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Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria

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The mid-Silurian Major Mitchell Sandstone of the Grampians Group outcrops at Mt Bepcha, western Victoria, represent a prograding fluviodeltaic sequence comprising four lithofacies and five ichnofacies. The stratigraphically lowest Interbedded Sandstone/Siltstone Facies is characterised by thin sandstone and siltstone beds with soft-sediment deformation and scours with gravelly lag deposits. This lithofacies contains *Thalassinoides*, *Palaeophycus*, *Rhizocorallium* and intrastratal burrows, together indicative of the Cruziana Ichnofacies, and is interpreted as a shallow-marine depositional environment on a low-energy delta front with minor tidal influences. The overlying Massive Sandstone Facies lacks silt, and consists of predominantly massive and some plane-laminated sandstone, abundant *Skolithos linearis*, rare *Palaeophycus* and a single small *Cruziana problematica*; the trace-fossil assemblage is assigned to the Skolithos Ichnofacies. This facies is believed to have been deposited in a marine high-energy shoreface environment with continuously shifting sands, affected by periodic flooding events from the mouth of a nearby river. Above this is the Trough Cross-bedded Facies, which contains trough cross-bedding with gravelly lag deposits, a northwest palaeocurrent direction and large *Taenidium barretti* burrows (Burrowed Ichnofacies). This facies also contains abundant plane-laminated sandstone with a northeast–southwest palaeocurrent direction and ichnofossils of *Scoyenia* and *Daedalus*, representing the Scoyenia Ichnofacies. The Trough Cross-bedded Facies is interpreted to have been deposited in shallow low-sinuosity channels by overbank-flooding events, most likely on a delta plain. The uppermost facies, the Plane-laminated Facies, contains thin beds of current-lineated, plane-laminated graded coarse to fine sandstone that preserve arthropod trackways (Arthropod Ichnofacies). This facies was deposited on a periodically sheet-flooded, subaerially exposed delta plain.

KEY WORDS: fluviodeltaic, Grampians Group, ichnology, sedimentology, Silurian, Victoria.

INTRODUCTION

The Grampians Group is a sparsely fossiliferous Early Palaeozoic succession of dominantly quartzose sandstone, and outcrops prominently as the Grampians and Black Ranges in western Victoria (Figure 1). Its age, sedimentology and ichnology have all been the subject of controversy and reinterpretation.

The Grampians Group was originally believed to be Late Devonian to Early Carboniferous in age (Spencer-Jones 1965), but subsequent studies have shown that the strata are unconformably overlain by Early Devonian volcanics (Simpson & Woodfull 1994) and intruded by Early Devonian granites (Gleadow & Lovering 1978; Gray 1990). Siltstones in the upper to middle part of the succession (near the top of the Silverband Formation) contain rare fish fossils originally dated as Late Silurian to Devonian (Turner 1986); this age has since been revised to no earlier than Middle Ludlovian (Burrow & Turner 2000). Cayley and Taylor (1997) suggested that sedimentation of the Grampians Group could have begun in the Late Ordovician.

The sedimentology of the Grampians Group has been interpreted in substantially different ways. Jones (1993) argued that the Grampians Group represented mostly low-relief braidplains deposited by sheet flooding of ephemeral rivers, whereas George (1994) attributed sedimentation predominantly to tidal processes. Other authors (Spencer-Jones 1965; Jenkin 1989; Cayley & Taylor 1997) favoured an alternation of fluvial and shallow-marine environments.

At Glenisla Homestead, in the western Grampians region near Mt Bepcha (Figure 1), a number of trackways are preserved in Grampians Group sandstone slabs paving a courtyard. One of these trackways was interpreted by Warren *et al.* (1986) as the oldest evidence of tetrapod footprints. However, Clack (1997) believed that this trackway was probably formed by an arthropod. Nevertheless, the Glenisla trackways are still of significance, as they provide additional evidence of the Siluro-Devonian Gondwanan arthropodan terrestrial invasion of the land, also shown by similar Australian trackways described from the ?Late Ordovician to Early Silurian Tumblagooda Sandstone, Western Australia (Trewin & McNamara 1995; McNamara & Trewin 2002).

The aims of this paper are to describe the sedimentology and ichnology of the Grampians Group strata at

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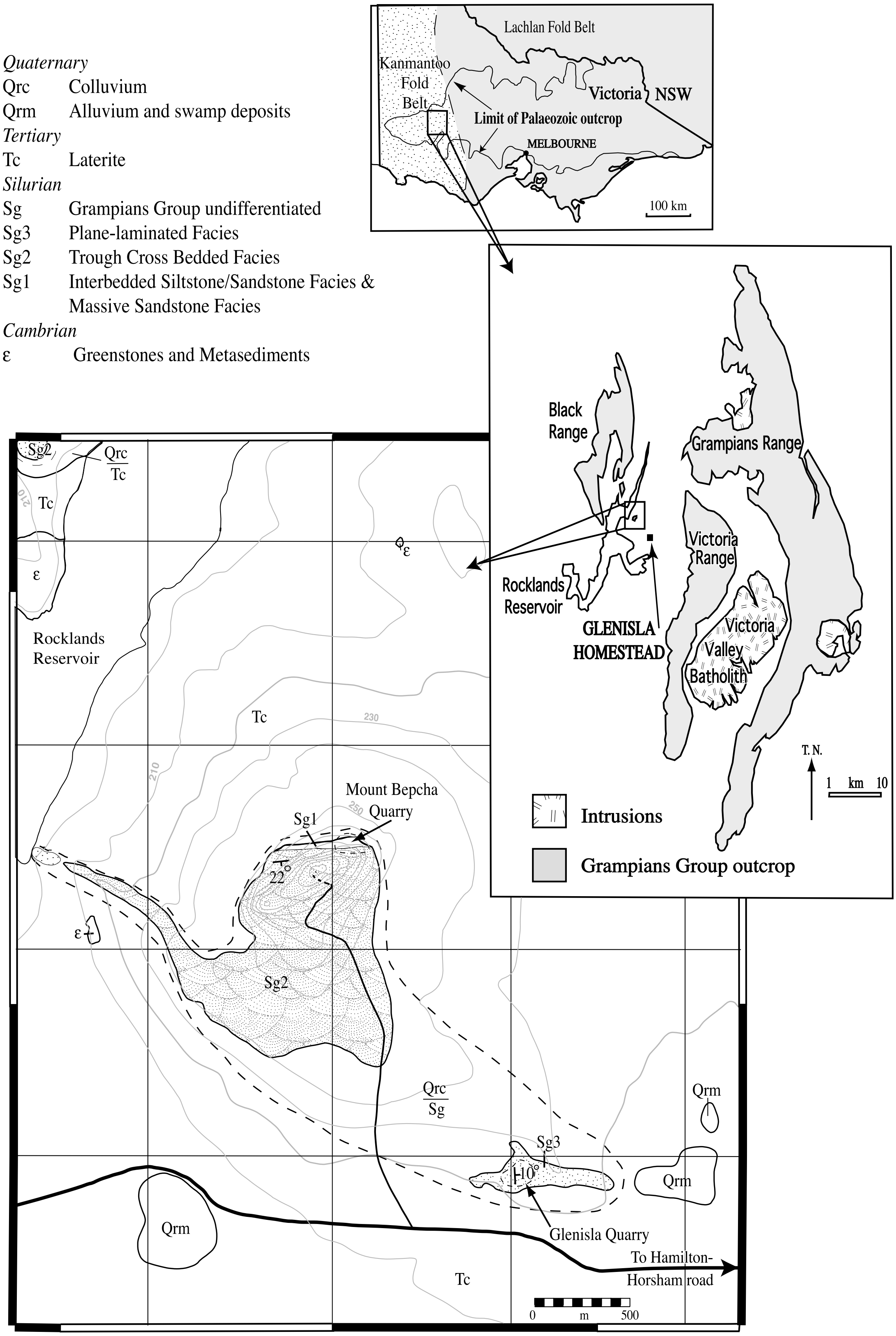


