Gondwanan sedimentary province.
4. Some authors have suggested that non-marine bivalves would be biostratigraphically useful for correlating late Palaeozoic deposits (Davies & Trueman 1927, Broadhurst 1959, Trueman & Weir 1946–1959, Zhu *et al.* 2005). It may be valid to differentiate ecological variations (morphotypes), especially in, for example, Carboniferous strata of northwest Europe (Vasey & Bowes 1985). However, in many situations, species definition must also be based on morphotypes because key characters for taxonomical studies (e.g., muscle scars, hinges) are not commonly preserved. This may result in excessive taxonomical splitting (see Lucas *et al.* 2006). Considering the high endemic potential of freshwater organisms, and the usually poor preservation of bivalves from such upper Palaeozoic environments, a well-defined biostratigraphy based on bivalves is likely unachievable. In the case of the Brenton Loch Formation, it is possible that the preserved bivalves were endemic, as the sedimentological interpretation points to an isolated freshwater environment. Hence, any correlation and comparison with other late Palaeozoic occurrences can only be tentative.

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