

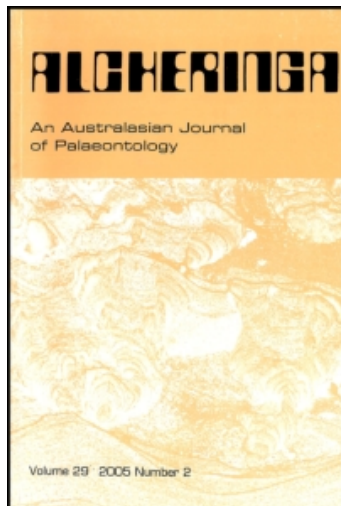
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Permian bivalve molluscs from the Gai-As Formation, northern Namibia: systematics, taphonomy and biostratigraphy

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Permian bivalve molluscs from the Gai-As Formation, northern Namibia: systematics, taphonomy and biostratigraphy

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Fossil bivalves from two horizons in the Gai-As Formation of NW Namibia are tentatively correlated with mid-Permian taxa of the Passa Dois Group of Brazil, supporting the concept that the Paraná Basin extended into Africa. The Namibian fauna includes a new genus and species, *Huabiella compressa*, which was previously confused with Brazilian taxa. The taphonomy of the bivalve-rich strata indicates deposition under the influence of episodic events, such as storms. The Gai-As Formation directly overlies the mesosaurid-bearing deposits of the Huab Formation, indicating a significant unconformity when compared with the more complete succession of the Passa Dois Group, Paraná Basin, Brazil. The studied bivalve assemblages are no younger than 265 ± 2.5 Ma (mid-Permian), based on U/Pb radiometric dating of zircons from tuffs.

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Key words: Bivalvia, Megadesmidae, Permian, Huab area, Gai-As Formation, biostratigraphy, Rio do Rasto Formation.

DURING the late Palaeozoic, large areas of western Gondwana (South America and Africa) were covered by an extensive inland sea in which part of the Permian successions of the Paraná (Brazil, Argentina, Paraguay and Uruguay), Karoo (South Africa) and Huab (NW Namibia) basins were deposited. In the late Early Permian, this large inland sea was either isolated or had a restricted connection to the Permian oceans. As demonstrated by the Permian succession of the Paraná Basin (*ca* 281–265 Ma, Holz *et al.* 2010), this inland sea was very

shallow, with variable salinity regimes (hypersaline, brackish and freshwater) due to climatic changes (humid to arid: Rohn 1994, Holz *et al.* 2010). Benthic faunas within this inland sea were dominated by bivalve molluscs that flourished despite the conditions of high environmental stress and extreme geographic isolation (Mendes 1952, Runnegar & Newell 1971, Simões *et al.* 1998, 2000). This is one of the oldest known examples of a molluscan long-lived fauna that evolved within an epeiric sea (Wesselingh 2007). The fauna was endemic, with high morphological disparity and was dominated by megadesmid bivalves, which had clearly evolved from marine ancestors

(Runnegar & Newell 1971, Simões *et al.* 1997, 1998).

At least 24 generic names had been applied to bivalves from the Paraná Basin prior to the publication of the benchmark monograph on Permian Passa Dois Group molluscs by Runnegar & Newell (1971). None of these names has been applied to species or genera found outside the Paraná Basin (Runnegar & Newell 1971). Cooper & Kensley (1984) were the first authors to record bivalves in the Permian deposits of the South African Waterford Formation, Ecca Group (Karoo Basin), ascribing them to typical Permian genera of the Paraná Basin. Consequently, the bivalves could no longer be considered endemic to the Paraná Basin, although Dickins (1992, p. 989) did not fully accept the identifications of the African forms by Cooper & Kensley (1984). As a result, this particular Karoo Basin fauna needs to be fully revised and re-described. Therefore, the occurrence of Permian bivalves in common with the Paraná Basin (Brazil, Uruguay and Paraguay) in deposits of the Karoo Basin has remained questionable.

A new Permian bivalve occurrence was recorded in lacustrine deposits of the Gai-As Formation (Huab Basin, NW Namibia) by Ledendecker (1991, 1992), who identified *Terraia altissima* (Holdhaus, 1918), a taxon known from the upper portion of the Passa Dois Group (Rio do Rasto Formation) of the Paraná Basin in Brazil and Uruguay. This information was confirmed by Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), and further occurrences were recorded, together with the discovery of bivalves tentatively assigned to *Leinzia similis* (Holdhaus, 1918). Unfortunately, these bivalve molluscs were not properly figured or described. Given the importance of bivalves for biocorrelation and the need for detailed descriptions of the fossil assemblage, the German sedimentologists contacted Brazilian palaeontologists and sent the fossils for further study. This paper aims to: (1) identify

and describe the Permian bivalves of the Gai-As Formation, Namibia; (2) compare the fauna with coeval assemblages of the Paraná Basin, Brazil; and (3) describe the taphonomic features of the bivalve assemblages.

Geological setting

The Permian succession of the Huab area in northern Namibia (Fig. 1) comprises two sedimentary successions that include fluvio-marine deposits (Verbrandeberg, Tsarabis and Huab formations) and lacustrine deposits (Gai-As and Doros formations; Figs 2, 3). These deposits were described by Stranistreet & Stollhofen (1999), Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), and their relevant results are summarized below.

The lacustrine sequence, yielding unique bivalve shells, reaches 170 m thick and initiates with the Gai-As Formation, which is divided into lower and upper subunits (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000; Fig. 3). The Gai-As Formation is separated from the underlying marine, mesosaurid-bearing deposits of the Huab Formation by a significant hiatus (Wanke 2000), and is succeeded unconformably by the sandy deposits of the Doros Formation. The Gai-As and Doros formations represent an overall shallowing and coarsening-upward interval (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000). The lower Gai-As deposits comprise 65 m of laminated claystones and mudstones representing a hemi-pelagic facies association, whereas the upper Gai-As deposits comprise mainly mudstones with interbedded limestones, sandstones and fallout tuffs resembling a shallowing-upward lacustrine association. The overlying Doros Formation is characterized by sandstones and conglomerates with subordinate interbeds of mudstones and limestones representing a lake-margin facies association.