Figure 1 Location and geological map of Mt Bepcha. Note the location of Glenisla Homestead.

Mt Bepcha, including the beds that yielded the arthropod trackways. By determining a detailed depositional environment for this part of the sequence, the study will also decide whether the arthropod trackways were formed terrestrially or subaqueously, and therefore whether they help to illustrate the early invasion of the land by arthropods. The trackways themselves will be described in detail elsewhere.

GEOLOGICAL SETTING

The Grampians Group is composed of three units; in stratigraphic order these are the Red Man Bluff Subgroup, Silverband Formation and Mt Difficult Subgroup (Spencer-Jones 1965; Cayley & Taylor 1997). The uppermost formation of the Red Man Bluff Subgroup is the 450 m-thick Major Mitchell Sandstone that directly underlies the fossiliferous Late Silurian Silverband Formation, and so is probably mid-Silurian.

Mt Bepcha in western Victoria (Figure 1) is a low-angle cuesta dipping to the southeast, and attains a height of 360 m a.s.l. The steep northwest-facing escarpment gives excellent exposures of over 100 m of gently dipping sandstones assigned to the Major Mitchell Sandstone by Cayley and Taylor (1997). The contact with underlying Cambrian low-grade metamorphics does not outcrop, but the base of the Major Mitchell Sandstone in this area is the subhorizontal Marathon Fault, along which the entire Grampians sequence has been thrust (Cayley & Taylor 1997, 1999). In Glenisla Quarry (1.4 km to the southeast of Mt Bepcha) (Figure 1), a separate 10 m-thick sandstone unit is exposed. Although 1 km without outcrop separates Glenisla Quarry and Mt Bepcha, the consistent low-angle dip at the two localities, and lack of evidence of faulting between them, indicates that the sandstone at the quarry is stratigraphically some 170 m above the uppermost bed exposed at Mt Bepcha.

Glenisla Homestead, 4.8 km southeast of Mt Bepcha (Figure 1), is constructed of sandstone blocks that came from both Mt Bepcha Quarry, located at the base of the peak, and Glenisla Quarry. The lithologies from both quarries are quite distinctive, being pink and white interbedded sandstone/siltstone in the former, and plane-laminated generally brown-orange sandstone at the latter. As a result, the provenance of the sandstone blocks in the homestead and courtyard can be determined with certainty.

METHODS

The Mt Bepcha area was mapped in detail, and from the stratigraphic sections compiled the Major Mitchell Sandstone was subdivided into four lithofacies, from base upwards: the Interbedded Sandstone/Siltstone Facies, Massive Sandstone Facies, Trough Cross-bedded Facies and Plane-laminated facies, and five ichnofacies: Cruziana Ichnofacies, Skolithos Ichnofacies, Burrowed Ichnofacies, Scoyenia Ichnofacies and Arthropod Ichnofacies. As well as recording the ichnogenera present, the degree of bioturbation was determined for each bed using the Ichnofabric Index of Bromley (1997). An Ichnofabric Index of 1 (i.e. 0% bioturbation) in a bed is the most common, and the degree of bioturbation never exceeds 60% (upper limit for Ichnofabric Index 4).