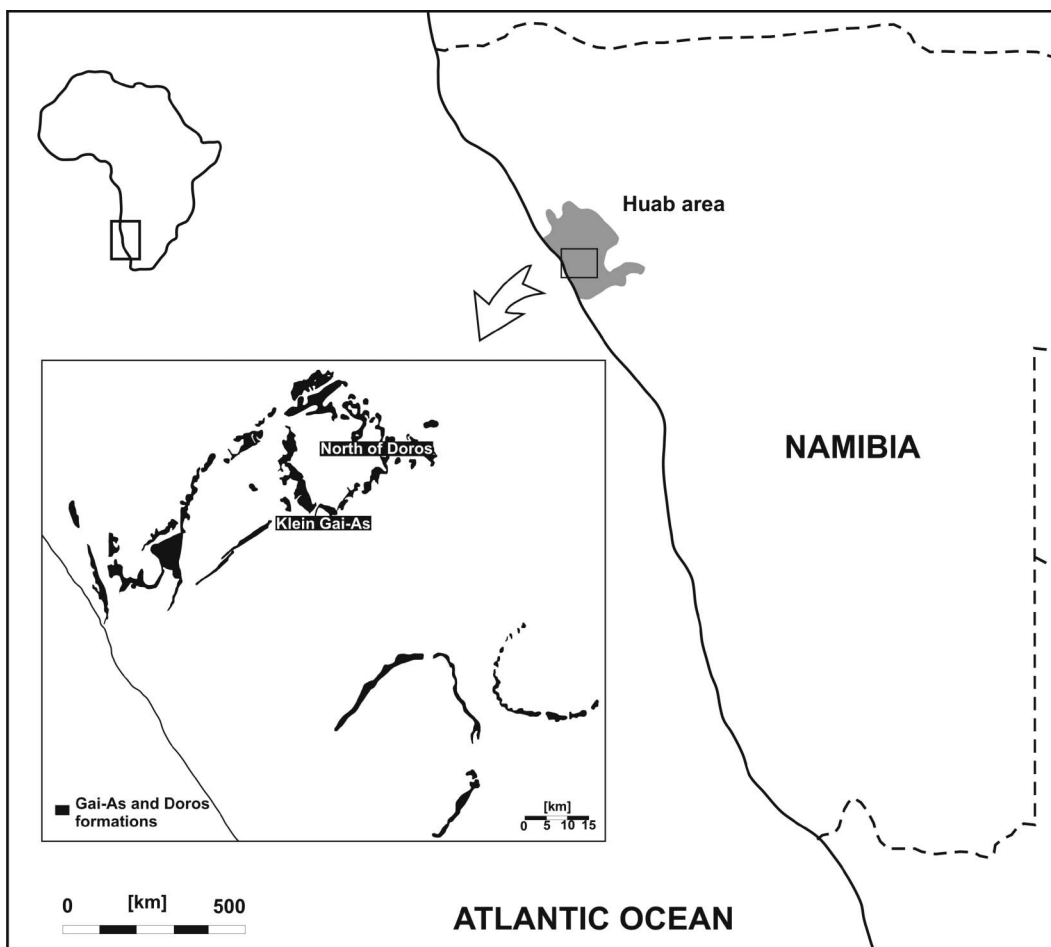
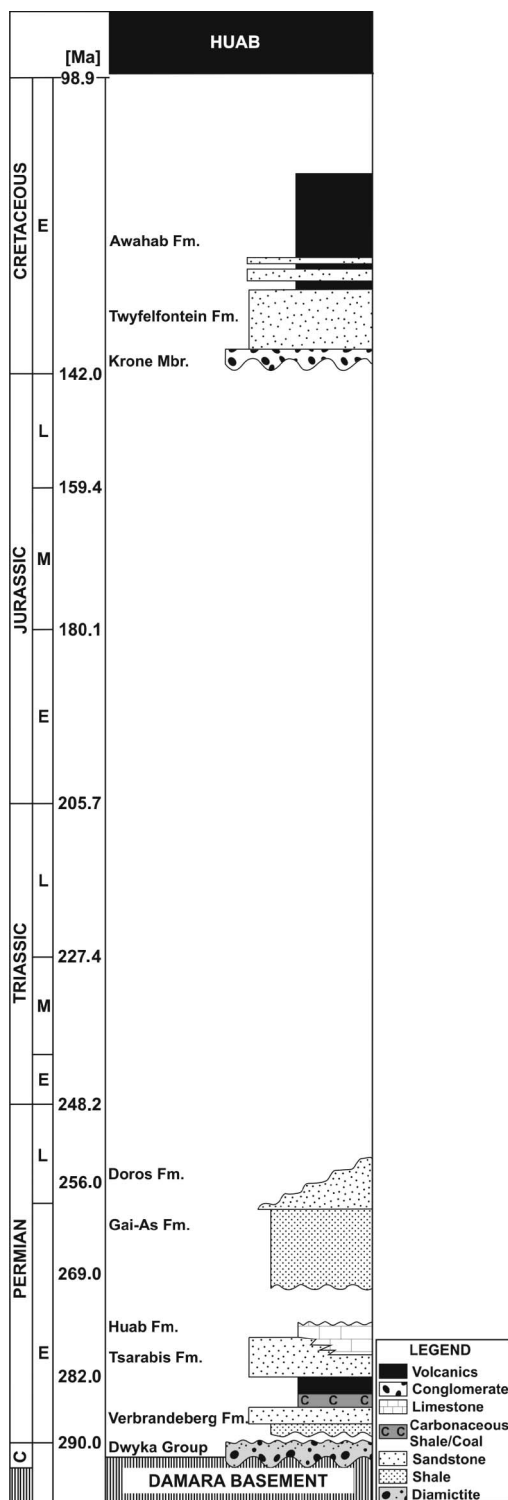


Fig. 1. Schematic map of the Huab area, northwest Namibia (modified from Catuneanu *et al.* 2005). Inset: map of the outcrop belts of Gai-As Formation, and the type localities of the sections measured at the Klien Gai-As and north of Doros (see also Fig. 3, modified from Stollhofen *et al.* 2000).

Within the lacustrine sequence, bivalves occur in both the lower and upper Gai-As deposits (Fig. 3). The lower unit of the Gai-As Formation, from which some of our samples were derived, is widespread in the central Huab region. According to Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), the basal strata of the Gai-As Formation comprise reddish to violet, mostly laminated argillaceous to silty shales, containing 1–3 cm thick tabular interbeds of normally graded, medium-grained sandstones and a few 10–50 cm thick, lami-

nated limestone beds (Fig. 3). This informally named lower Gai-As Formation (Stollhofen *et al.* 2000) contains at least two widespread beds with conspicuous concentrations of bivalve shells (Wanke 2000).

The informally named upper Gai-As Formation (Stollhofen *et al.* 2000), thins from 80 m at the Namibian coast to 10–20 m thickness inland and comprises red–violet mudstones containing minor tabular sandstone interbeds, laminated or small-scale cross-bedded limestone, and fallout tuff deposits. Eastwards, intense



pedogenic modification is apparent. The fine- to medium-grained sandstones, 1–10 cm thick, are normally graded and show rare hummocky cross-bedding, basal load casts, wave-rippled tops and *Monocraterion*-like escape structures (Holzfoerster 2000, 2002, Wanke 2000). They are interpreted as tempestite or turbidite beds arranged in a thickening- and coarsening-upward architecture. At least four horizons of interlaminated limestone/sandstone beds (single layers 2–5 cm thick) contain conspicuous concentrations of articulated and disarticulated bivalve shells.

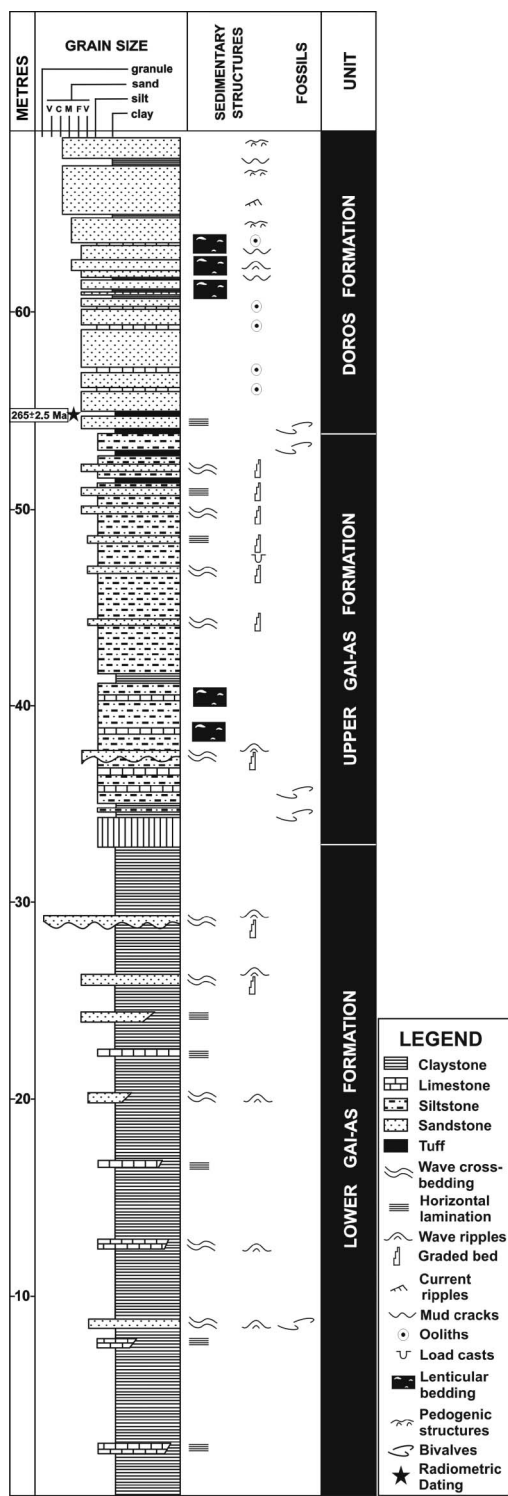
Systematic palaeontology

Nearly 20 small (15 cm long) slabs of fossiliferous sediment from the Gai-As Formation were available for study, originally collected in Namibia by one of us (Frank Holzfoerster). The bivalves occur in mudstone and very fine sandstone. The samples are housed in the scientific collection of the Zoology Department of the São Paulo State University, Botucatu campus, under the code DZP. The material comprises 28 shells, some of which were mechanically extracted, following standard palaeontological techniques described by Feldmann *et al.* (1989). However, many shells were kept in the original matrix for taphonomic studies.