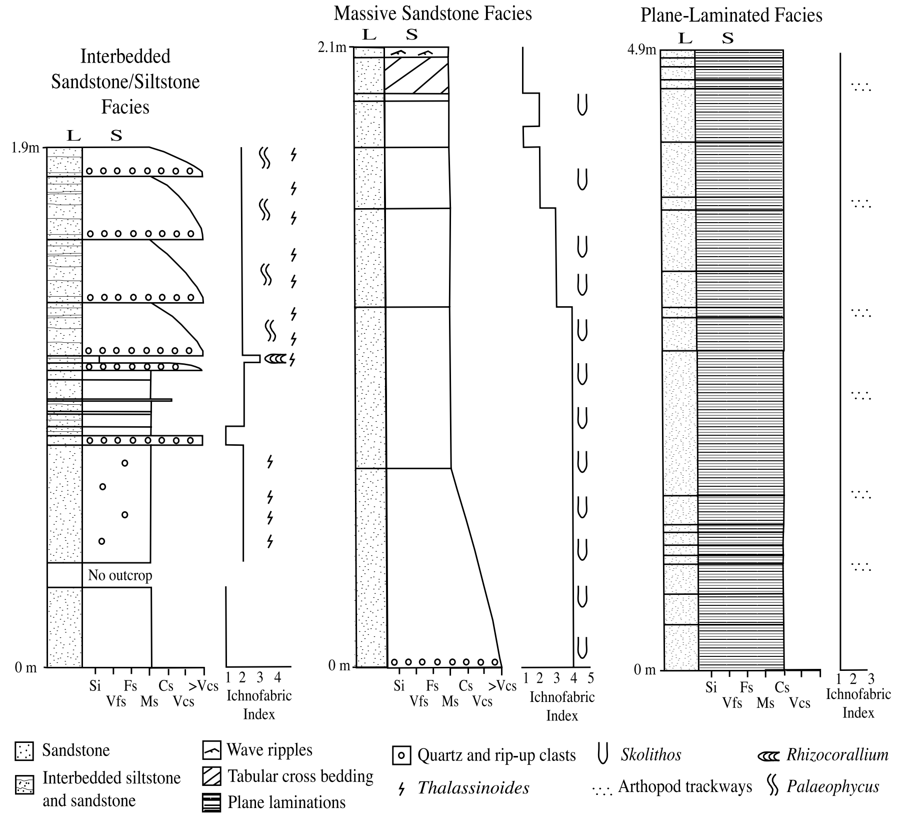


Figure 2 Representative stratigraphic sections of facies, showing lithologies (L), sedimentary structures (S), ichnofauna and ichnofabric index. Note that each section is to a different scale. Cs, coarse sandstone; Fs, fine sandstone; Ms, medium sandstone; Si, siltstone; Vcs, very coarse sandstone; Vfs, very fine sandstone.

LITHOLOGIES

The Major Mitchell Sandstone at Mt Bepcha consists predominantly of sandstone, with interbedded siltstone (in the lower part of the section). Both lithologies are pink or white on fresh surfaces but weather grey. The sandstone is fine- to coarse-grained, texturally mature, porous quartz arenite containing monocrystalline (probably largely plutonic igneous) quartz, along with varying, small amounts of vein and polycrystalline metamorphic quartz, and accessory biotite, iron oxide, muscovite, zircon, tourmaline and sericite. The sericite represents recrystallised interstitial clay, and can reach 5% in some lower porosity sandstones. The cement comprises both syntaxial silica overgrowths and pore-rimming (sometimes isopachous) iron oxide and/or chalcedony. Cobbles of vein quartz and, less commonly, mudstone and sandstone rip-up clasts, are present in some beds. The siltstone is identical in composition to the sandstone but is finer-grained.

At Glenisla Quarry, the sandstone has more metamorphic quartz (13%) and chert clasts (2%), and ranges from quartz arenite to quartz wacke in individual fining-upward sequences a few millimetres to a few centimetres thick. The quartz wacke has up to 20% silt-sized, dominantly quartz matrix.

FACIES

Interbedded Sandstone/Siltstone Facies

LITHOFACIES

The Interbedded Sandstone/Siltstone lithofacies is approximately 30 m thick at Mt Bepcha Quarry on the north-western face of Mt Bepcha (Figure 1), and quarried blocks from this facies are common in the walls of Glenisla Homestead.

This lithofacies comprises alternating thin, planar beds of pink, medium-grained sandstone 3–10 mm thick (Figure 2) and white siltstone (1–3 mm, rarely up to 3 cm thick). The beds are laterally continuous, except where they are disrupted by bioturbation.

Soft-sediment deformation is the most common sedimentary structure present; large, up to 10 cm diameter, pillows of sandstone press down into the underlying siltstone, pushing up small flames. Water-escape structures are rarely present as vertical columns through the sandstone.

Occasional thicker sandstone beds with dune trough cross-bedding are found in this facies, forming scours up to 40 cm deep. Rarely there are thin films of silt between successive foresets (only found preserved in sandstone blocks in the walls of Glenisla Homestead), and these are interpreted to be mud drapes (Figure 3a). The lag deposits at the base of the scours (Figure 2) contain clasts of vein quartz 1–10 cm across, along with minor grey, very angular to subrounded mudstone rip-ups, and very rare, 3 cm, rounded, green, medium-grained sandstone clasts. These lags show some grading upwards, in that the coarse- to medium-grained sand matrix surrounding the clasts increases from 40 to 100% upwards. Minor symmetrical wave ripples sometimes occur on the tops of the trough cross-beds. Palaeocurrent directions were impossible to obtain for this facies due to poor outcrop.

ICHNOFACIES

The beds show an ichnofabric index of 1–3, and in some sections (Figure 2), a relatively high proportion (50%) of beds have an Ichnofabric Index of 2 (minor amount of bioturbation). More intense bioturbation (Ichnofabric Index 3) is also evident. There is a decrease in the degree of bioturbation up the sequence, corresponding to a change towards a more sand-dominated lithology.

Four types of ichnofossils are present: *Thalassinoides* (most abundant), *Palaeophycus*, *Rhizocorallium*, and moderately large unidentified burrows. These occur both within the siltstone beds and crossing the siltstone and sandstone beds.

Thalassinoides (Figure 4a) occurs in two forms: circular to subcircular vertical burrows, and horizontal linear elongate tubes. Both are less than 3 cm in diameter and lack wall ornamentation. Large rounded sections in the horizontal burrows might be intersection points between the vertical and horizontal components, where the animal had enough room to turn around. Because of their similar size and morphology, the horizontal and vertical burrows probably functioned as a domichnion for the constructor. Burrow mottling most likely attributable to *Thalassinoides* also occurs as poorly preserved epichnial ridges of pink sandstone extending into the siltstone beds.

Burrows of similar morphology are formed by extant callianassid shrimps (Order Decapoda) (Bromley 1997). Decapods, however, had not evolved in the Middle Silurian, but their ancestors, the Phyllocarida, range from the Cambrian through to the present (Clarkson 1996). Although phyllocarids are filter feeders, they resemble shrimps, except for their very large carapaces, and they might have formed similar dwelling structures to callianassids (Bromley 1997).

Palaeophycus (Figure 4c) is found in slabs of light pink siltstone in the walls of Glenisla Homestead, which also contain abundant *Thalassinoides*. *Palaeophycus* occurs as substratal, exichnial burrows that are long (up to 14 cm), thin (<0.5 cm) and gently curved. They lack wall ornamentation and do not branch, but occasionally cross previously formed burrows.

Palaeophycus has been interpreted as a substratal repichnion (Hantzschel 1975) or a domichnion (Bromley 1997), formed by an arthropod (Hantzschel 1975), polychaete (Bromley 1997) or predacious annelid or annelid-like animal (Hiscott *et al.* 1984). *Palaeophycus* in the Major Mitchell Sandstone appears to have a repichnial function because the burrows are parallel to the bedding, cross one another and are gently curved, suggesting formation as the animal burrowed its way through the sediment.

The only specimen of *Rhizocorallium* (Figure 4b) was found associated with *Thalassinoides* in a siltstone bed. It is a straight, subhorizontal hypichnion, 11 cm long, 3 cm wide and 3 mm deep, containing protrusive spreite parallel to bedding. The maximum width between individual meniscate backfills is approximately 1 mm, and this distance decreases as the backfills approach the external walls. The burrow dips at an extremely shallow angle to bedding, and was formed during sedimentation as the animal maintained its relative depth within the sediment, while moving laterally during feeding (Seilacher 1967). There is no tapering of the spreite due to growth of the organism, so the burrow is probably a fodinichnion, produced by an arthropod or worm-like creature.

Moderately large burrows found parallel to bedding homogenise the sandstone and siltstone beds and cannot be attributed to an ichnogenus. They are circular to elliptical with a radius of 5–5.5 cm (occasionally up to 14 cm), and were probably formed by a large worm-like creature (polychaete?) that ingested and then excreted homogenised sediment, thus forming a temporary substratal fodinichnion.

Based on the presence of *Thalassinoides*, *Rhizocorallium* and *Palaeophycus*, this ichnofacies can be assigned to the archetypal Cruziana Ichnofacies of Seilacher (1967), even though the nominate ichnogenus, *Cruziana*, is absent.

INTERPRETATION

This ichnofacies suggests a relatively shallow-marine depositional environment. Seilacher (1964) showed that the Cruziana Ichnofacies from the Ordovician Khabour Quartzite, Northern Iraq, represents littoral to sublittoral marine environments, where deposit feeders and fodinichnia are abundant, especially *Rhizocorallium* and *Thalassinoides*. Vos (1977) described these trace fossils from an Upper Palaeozoic delta system in southern Morocco, where they occur in interbedded sandstone and siltstone with soft-sediment deformation. These lithofacies and ichnofacies were interpreted as a nearshore delta-front environment, with some tidal and wave reworking of sediments.

The presence of silt at Mt Bepcha indicates low-energy conditions in the nearshore marine environment, below daily fairweather wave-base. This is also evident in the trace-fossil association. The abundant horizontal or sub-horizontal fodinichnia, repichnia and domichnia require quiet conditions for the colonisation and construction of these burrowing systems. The vertical components of the domichnial *Thalassinoides*, which extend into the sandstone beds as burrow mottling, would take some time to construct.

This ichnofacies shows a decrease in the degree of bioturbation up the sequence (Figure 2), corresponding to a change towards a more sand-dominated lithology. As the depositional environment shallowed from nearshore to

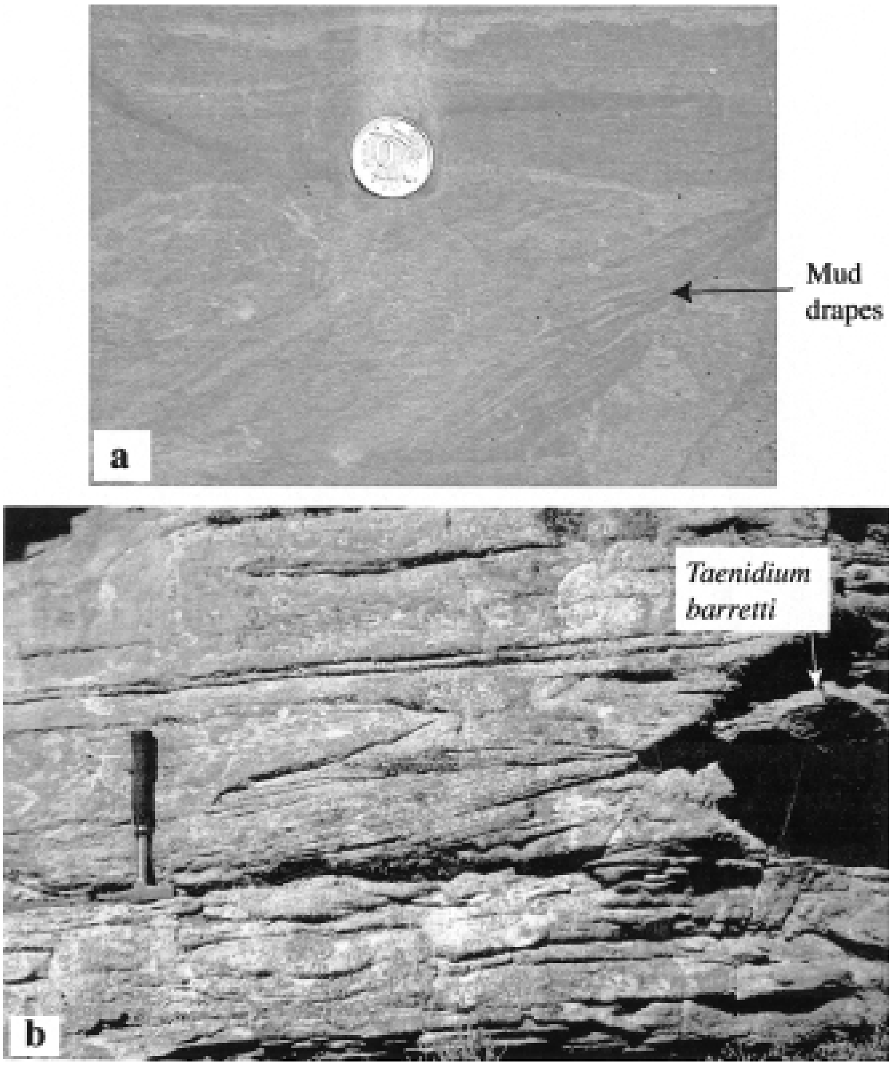


Figure 3 (a) Mud drapes, Interbedded Siltstone/Sandstone Facies; slab of rock in Glenisla Homestead (605500E 5877500N); coin is 24 mm in diameter. (b) Large-scale trough cross-bedding showing *Taenidium barretti* burrow, Trough Cross-bedded Facies, northern cliffs of Mt Bepcha (602000E 5881500N); hammer for scale.