The suprageneric systematics for the anomalodesmatans and crassatellaceans follows Morris *et al.* (1991). The morphological terminology and systematic classification of megadesmids is based on Mendes (1952), Runnegar & Newell (1971), Runnegar (1974) and Simões *et al.* (1997). The mode of life of Gai-As bivalves has been interpreted from shell morphology, dimensions and muscle scars (where preserved) following Stanley (1970).

Fig. 2. Sedimentary succession of the Huab area, northwest Namibia (modified from Stollhofen *et al.* 2000).

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Subclass HETEROCONCHIA Hertwig, 1895
Superorder HETERODONTA Neumayr, 1883
Order VENEROIDA Adams & Adams, 1856
Superfamily CRASSATELLOIDEA Férusac, 1822
Family Uncertain

Terraia Cox, 1934

Type species. Terraia altissima (Holdhaus, 1918); Late Permian, Brazil.

Terraia sp. cf. **T. altissima** (Holdhaus, 1918) (Fig. 4A–E)

Material examined. Four single silicified shells (DZP-18706, 18707, 18708, 18711) and one internal mould (DZP-18710).

Locality and unit. Huab region, Namibia, lower Gai-As Formation, Huab Sedimentary Basin.

Age. Permian, Wordian.

Description. Shell small, equivalved, inequilateral, elongate (Table 1). Two well-defined

Specimen	Valve	Length	Height	Elongation
		(mm)	(mm)	Index
DZP-18700	Left	–	4.23	–
DZP-18706	Left	11.07	6.79	1.63
DZP-18707	Left	7.86	4.48	1.75
DZP-18710	Right	–	13.04	–
DZP-18711	Left	14.63	9.69	1.50

Table 1. Dimensions of specimens of *Terraia* sp. cf. *T. altissima*

Fig. 3. Composite stratigraphic section of the Gai-As and Doros formations, measured at the Klien Gai-As and north of Doros type localities (see Fig. 1), showing the stratigraphic position of the bivalve shell beds studied (modified from Stollhofen *et al.* 2000).

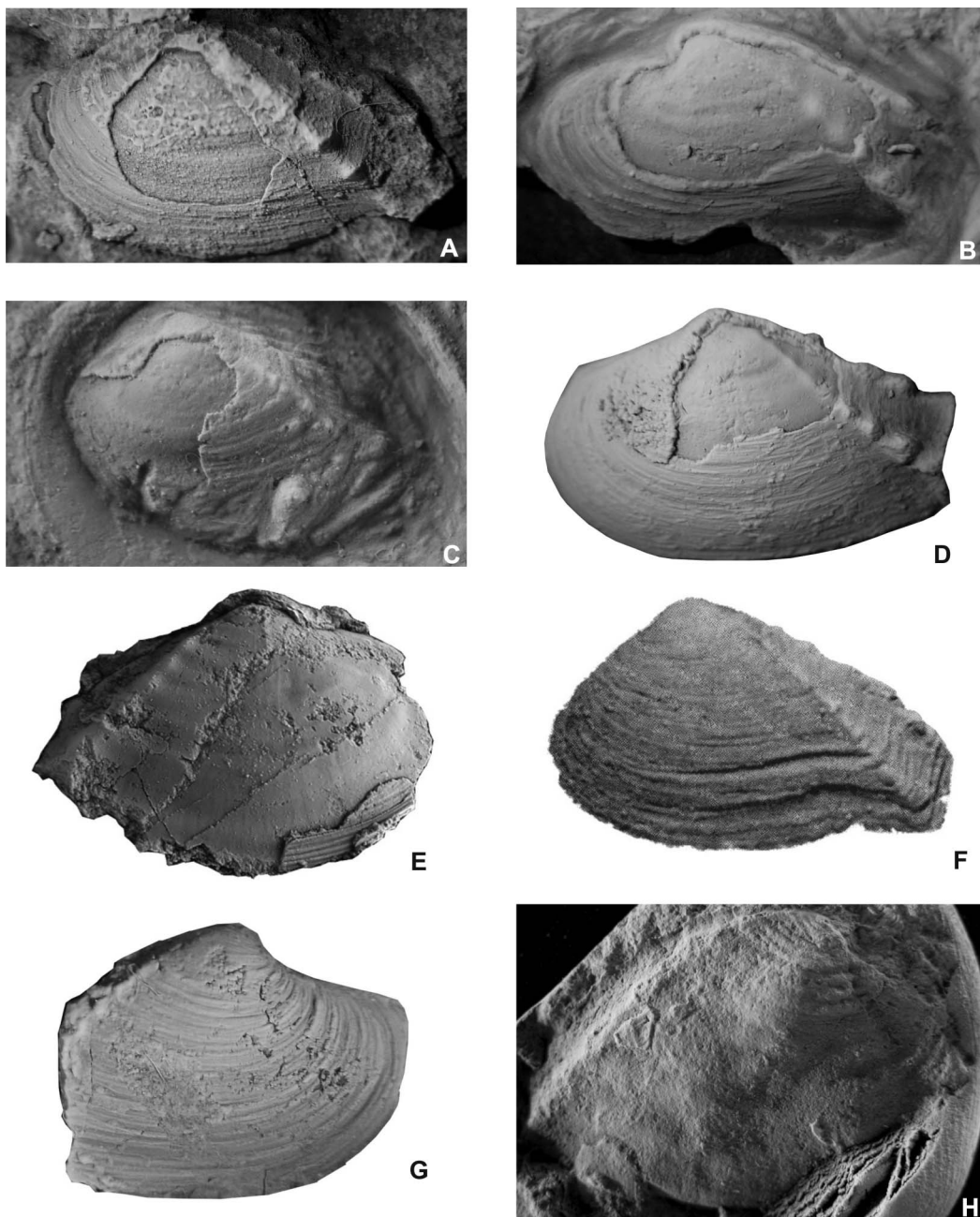


Fig. 4. A–E, *Terraia* sp. cf. *T. altissima* (Holdhaus, 1918), Gai-As Formation, Huab area, Permian. A, External view of silicified left valve, DZP-18706, $\times 5.1$; B, External view of silicified left valve, DZP-18707, $\times 7.9$; C, External view of silicified left valve, DZP-18700, $\times 7.0$; D, External view of silicified left valve, DZP-18711, $\times 3.8$; E, Internal mould with silicified shell remains, right valve view, DZP-18710, $\times 3.2$; F, *Terraia altissima*, Passa Dois Group, Paraná Basin, external view of a silicified left valve, FAC Pal.1868 (figure from Runnegar & Newell 1971), $\times 2.8$; G–H, *Terraia* sp. cf. *T. curvata* (Reed, 1929), Gai-As Formation, Huab area, Permian. G, External view of incomplete silicified right valve, DZP-18712, $\times 9.3$; H, Plasticine cast of external mould of right valve, DZP-18709, $\times 3.2$.

posterior umbonal carinae extending from umbonal region to the postero-dorsal and postero-ventral angles, each ridge bearing 6–7 visible protuberances (knobs; Fig. 4A–D), which are visible in the internal moulds (Fig. 4B, E). The ventral carina is always stronger; the dorsal carina borders the escutcheon. Umbones low, extending beyond the dorsal margin, with slightly prosogyrous beaks. Anterior margin strongly rounded (Fig. 4B); ventral margin broadly arcuate (Fig. 4D); posterior margin angular where intercepted by the two posterior carinae, and straight between (Fig. 4B). External ornament of co-marginal spaced growth lines. Ligament, muscle scars and hinge features unknown.