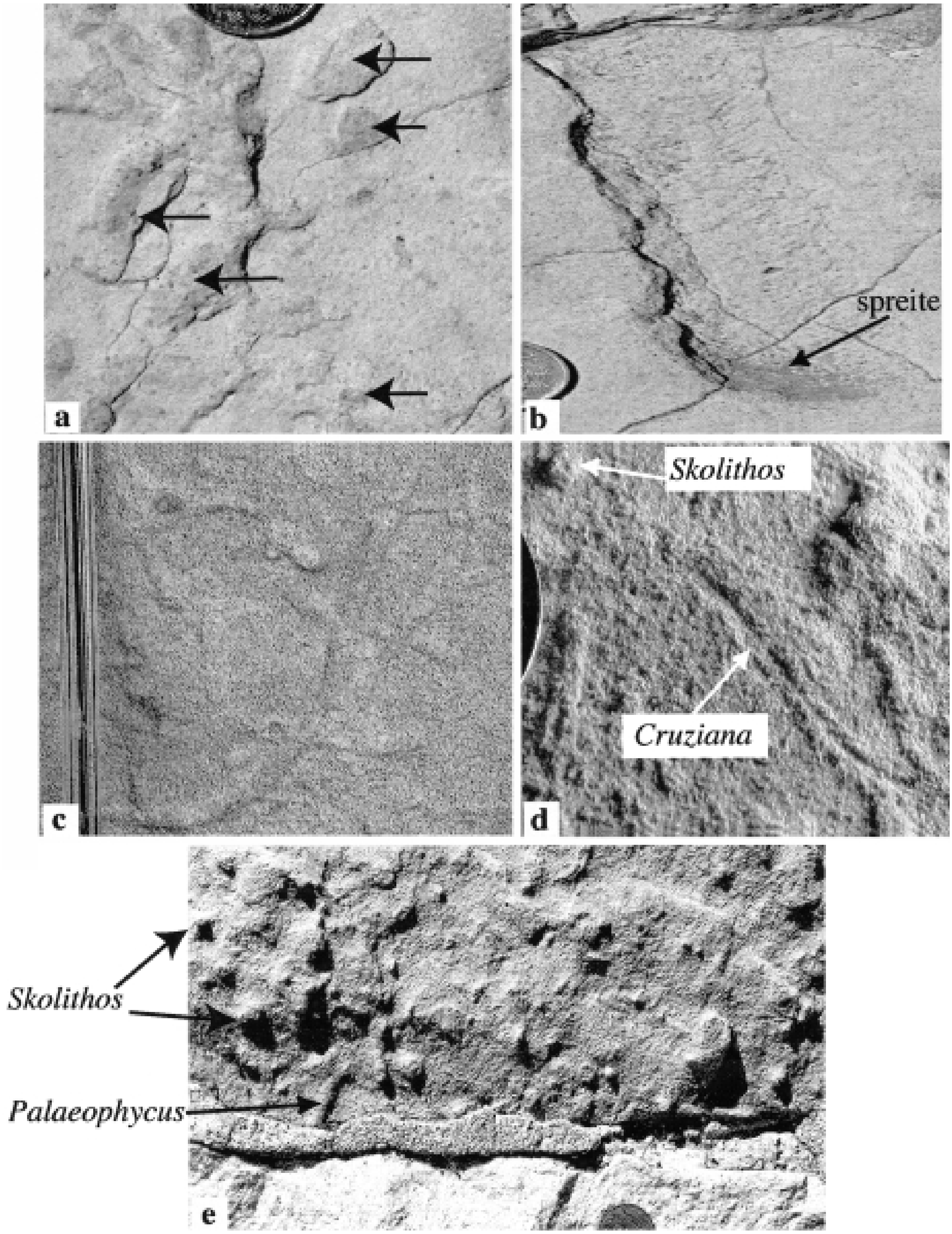


Figure 4 (a) *Thalassinoides*, Interbedded Siltstone/Sandstone Facies, Mt Bepcha Quarry (602000E 5881500N). (b) *Rhizocorallium* with well-defined arrowed spreite, Interbedded Siltstone/Sandstone Facies, Mt Bepcha Quarry (602000E 5881500N). (c) *Palaeophycus* burrows, Interbedded Siltstone/Sandstone Facies; slab in Glenisla Homestead (605500E 5877500N); pen for scale. (d) *Cruziana problematica* trails and *Skolithos linearis* burrows, Massive Sandstone Facies, Mt Bepcha Quarry (602000E 5881500N). (e) Dense *Skolithos linearis* (ichnofabric index 4) and occasional *Palaeophycus* burrows, Massive Sandstone Facies, slab in Glenisla Homestead (605500E 5877500N). Coin (a, b, d, e) is 24 mm in diameter.

middle shoreface, less silt was deposited due to the increase in energy, and the amount of biological activity by horizontally burrowing organisms decreased.

The massive or cross-bedded medium-grained sandstones of the Interbedded Sandstone/Siltstone Facies correspond to lithofacies Sm of Miall (1978, 1996) and have structures indicative of rapid sedimentation (pillows and flames and water escape). These beds were deposited during flooding events from a nearby river, when a rapid influx of medium-grained sand deformed the underlying siltstone bed. Thus, the facies probably represents a delta front.

The thicker sandstone beds with large dune trough cross-bedding and basal lags correspond to lithofacies Ss and St of Miall (1977, 1996) and Se of Cant and Walker (1976). Occasionally, the cross-beds show mud drapes (facies Fm of Miall 1978, 1996) are indicative of tidal deposits (Reineck & Singh 1980). The dune cross-beds are sometimes overlain by symmetrical wave ripples (facies Sr of Miall 1978, 1996), and these beds probably formed as small longshore bars in a tidally influenced middle shoreface depositional environment. Where the dune trough cross-beds lack mud drapes, they formed above fairweather wave-base, where the silt was kept in suspension.

Lithofacies resembling the Interbedded Sandstone/Siltstone lithofacies at Mt Bepcha have been described from elsewhere in Australia and overseas. The Cretaceous Reconcavo Basin in Brazil contains a Disturbed Sandstone – Mudstone Facies characterised by interbedded siltstone and sandstone with soft-sediment deformation (DeVries Klein *et al.* 1972), and was interpreted as delta-front sedimentation.

The Permian Snapper Point Formation of the southern Sydney Basin contains strongly bioturbated, interbedded sandstone and siltstone with trough cross-bedding, interpreted as a braidplain delta prograding into a shallow-marine shelf environment (Tye *et al.* 1996). Within Unit A (Bioturbated Muddy Sandstone: Barrier Foot), which was deposited on a barrier beach facing the open ocean, Carey (1978) recognised a middle shoreface facies characterised by the presence of *Rhizocorallium*, and a lower shoreface facies with *Zoophycos*? and *Taenidium*. The Snapper Point Formation is similar to the facies at Mt Bepcha, but contains abundant hummocky cross-stratification, indicating that the shelf was storm-dominated, whereas the shallow-marine environment of the Major Mitchell Sandstone was protected in some way, and shows little or no evidence of storm activity.