Remarks. The shell shape and external ornament of the Gai-As specimens are very similar to *Terraia altissima* (Fig. 4F), which is common in bivalve assemblages from the basal part of Rio do Rasto Formation, Paraná Basin, Brazil. The six to seven protuberances (knobs) on the posterior-umbonal carinae are similar to those found in specimens of *T. altissima* from the Paraná Basin (Runnegar & Newell 1971, p. 49, fig. 21, Rohn 1994, p. 361, fig. 169-1), but the Namibian specimens lack the slight flexure of the ventral margin anterior to the posterior-umbonal carina (see Fig. 4F). The hinge is not visible in the Huab material, making a more accurate comparison with specimens figured by Runnegar & Newell (1971) difficult. Consequently, the Namibian specimens are identified as *Terraia* sp. cf. *T. altissima* (Holdhaus 1918).

Terraia* sp. cf. *T. curvata (Reed, 1929) (Fig. 4G–H)

Material examined. One silicified shell (DZP-18712) and one external mould (DZP-18709).

Locality and unit. Huab region, Namibia, lower and upper Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small, subtriangular (Table 2), anterior margin broadly rounded and slightly angular where it intercepts dorsal margin; dorsal margin posterior to umbo, slightly arched, descending steeply to small obliquely truncated respiratory margin. External surface of shell with two arched, posterior umbonal carinae; the second carina being close to dorsal margin. Posterior margin appears truncated between the carinae. Umbones low, subcentral, with slightly prosogyrous beaks. External ornament of co-marginal spaced growth lines. Hinge and muscle scars not preserved.

Remarks. The Gai-As Formation specimens are very similar to *Terraia curvata* described from Brazil by Reed (1929, pl. I, figs 6, 7). The muscle scars and hinge are not preserved in the Namibian specimens, making a more accurate comparison difficult. *Terraia curvata* occurs with *Terraia altissima* in the Serrinha beds of the Rio do Rasto Formation, Paraná Basin. These forms are morphologically similar, and Mendes (1952) tentatively suggested that *Terraia curvata* might be a junior synonym of *T. altissima* (for discussion, see Beurlen 1953, 1954). Beurlen (1954, 1957), however, regarded the general shell profile and hinge structure of both species as distinct. The Namibian specimens of *Terraia* sp. cf. *T. curvata* have

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18709	Right	19.43	–	–
DZP-18712	Right	–	4.13	–

Table 2. Dimensions of specimens of *Terraia* sp. cf. *T. curvata*.

a more equilateral shell that bears two well-defined arched carinae. The shell of *Terraia altissima* on the other hand, is more posteriorly elongated and has straighter posterior carinae, which bear well-defined projections. As specimens of *Terraia curvata* from the Paraná Basin (Serrinha Member), show well-preserved anterior muscle scars and hinge features (see Reed 1929), which are unknown in the Gai-As bivalves, we have identified the Namibian specimens as *Terraia* sp. cf. *T. curvata*.

Superorder ANOMALODESMATA Dall, 1889

Order PHOLADOMYOIDA Newell, 1965

Superfamily PHOLADOMYOIDEA
(King, 1844) Gray, 1847

Family MEGADESMIDAE Vokes, 1967

Huabiella gen. nov.

Type-species. *Huabiella compressa* gen. et sp. nov.

Diagnosis. Shell small, compressed, very elongate and posteriorly expanded. Anterior margin of shell with poorly defined expansion; umbonal carina well marked, extending diagonally from beak to posterior-ventral margin.

Etymology. After the Huab area in northern Namibia.

Remarks. *Huabiella* can be distinguished from other Permian bivalves by a combination of external and internal characters. A well-defined rostrum is present in *Leinzia* Mendes, but absent in *Huabiella*. We do not consider the similar pattern of ornamentation of *Huabiella* (from Namibia) and *Leinzia* (from the Paraná Basin) to be a strong argument for con-specificity. Hammer (2000) has shown that the growth processes responsible for the concentric commarginal ribs in bivalves, result from an

oscillation in the regulatory system involving purely mechanical factors. This evaluation seems valid since among Permian megadesmids of the Paraná Basin, commarginal ribs are found in genera as distinct as *Cowperesia* Mendes, 1952 and *Leinzia*. The main difference between *Huabiella* and *Leinzia*, besides the shell shape, is the absence of a well-defined rostrum in the anterior margin of the Namibian genus. The anterior margin of *Huabiella* shells has a small projection, very similar to that found in *Holdhausiella* Mendes, 1952 and *Favalia* Mendes, 1962 from the Corumbataí and Teresina formations (see Runnegar & Newell 1971, p. 41, fig. 16 and p. 43, fig. 17, respectively). However, in *Holdhausiella* and *Favalia* the hinge is edentulous and the posterior margin of the shell is straight.

Huabiella compressa sp. nov. (Fig. 5A–K)

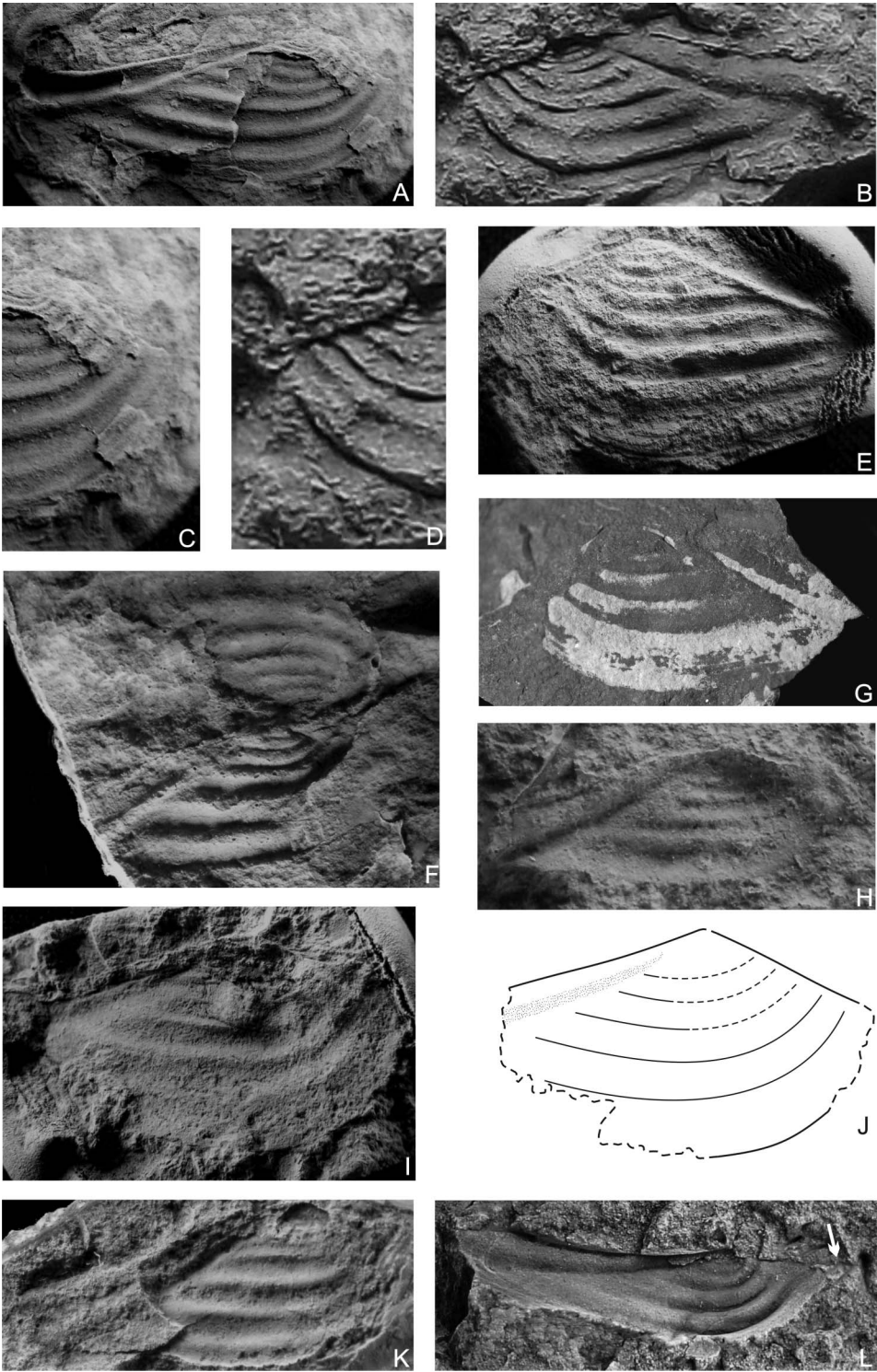
Type material. Six internal moulds (DZP-18687, 18690, 18691, 18692, 18693) and two external moulds (DZP-18688, 18689). Holotype, DZP-18686. Paratypes, DZP-18687, 18688, 18689, 18690, 18691, 18692, 18693.