Unit 4 of the Mt Baldwin Formation of the Early Cambrian Georgina Basin in central north Australia is a coarsening-upward sandstone sequence, with water-escape structures, laminated siltstone, rip-up clasts and mud drapes (Eyre 1994). It is interpreted to have been deposited in a shallow-marine tidally influenced environment, representing the distal portion of a braided alluvial plain.

Thus, the depositional environment of the Interbedded Sandstone/Siltstone lithofacies at Mt Bepcha is believed to have been relatively shallow marine, predominantly middle shoreface, and probably represented a low-energy delta front with minor tidal influences. Periodic flooding events interrupted silt deposition with the deposition of medium-grained sand. During times of low energy and silt deposition, fodinichnia, repichnia and domichnia were established. The degree of bioturbation decreases with increasing grainsize up the sequence, suggesting a progradation of the delta front and subsequent shallowing of sea-level.

Massive Sandstone Facies

LITHOFACIES

This lithofacies overlies the Interbedded Sandstone/Siltstone Facies on the northwestern face of Mt Bepcha. It is approximately 7.5 m thick, and characterised by massive beds of coarse- to medium-grained sandstone, 20–80 cm thick; siltstone interbeds are lacking (Figure 2). Most beds are structureless except for the preservation of vertical burrows, but occasionally present are dune and ripple cross-bedding and plane-lamination (facies Sm, St, Sr, Sh of Miall 1977; Miall 1978, 1996). Lag deposits of vein quartz clasts (up to 10 cm in diameter and comprising approximately 10% of the rock) are present at the bases of some sandstone beds and decrease in diameter up the bed.

The relatively rare trough cross-bedded and rippled beds are similar to those in the Interbedded Sandstone/Siltstone Facies, and occur as dune trough cross-beds overlain by symmetrical ripples. No palaeocurrents were measured due to poor outcrop.

The plane-laminated beds occur in the upper parts of the Massive Sandstone Facies, as laminae less than 3 mm thick stacked in beds 5–40 cm thick, and represent higher energy conditions of the upper to middle flow regime. These beds often overlie graded sandstone beds with basal-lag deposits, and might erode the tops of trough cross-beds.

ICHNOFACIES

The Massive Sandstone Facies is characterised by a high-abundance but relatively low-diversity ichnofauna (Figure 2), with three ichnospecies present. These are very abundant *Skolithos linearis*, and single examples of *Palaeophycus* (identical to that in the Sandstone/Siltstone Facies), found among *S. linearis* in slabs in the walls of Glenisla Homestead (Figure 4e), and *Cruziana problematica*, preserved only on a single piece of plane-laminated sandstone float (Figure 4d). This assemblage represents Seilacher's (1967) Skolithos Ichnofacies because *S. linearis* is present in such large numbers.

S. linearis (Figure 4d, e) is a straight, vertical domichnial tube, found in the massive and plane-laminated beds. These burrows never curve, branch or deviate from vertical. They are 2–8 cm long and have a circular cross-section with a diameter of 0.5–0.8 cm. The upper end opens to the palaeosurface, and has a small dome-like epichnial chimney above this surface. The lower end tapers to a fairly blunt tip. Often, specimens that have been broken parallel to the long axis show a thin coating of iron oxide around the interior wall of the burrow.

S. linearis occurs in great numbers in this facies; most beds with *S. linearis* record an Ichnofabric Index of 3 (30% bioturbation) and occasionally reach 4 (60%) (Figure 2). Beds with such a high density are named piperock, and are common in Palaeozoic marine sediments worldwide (Droser 1991).

The beds that contain *S. linearis* usually have very prominent upper surfaces, where the tops of the burrows all terminate. The burrows often extend downwards into the lag horizons at the bottom of beds or into underlying beds. Occasionally, the base of a bed with *S. linearis* is not bioturbated, probably because deposition was so rapid there was insufficient time for the *S. linearis*-producing organisms to completely colonise the sediment (Droser & Bottjer 1989; Droser 1991).

S. linearis tubes show no evidence of grazing, and appear to represent dwelling burrows. They were probably produced by filter-feeding polychaete, sipunculan and/or phoronid worms (Bromley 1997).

The single specimen of *C. problematica* (Figure 4d) is a short, sinusoidal trail 3 cm long, curving around the chimneys of *S. linearis*. The trail comprises two lateral epichnial ridges with a thin median groove, which extends the length of the trail, and is 0.5–1 mm wide. The lateral ridges are commonly asymmetrical, the right ridge being slightly wider than the left, measuring 2 mm and 1 mm, respectively. Angled scratch marks approximately 1 mm apart, produced by the legs of the organism that formed the trail, occur either side of the ridges; the angle of V created by the scratches is greater than 90°.

The animal that created the *C. problematica* trail probably had many pairs of jointed legs that propelled the body by a metachronal action (Anderson 1996). In marine environments, the usual suspects are trilobites, but notostracan branchiopods and gastropods may have created *Cruziana* traces in fluvial facies (Hantzschel 1975).

INTERPRETATION

S. linearis is generally regarded as indicative of high-energy, typically upper-shoreface marine environments (Seilacher 1967). The filter feeders that formed the *S. linearis* burrows needed currents streaming across their filaments so that nutrient particles in the water column could be filtered out (Walker & Bambach 1974). For filter feeders like *S. linearis* to flourish, they must have lived in a relatively dynamic environment. The high energy and shifting sand substrate represented difficult conditions to which few animals could adapt, resulting in a low-diversity, high-abundance fauna.

Droser and Bottjer (1989) interpreted *Skolithos* piperock in the Lower Cambrian Zabriskie Quartzite in California, the Middle Ordovician Watson Ranch Quartzite in Utah, and the Silurian Tuscarora Formation in Pennsylvania as forming in high-energy nearshore environments. Tankard and Barwis (1982) identified *Skolithos* from a distributary mouth bar in a wave-dominated delta environment in the Devonian Bokkeveld Basin of South Africa. The Crow Head Member of the Lower Cambrian Bradore Formation in eastern Canada generally lacks sedimentary structures but contains abundant *Skolithos*, and is believed to represent estuarine deposition (Hiscott *et al.* 1984). The *Skolithos–Diplocraterion* ichnofauna from the ?Late Ordovician to Early Silurian Tumblagooda Sandstone, Western Australia, probably inhabited large bedforms in a tidally influenced shallow-marine environment (Trewin & McNamara 1995). Bradshaw (1981) described *Skolithos* from shallow-marine facies of the Devonian Taylor Group in Antarctica, but Woolfe (1990) and Wizevich (1997) disputed the environmental interpretation, suggesting instead fluvial and aeolian environments. Nevertheless, in the majority of cases where *Skolithos* has been reported, the environment is clearly shallow marine and high energy.