Diagnosis. *Huabiella* shell ornamented by regularly spaced angular commarginal rugae.

Locality and unit. Huab region, Namibia, upper Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small, very elongate, posteriorly expanded, equivalved, inequilateral, compressed to very compressed (Table 3). Dorsal and ventral margins subparallel; umbones low, beaks slightly prosogyrous. Anterior dorsal margin only slightly pronounced anteriorly; posterior margin straight or nearly so. Umbonal carina well marked, narrow and sharply rounded, extending diagonally from beak to posterior-ventral angle; delimiting a smooth, concave,



Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18686	Left	31.28	12.10	2.58
DZP-18687	Left	13.58	4.44	3.05
DZP-18688	Left	—	14.42	—
DZP-18689	—	—	—	—
DZP-18690	Left	—	14.67	—
DZP-18691	Left	16.27	—	—
DZP-18692	Left	15.71	6.78	2.32
DZP-18693	Left	—	10.23	—

Table 3. Dimensions of specimens of *Huabiella compressa* gen. et sp. nov.

elongate, triangular area below posterior dorsal margin. External ornamentation of regularly spaced rounded co-marginal rugae, separated by angular grooves. Rugae terminate abruptly against the posterior-umbonal carina without any projections. Ligament external, parivincular. Hinge and muscle scars unknown.

Discussion. *Huabiella compressa* superficially resembles *Leinzia similis* (Fig. 5L) from the middle to upper part of the Serrinha Member (Rio do Rasto Formation), and understandably, some authors (Stollhofen *et al.* 2000, Wanke 2000) have preliminarily assigned the Gai-As shells to this species. However, despite the relatively poor preservation of the examined specimens, the small anterior expansion in *H. compressa* is in no way comparable to the anterior rostrum of *Anhembia froesi* Mendes and *L. similis*. The anterior expansion observed in *Huabiella compressa* is more similar to that recorded in other Permian megadesmids, such as

Holdhausiella elongata (Holdhaus, 1918) and *Favalia arcuata* Mendes, 1962. In addition, *Huabiella compressa* shells lack protuberances at the intersection of the umbonal carina with the co-marginal rugae, or spinose projections along the posterior dorsal margin as in *L. similis* (see Runnegar & Newell 1971, p. 53). It should be noted that *Huabiella compressa* is very similar to specimens figured by Beurlen (1957, pl. 4, figs 23, 34–36) from the Serrinha Member of the Rio do Rasto Formation. These specimens were designated *Leinzia curta* Beurlen, 1957, but were never formally described and no type material was selected. The illustrations are hand drawings and not photos. *Leinzia curta* should, therefore, be regarded as a *nomen nudem*. Rohn (1994, fig. 167-6) also recorded bivalves from the Serrinha Member that were similar to Beurlen’s drawings, but these were never fully described.

Cowperesia Mendes, 1952

Discussion. Runnegar & Newell (1971) suggested that *Cowperesia* Mendes, 1952 is a junior subjective synonym of *Pyramus* Dana, 1847. The following generic characters are listed for *Pyramus* by Runnegar & Newell (1971, p. 35): ‘shell oval, equivalved, with low umbones, inwardly directed beaks, and rounded to angular posterior umbonal slopes; lunule and escutcheon narrow, often poorly defined; valve margins closed anteriorly and ventrally, but usually with small siphonal gape; shell smooth or with ornament of coarse concentric ribs; ligament opisthodetic, parivincular, external,

Fig. 5. A–H, J, *Huabiella compressa* gen. et sp. nov., Gai-As Formation, Huab area, Permian. A, Plasticine cast of internal mould of left valve, holotype DZP-18686, × 1.8; B, Left valve view of internal mould, paratype DZP-18687, × 4.3; C, Detail of anterior region, paratype DZP-18686, × 2.7; D, Detail of anterior region, paratype DZP-18687, × 6.9; E, Plasticine cast of external mould of left valve, paratype DZP-18688, × 2.3; F, Latex cast of external mould of splayed valves, paratype DZP-18689, × 3.7; G, Internal mould of left valve, paratype DZP-18691, × 3.2; H, Latex cast of internal mould of left valve, paratype, DZP-18692, × 3.2; I, Plasticine cast of internal mould of left valve, paratype DZP-18690, × 2.3; J, Drawing representation based in the same specimen, × 2.3; K, Latex cast of internal mould of left valve, paratype DZP-18693, × 2.4; L, *Leinzia similis*, Serrinha Member, Rio do Rasto Formation, Paraná Basin, external mould of left valve, arrow indicates the characteristic anterior expansion of this species, DGP 7-85, × 2.7.

attached to short dorsally reflected nymphs; hinge virtually edentulous or with variably developed tooth beneath beak of right valve and socket in left; valve margin in front of socket may be thickened to fit beneath corresponding edge of right valve; true lateral teeth absent; adductor muscle scars subequal; pallial line relatively wide, continuous, not extended above adductor scars; pallial sinus small or absent; pedal protractor and anterior and posterior retractor scars present in all species; elevator muscle scar present in most species at apex of umbonal cavity'.

Based on these characters, we had difficulty accepting the suggested synonymy of *Cowperesia* and *Pyramus* for the following reasons: 1, adult shells of *Cowperesia* are very small, compressed to very compressed, whereas shells of *Pyramus* are normally large and inflated; 2, the elevator scar is absent in all specimens of *Cowperesia*, as are the adductor accessory muscle scars 'a', 'b', and 'ava' figured for *Pyramus* (see Runnegar 1966, 1967); 3, the lunule and escutcheon are absent in *Cowperesia*, but are usually present in *Pyramus*; 4, the ornamentation of *Cowperesia* shells is typically of fine co-marginal rugae, which differs from the coarser concentric ribs of *Pyramus*; 5, the pallial sinus of *Cowperesia* is deeper than that present in most species of *Pyramus*; 6, the hinge of *Cowperesia* always bears a blunt tooth in the right valve, whereas *Pyramus* is normally edentulous.

Cowperesia emerita (Reed, 1929) (Fig. 6A–H, J–K)

Material. Six specimens with silicified shell remains (DZP-18696, 18697, 18699, 18700, 18701, 18702) and six internal moulds (DZP-18694, 18695, 18698, 18703, 18704, 18705).

Locality and unit. Huab region, Namibia, lower Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small (Table 4), subtriangular, equivalved, equilateral, equant to moderately elongate (elongation index: 1.17–1.24), very compressed (inflation = obesity index of 2.26). Two well-defined, slightly curved posterior umbonal carinae present, one extending from the umbonal region to the postero-ventral angle and the other close to the posterior dorsal margin (Fig. 6A, C). Very weak projections evident where co-marginal growth lines cross the umbonal carina. Projections not visible on internal moulds (Fig. 6D). External ornament of fine, co-marginal growth lines, superimposed by widely spaced, broad co-marginal rugae that are apparent on internal moulds (Fig. 6B, D). Umbones low with pointed prosogyrous beaks. Well-marked muscle insertion scars visible on the umbonal region of internal moulds (Fig. 6J, K), with radiating striated muscle tracks below (Fig. 6D, E). Right valve with well-developed triangular tooth below beak (Fig. 6G, L). Left valve has large triangular socket below beak, and a well-defined tooth to anterior (Fig. 6H, I). Lateral teeth absent.

Remarks. *Cowperesia anceps* (Reed, 1935), *C. emerita* (Reed, 1935), and *C. camposi* Mendes, 1952 are the only known species of *Cowperesia*. However, *C. camposi* may be conspecific with *C. anceps*, as the type specimens are similar to Reed's original illustrations and only small differences in ornamentation separate the two species (Runnegar & Newell 1971). As far as we know, *C. anceps* and *C. emerita* do not occur together at the same stratigraphic level in the Permian of the Paraná Basin. The Namibian material closely resembles *C. emerita* in shell shape, ornamentation and hinge features (see Fig. 6J, L for comparison). This is further supported by

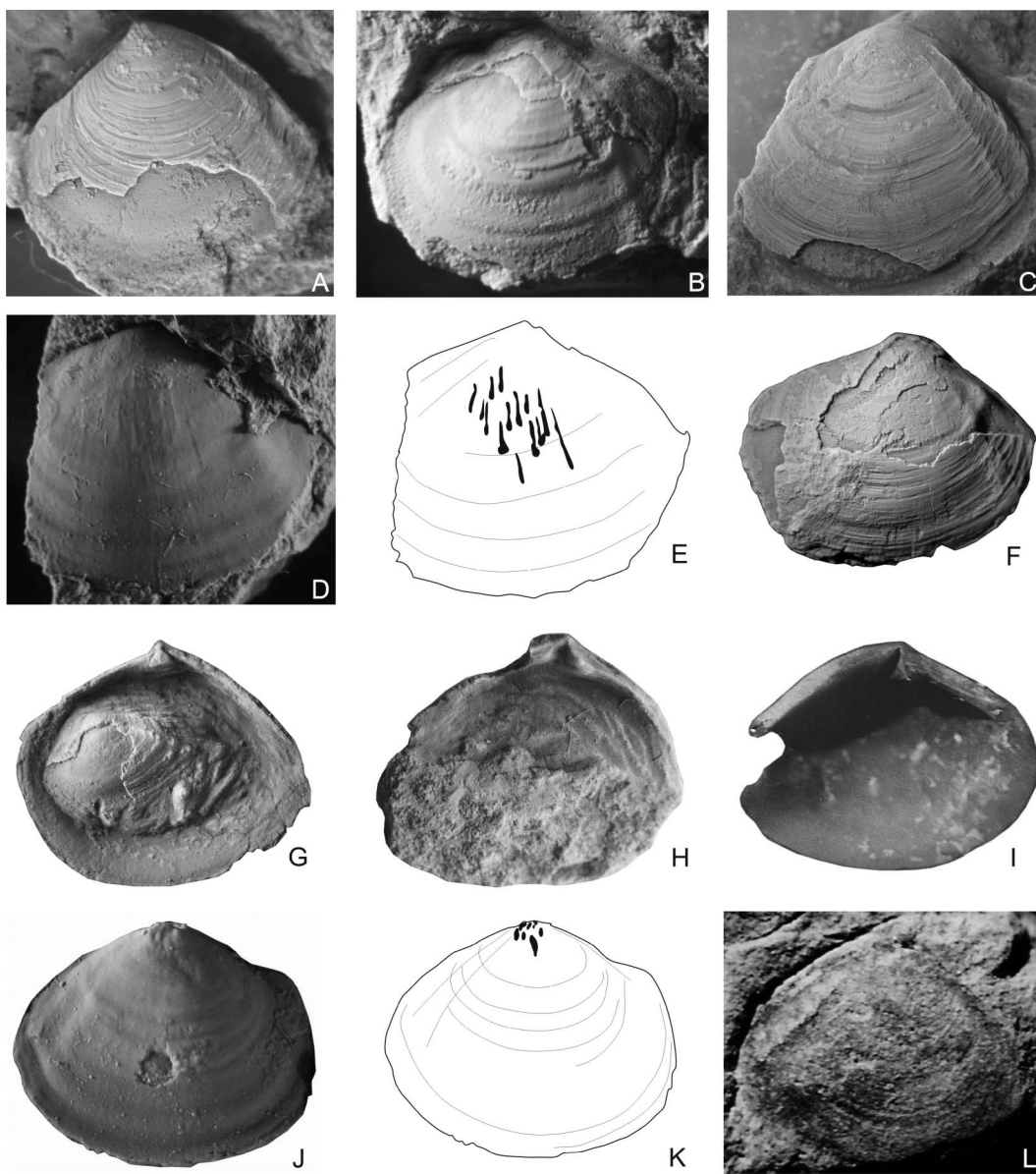


Fig. 6. A–H, J–K, *Cowperesia emerita* (Reed, 1929), Gai-As Formation, Huab area, Permian. I, L, *Cowperesia emerita* (Reed, 1929), Rio do Rasto Formation, Paraná Basin, Permian, specimens illustrated by Rohn (1994). A, External view of silicified left valve, DZP-18697, $\times 5.0$; B, Incomplete internal mould with silicified shell remains, left valve, DZP-18699, $\times 5.4$; C, External view of silicified left valve, DZP-18696, $\times 6.0$; D, Internal mould of right valve, DZP-18703, $\times 5.6$; E, Drawing representation of muscular pits, based in the same specimen, $\times 5.6$; F, Incomplete internal mould with silicified shell remains, left valve, DZP-18702, $\times 4.3$; G, Internal view of silicified right valve showing hinge features, DZP-18700, $\times 4.3$; H, Internal view of silicified left valve showing hinge features, DZP-18701, $\times 6.5$; I, Internal view of silicified left valve, showing the hinge features, $\times 3.2$; J, Internal mould of right valve, DZP-18698, $\times 10.0$; K, Drawing representation of muscular pits, based on the same specimen, $\times 10.0$; L, Internal mould of a right valve, $\times 3.3$.

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18696	Left	—	7.55	—
DZP-18697	Left	7.89	7.56	1.04
DZP-18698	Right	4.09	3.52	1.16
DZP-18699	Left	6.86	5.92	1.15
DZP-18700	Right	9.22	8.03	1.14
DZP-18701	Left	—	—	—
DZP-18702	Left	9.36	7.95	1.17
DZP-18703	Right	—	6.83	—

Table 4. Dimensions of specimens of *Cowperesia emerita*.

specimens from the upper part of the Teresina Formation in the Tiaraju region (Klein 1997), Rio Grande do Sul State, and from the Serrinha Member of the Rio do Rasto Formation, illustrated by Rohn (1994, p. 358, fig. 166-1a, b; p. 360, fig. 168-7-9).

Palaeoautoecology

The bivalve fauna of the Gai-As Formation is of low diversity, particularly when compared with coeval faunas of the mid-Permian deposits of the Paraná Basin (see Runnegar & Newell 1971, Simões *et al.* 1998). However, the Huab fauna is dominated by the same bivalve groups that are found in the Passa Dois Group of the Paraná Basin, namely megadesmids and veneroids. In this context, the abundance of megadesmid genera is of particular interest because they are also common in Permian marine faunas of Australia and New Zealand (see Runnegar 1967, Runnegar & Newell 1971, Simões *et al.* 1997). Megadesmids were infaunal, suspension-feeding bivalves that appear to have had robust shells with a stout opisthodontic ligament, edentulous hinge or have a blunt tooth in the right or both valves (Runnegar 1967, Runnegar & Newell 1971, Simões *et al.* 1997). They were active infaunal bivalves (shallow, intermediate and deep

burrowers) that flourished in shallow waters with soft substrates (Runnegar & Newell 1971, Runnegar 1974, Simões *et al.* 1997).

Cowperesia emerita and *Huabiella compressa* are the typical megadesmids of the lower and upper Gai-As Formation, respectively. *Cowperesia emerita* has thin, very compressed and non-elongated shells (elongation index 1.04–1.17; see Stanley 1970). The occurrence of closed-articulated shells of *C. emerita* in very fine sediments of the lower Gai-As Formation (Fig. 7G) indicates that this species may have lived in a soupy, fine-grained substrate. As commented by Stanley (1970), owing to the maintenance of negative buoyancy, a good strategy in such conditions of soft, muddy bottoms is to keep the shell thin and compressed. Species of *Cowperesia* from the Paraná Basin bear deeply impressed anterior, protractor muscle scars in addition to a small, but very well defined pallial sinus. These features may indicate an active, intermediate, burrowing lifestyle (see Runnegar 1974). Similar conclusions may be applicable to *Huabiella compressa* shells, of which the splayed valves are also found in fine-grained sediments. As the species name indicates, their shells are compressed, thin, non-gaped, and very elongate (elongation index 2.32–3.05, see Stanley 1970). Again this may be a strategy for bouyancy in a fine-grained substrate of low density and viscosity (Stanley 1970), with a shallow to intermediate burrowing strategy.