C. problematica is the only *Cruziana* species not found in quiet, deep-marine environments (Bromley & Asgaard 1979). The *Cruziana* trail at Mt Bepcha was probably formed by a trilobite crawling around the chimneys of the *S. linearis* burrows. The lack of siltstone in the Massive Sandstone Facies indicates that these sediments were deposited above fairweather wave-base, although trilobites occur most commonly below fairweather wave-base (Clarkson 1996), accounting for the rarity of *Cruziana* in this facies.

The depositional environment for the Massive Sandstone Facies is therefore interpreted to be a high-energy, upper-shoreface environment, above fairweather wave-base, so the sea-floor sands were continually shifting as they were reworked by waves. The characteristic, periodic sudden influxes of sandy sediment were probably caused by flooding events from the mouth of a nearby river, so this facies, like the underlying Interbedded Sandstone/Siltstone Facies, represents a delta front, but in shallower water closer to the river mouth, where higher-energy, more turbulent waters persisted. Thus, the change from the Interbedded Sandstone/Siltstone Facies to the overlying Massive Sandstone Facies was probably caused by progradation of the delta.

The Massive Sandstone Facies shows some cyclicity in sedimentary structures, with high-energy deposits (coarse basal lags, dune trough cross-bedding) overlain by massive beds with high degrees of bioturbation formed during times of quiescence. The energy of the environment was too high to preserve ripples (except in rare instances), and was strong enough to keep the finer sediments in suspension. The animals that produced the *Skolithos* burrows would have been buried by the high-energy flooding events, and many of them might not have survived, but they were able to colonise the newly deposited sands during the following extended periods of quiescence.

Similar facies occur both stratigraphically higher and lower in the Grampians Group. Jenkin (1989) and George (1994) described *Skolithos* piperock, associated with abundant cross-bedding and broad, shallow channels from the Red Man Bluff and Silverband Formations. They interpreted these facies as subtidal deposits with large sandwaves; the lack of mud drapes was believed to indicate a high-energy ebb-tidal delta environment.

Facies resembling the Massive Sandstone Facies have been described from elsewhere. Facies 4 of the Ordovician Mweelrea Group of western Ireland consists of sharp-based, internally laminated, laterally persistent beds formed as prograding marine sands of an alluvial fan-delta (Pudsey 1984). Howard (1972) described an Upper Shoreface Facies from the Upper Cretaceous of east-central Utah, characterised by fine- to medium-grained sandstones, distinctly laminated, with rare ripple and trough cross-beds and a low-diversity, high-abundance ichnofauna.

Trough Cross-bedded Facies

LITHOFACIES

This lithofacies has an overall thickness of approximately 70 m and extends from the foot of the northwestern face of Mt Bepcha to the summit (Figure 1). It consists of coarse- and fine-grained quartz arenite; the lack of silt means it is very resistant to erosion and so forms near-vertical cliff faces. The contact between this facies and the underlying Massive Sandstone Facies is gradational with some interdigitating.

The Trough Cross-bedded Facies comprises large trough cross-beds (facies St of Miall 1978, 1996) and thin plane-laminated sands (facies Sh of Miall 1978, 1996).

The large trough cross-beds (Figure 3b) are 15–45 cm thick and form scours 1–5 m wide filled with coarse- to medium-grained sandstone. They grade upwards (normal to the dip of the dune foresets) from a basal lag composed of vein quartz clasts up to 10 cm across in a matrix of ~90–95% medium-grained sandstone.

The plane-laminated sandstones are relatively thin beds (10 cm to 1 m thick) comprising individual plane laminations 2 mm to 1 cm in thickness, with well-developed current lineations. These beds extend laterally only 1–3 m, and either merge into or are scoured and truncated by trough cross-beds (Figure 3b).

PALAEOCURRENTS

Palaeocurrent directions were determined from trough cross-beds preserved in 3-D form and from current lineations in the plane-laminated sandstones (Potter & Pettijohn 1977); both were plotted on frequency-corrected rose diagrams (Nemec 1988). The palaeocurrent directions from trough cross-beds average northwest (Figure 5a), with a mean vector trending 320°, but range from north-northeast to west-southwest (standard deviation 74°). The magnitude of the mean vector (r) is relatively low (0. 1732), confirming the relatively large spread. Statistical analysis of the variance about the mean vector of the trough cross-bed palaeocurrents, using both Snedecor's F-test and the Rayleigh Test (Potter & Pettijohn 1977; Krause & Geijer 1987), does not show a significant difference from the variance of a uniform distribution at a 5% level of significance.

Current lineations were measured as a trend and plunge (Figure 5b). Mean and variance were calculated for the axially bimodal von Mises type distribution of data (Mardia 1972), and the Rayleigh Test for uniformity applied to show whether the data was random or directional (Batschelet 1981). The mean directional vector is towards 43° and/or 223° with a circular variance of 0.0262; application of the Rayleigh Test resulted in rejection of the null hypothesis that the distribution was random ($P < 0.001$ at a 5% level of significance). Thus, the results show that the palaeocurrents forming the current lineations were flowing towards either the northeast or southwest or both, with very little variation in the direction of flow.

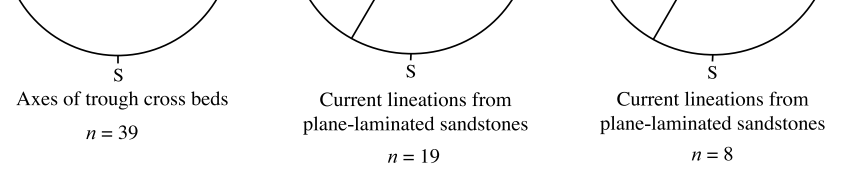
ICHNOFACIES

Two ichnofacies are present in the Trough Cross-bedded Facies, the Scoyenia Ichnofacies associated with the trough cross-beds, and the Burrowed Ichnofacies in the plane-laminated sandstone.

The trace-fossil suite found in the plane-laminated sandstones consists of the ichnogenera *Daedalus* and *Scoyenia*, although they do not occur together, with *Scoyenia* present lower in the sequence. This assemblage is typical of Seilacher's (1967) Scoyenia Ichnofacies.