Terraia sp. cf. *T. altissima* is elongate to very elongate (elongation index 1.50–1.63; see Stanley 1970). Both species (*Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*) have relatively robust shells. Similar to other thick-shelled Veneroida, these may have been active burrowers in shallow water substrates (Stanley 1970, p. 68, Runnegar & Newell 1971). The shells of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata* are always disarticulated and,

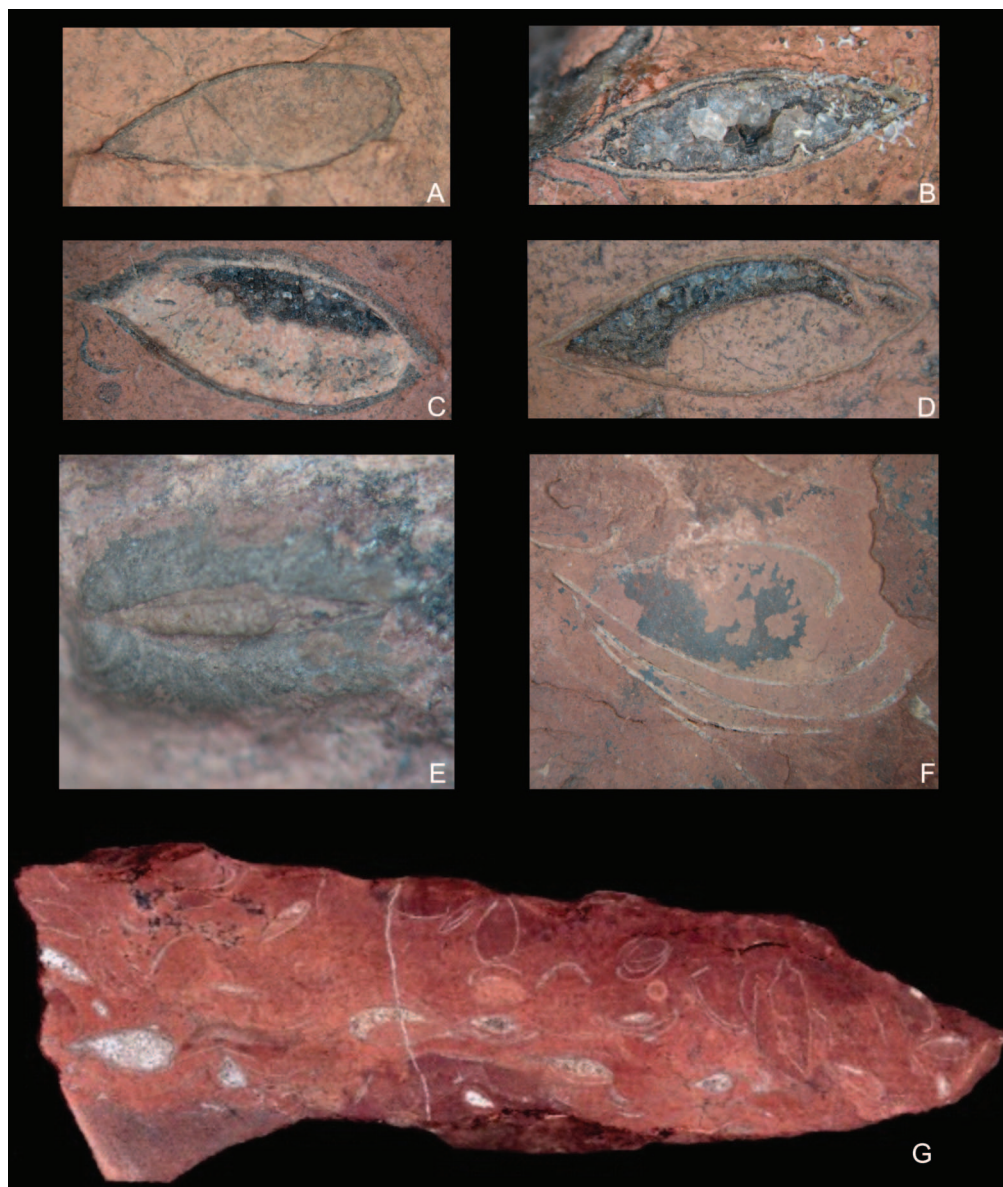


Fig. 7. Taphonomic features of bivalve shells of the lower Gai-As Formation. **A**, Shell filled by muddy sediments (matrix), $\times 6.0$; **B**, Articulated shells showing infillings that do not match with the surrounding matrix, $\times 6.0$; **C–D**, Bivalve shells with distinct geopetal infills, $\times 7.0$; **E**, Closed articulated valve with the external ligament preserved, $\times 20.0$; **F**, Nested concave-up shells, $\times 12.0$; **G**, Section showing articulated and disarticulated valves, chaotically oriented in the matrix, $\times 1.05$. Note the predominance of closed articulated bivalve shells in the lower portion of the sample.

owing to their different lifestyle, they may not have lived in direct association with the other forms (*C. emerita* and *H. compressa*) during life.

Taphonomy

The taphonomic analysis presented herein is probably biased, as the samples were primarily collected for taxonomic purposes

and not according to standard taphonomic procedures (e.g. Kidwell *et al.* 1986, Kidwell 1991, Kidwell & Holland 1991, Fürsich & Oschmann 1993, Simões & Kowalewski 1998). Fortunately, some slabs were large enough to be vertically sectioned for descriptions and allowed observation of some taphonomic characters (e.g. degree of packing and shell orientation). Since few samples were available, our analysis is only qualitative. The description follows the terminology suggested by Kidwell (1991) and Kidwell & Holland (1991).

The lower Gai-As Formation comprises a 35 m thick sequence of reddish to violet, mostly laminated mudrocks containing thin (1–3 cm) tabular interbeds of normally graded, fine- to medium-grained sandstones and a few laminated limestones, 10–50 cm thick (Fig. 3; Holzfoerster 2000, 2002, Wanke, 2000). In this succession, at least two extensive shale horizons incorporate layers, up to 4 cm thick, of accumulated bivalve shells (Wanke 2000). The bivalves are both articulated and disarticulated, and are chaotically distributed within the matrix (Fig. 7G). Closed articulated shells of *Cowperesia emerita* are common, and are associated with disarticulated valves of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*. Some closed articulated shells have fragile structures preserved, such as the ligament (Fig. 7E). The shells are silicified without signs of abrasion, encrustation or bioerosion. Some closed articulated specimens bear geopetal infillings of sediment (matrix) and calcite (Figs 7C, D). In some cases, disarticulated shells, including *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima*, are nested (Figs 6G, 7F).

The upper Gai-As Formation comprises a 10–80 m thick sequence of red violet mudstones with minor tabular sandstone interbeds, laminated or small-scale cross-bedded limestone, and laminated rhyolitic to dacitic fallout tuff (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000). Some inter-

laminated limestone/sandstone beds are characterized by conspicuous concentrations of *Huabiella compressa* shells in a single, 2–5 cm thick layer with sparse specimens of *Terraia* sp. cf. *T. curvata*. *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima* appear to be absent. All shells are represented by moulds (see also Stollhofen *et al.* 2000). The shells are commonly disarticulated and in a concave-down orientation. Rare splayed shells were also found (Holzfoerster 2000, 2002).

In summary, the bivalve assemblages of the lower and upper Gai-As Formation are formed by a mixture of autochthonous to parautochthonous species (*C. emerita* and *H. compressa*, respectively) and allochthonous (transported) shells (*Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*) when present. However, these observations must be viewed with caution owing to the small size of the examined collection.

Palaeoenvironment

Despite the qualifications outlined above, the bivalve shell concentrations of the Gai-As Formation exhibit a range of taphonomic signatures that are useful for palaeoenvironmental interpretations. At least two associations are present, characterized by particular preservational styles and taphonomic histories.

As indicated by Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), the thick succession of mudstones of the basal portion of the Gai-As Formation was deposited predominantly from suspension fallout in a hemi-pelagic setting within a large body of water. However, the calm background conditions that prevailed in this lacustrine environment were frequently disrupted by episodic high-energy events. For example, within the lower Gai-As section the sandstone beds were interpreted as event beds, such as tempestites and turbidites (Holzfoerster 2000, 2002, Stollhofen *et al.*

2000, Wanke, 2000). Indeed, the presence of chaotically disposed, stacked and nested bivalve shells in the matrix would supplement this, and the occurrence of specimens with closed articulated valves (*Cowperesia emerita*), some with preserved ligament (Fig. 7E), are good indicators of abrupt burial associated with high-energy events (see Aigner 1985, Fürsich & Oschmann 1986, 1993, Kidwell *et al.* 1986, Simões *et al.* 1996, Simões & Kowalewski 1998). Both *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima* were shallow burrowers, and the closed articulated shells that are chaotically arranged in the matrix are good indicators of disruption of bivalves that were alive prior to final burial. This disruption may have been caused by turbulent flows in offshore bottoms, as indicated by the presence of nested shells (Figs 6G, 7F) that were subsequently buried by very fine grained sediments from suspended mud. Although closed-articulated, some shells may represent winnowed and reworked re-fossilized material. For example, many articulated shells of *Cowperesia emerita* have geopetal structures (Fig. 7C, D), i.e. infillings clearly divided into sediments and calcite crystals—the calcite precipitated in the hollow upper space of the valves. According to the inclined position of the geopetal structures within the bed, it is easy to conclude that the shells were reworked. The infilling of some closed shells corroborates this interpretation because it is composed of sediment that is different from that of the muddy matrix that encloses the shells (Fig. 7B). Other specimens are completely filled with muddy sediment equivalent to the surrounding matrix (Fig. 7A). According to various authors (Seilacher 1973, Fürsich 1978, Brett & Allison 1998, Klein & Simões 1998, Simões & Torello 2003), these features suggest reworking and repeated burial of shells over long time periods on bottoms that were continuously being

affected by storms or turbidites (see also Wani 2001, p. 622).

Additional evidence for deposition under high-energy conditions with exhumed and disarticulated shells settling from suspension is manifest by the presence of concave-up, nested and disarticulated shells (Kidwell *et al.* 1986, Fürsich & Oschmann 1993, Simões *et al.* 1996, Simões & Kowalewski 1998). Hence, these taphonomic observations corroborate previous interpretations by Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000) based on sedimentological evidence alone.

The shell beds of the lower part of the Gai-As Formation are composite concentrations (*sensu* Kidwell 1991), deposited during high-energy events (storms or turbidity flows) that show disharmonic time-averaging (see Kowalewski, 1996; Simões & Kowalewski 1998). This taphonomic context is equivalent to many Permian shell beds of the Passa Dois Group of the Paraná Basin (see Klein & Simões 1998, Simões *et al.* 1996, Simões & Kowalewski 1998, Simões & Torello 2003, Neves 2009, Neves *et al.* 2010).

One of the main taphonomic features of the shell-rich layers in the upper part of the Gai-As Formation is the presence of articulated and disarticulated valves of *Huabiella compressa* in concave-down attitude to bedding (see also Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000). *Huabiella compressa* was a shallow burrower that may have lived in a soupy, fine-grained bottom, as suggested by their thin, compressed shells with commarginal rugae (see also Ghilardi 1999). The articulated specimens of *Huabiella compressa* are those with the two valves splayed open on the bedding plane. Because bivalve molluscs shells are known to dry out and splay, it is highly unlikely that open shells of *Huabiella compressa* lying at the sediment/water interface could have been transported intact and articulated (see also Allmon 1985, Selover *et al.* 2005). The splayed shells of *Huabiella*

may represent dead molluscs dislodged during high-energy events that became mixed with previously dead molluscs lying on the bottom. *Huabiella compressa* shells were elongate, nearly flat, with a small, opisthodontic, parivincular ligament and no hinge teeth (edentulous). It is arguable that the lack of teeth and the fragile ligament favour disarticulation if the shells are subjected to prolonged exposure on the sea floor. This suggests that, these splayed shells of *Huabiella* are good indicators of rapid (but not abrupt) burial. However, because splayed shells were preferentially preserved in a concave-down position, this may indicate that after settling, these shells experienced brief exposure to bottom currents that overturned both splayed and disarticulated shells into a more hydrodynamically stable position. The preservation of splayed shells in a concave-down position suggests low-energy conditions following the exhumation event but relatively rapid subsequent burial, preventing the complete disarticulation of valves (Cantalamessaa *et al.* 2005).

Biostratigraphy and correlation

The age and vertical and lateral extent of the Namibian Gai-As sediments are well resolved following the studies of Horsthemke (1992), Ledendecker (1992), Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000). Based on the occurrence of the bivalves, Horsthemke (1992) and Ledendecker (1992) correlated the Gai-As Formation with the Serra Alta, Teresina, and lower Rio do Rasto formations of Brazil, and with the Collingham to Waterford Formations of South Africa. However, studies by Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000) have demonstrated that in northern Namibia, coeval Permian beds to the entire post-Whitehill Formation (Ecca Group), Collingham to Waterford formations, in the Main Karoo Basins, of South Africa

and the greater part of the Passa Dois Group (Serra Alta and Teresina formations) of Brazil, are poorly preserved or missing (Stollhofen *et al.* 2000). Based on the probable presence of *Leinzia similis*, Stollhofen *et al.* (2000) suggested correlation of the Gai-As Formation with the informal *Terraia altissima* Biozone (Rohn 1994) of the Rio do Rasto Formation, Paraná Basin, Brazil. However, as revealed here, *Leinzia similis* is not recognized in Namibia, and the presence of *Cowperesia emerita*, indicates possible correlation with intervals of the lower portion (Serrinha Member) of the Rio do Rasto Formation. The occurrence of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata* in the Namibian fauna may constitute additional evidence for the bio-correlation above (but see comments in the section below). In addition, it is pertinent to note that *Huabiella compressa* is very similar to *Leinzia curta* (*nomen nudum*) recorded by Beurlen (1957), and to some non-described specimens illustrated by Rohn (1994, fig. 167-6), from the basal part of the Rio do Rasto Formation (Serrinha Member).

Radiometric dating of zircon grains from tuff beds within the top part of the Gai-As succession provide U/Pb ages of 265 ± 2.5 Ma (Holzfoerster 2000, 2002, Wanke 2000). This age, according to the International Stratigraphic Chart of 2009 (Walker & Geissman 2009), corresponds to the Wordian/Capitanian boundary in the Guadalupian (Middle Permian). More significantly, recent U/Pb ages obtained from zircon grains from ash-fall beds in coeval Permian rocks of the Paraná Basin indicate ages of 267 ± 17 Ma for the Teresina Formation, and 266.3 ± 4.6 Ma for the Serrinha Member of the Rio do Rasto Formation (Rocha-Campos *et al.* 2009). Consequently, the tuff layers are of probable equivalent age (Wordian) in both countries, reinforcing correlations made by previous authors (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000).

Summary

The discovery of typical South America Permian 'endemic' bivalves in Namibia reinforces the idea that the fauna of the Passa Dois Group (Mendes 1952, Runnegar & Newell 1971, Simões *et al.* 1998) was not confined to the South American portion of the Permian sea that covered the southern region of Gondwana during Wordian times. The lacustrine environment represented by the Namibian deposits was probably an extension of the huge epicontinental sea of the Paraná Basin. The best record of this fauna in terms of preservation, abundance and stratigraphic completeness is found in Brazil.

The Gai-As bivalve occurrences are potentially significant for stratigraphic correlation and age determination. The species identified as *Terraia* sp. cf. *T. altissima*, and *Terraia* sp. cf. *T. curvata* are not necessarily different to *T. altissima* and *T. curvata* in South America, but the Namibian forms lack the preservational details for definitive attribution to the Brazilian taxa. Therefore, future research in Namibia must focus on the search for better preserved specimens that may clarify the specific relationships between these species of *Terraia*.

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