Daedalus (Figure 6a) is found as both epichnial and hypichnial ridges on the upper and lower surfaces, respectively, of plane-laminated beds. These epichnial and hypichnial trails always have a continuous vertical burrow extending, respectively, above or below the exposed bedding surface. These burrows moved laterally in the sediment to form a spiral or meandering trail, which might cross over older meanders made by the same animal, but never the trails of different individuals. *Daedalus* can reach densities of up to 40% (upper limit of Ichnofabric Index 3).

The surficial trails range in width from 5 to 12 mm and can cover areas up to 70 cm^2. They extend vertically through the sediment as unbranched cylindrical or cone-shaped burrows (Figure 6a). The cylindrical burrows tend to be larger, ranging up to 9 cm wide, and the inverted cones are smaller, reaching a maximum depth of 5 cm. The latter, found in thinner plane-laminated beds, are formed as the burrow bends in towards the middle of the overall

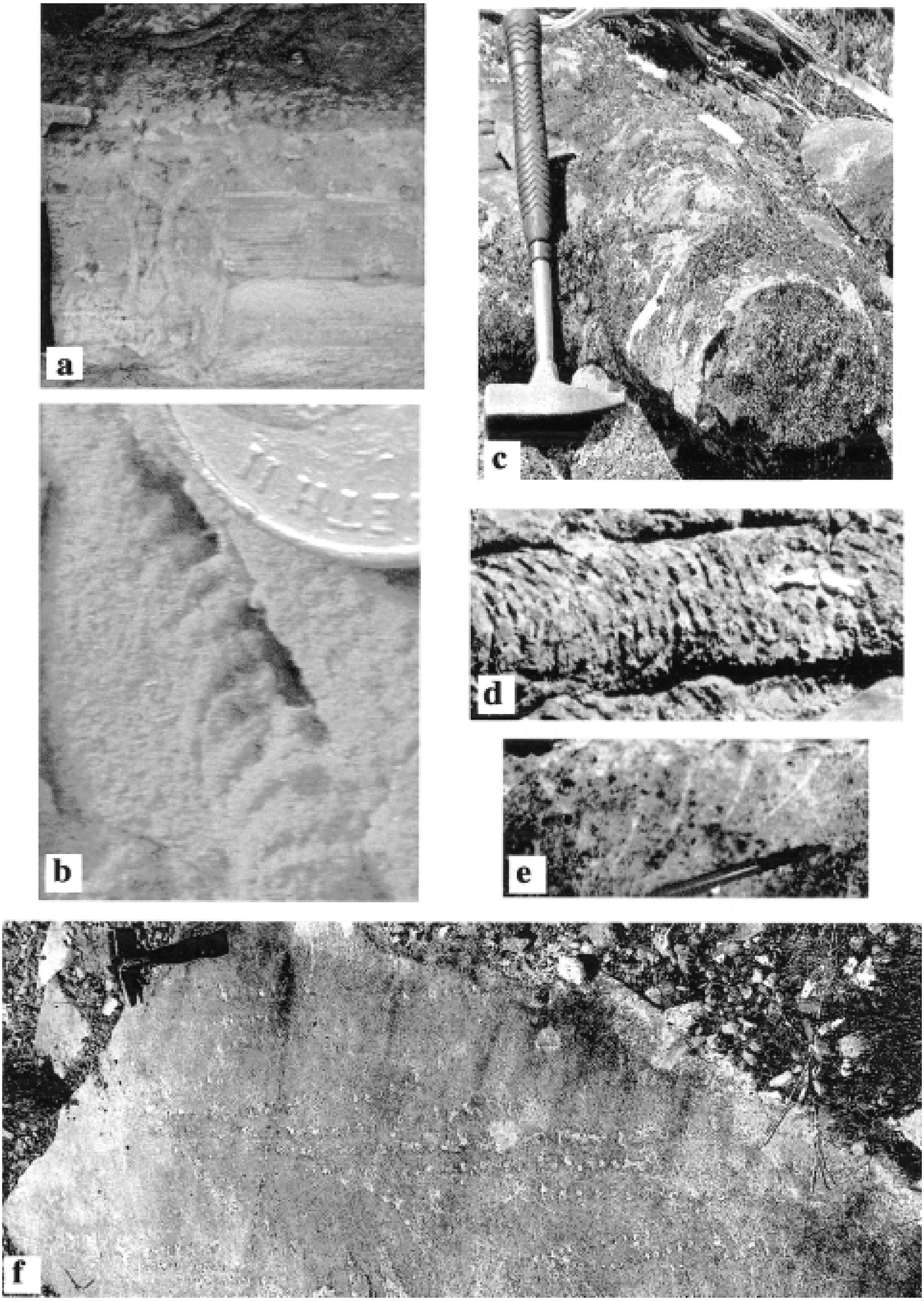


Axes of trough cross beds
$n = 39$

Current lineations from plane-laminated sandstones
$n = 19$

Current lineations from plane-laminated sandstones
$n = 8$

Figure 5 Frequency-corrected rose diagrams of palaeocurrent directions, with number of measurements (n). Data corrected for dip of bedding.


a
b
c
d
e
f

structure in smaller individuals (Trewin & McNamara 1995).

The Mt Bepcha *Daedalus* appears to be a combined pascichnial/dominichnial trace very similar to *Daedalus* sp. described from the Tumblagooda Sandstone of Western Australia by Trewin and McNamara (1995), who hypothesised that this ichnofossil was formed by a deposit-feeding polychaete worm of similar morphology to the creator of *Skolithos*. When the burrowing animal reached the maximum depth to which it could penetrate the substrate, it slowly migrated laterally within the sediment, feeding on surrounding sediments while searching for a point of access to greater depth (Trewin & McNamara 1995).

Scoyenia (Figure 6b) is found as both epichnial ridges and grooves on the tops and bases of the plane-laminated beds. The trails are fairly straight, or have a slight curvature, range in thickness from 4 to 12 mm and are approximately 10 cm long. They are formed intrastratally and both dorsal and ventral sides are preserved with either meniscate, sinuous or oblique backfill structures approximately 2 mm apart. There is no median groove, but two thin (<1 mm) lateral grooves are present.

The trails represent repichnial traces, probably formed by small arthropods as they travelled through the sediment at a shallow depth.

Within the trough cross-beds, only one ichnospecies is present: large intrastratal burrows here named the Burrowed Ichnofacies. The degree of bioturbation is low (1–10%). These burrows were previously described by Douglas and Kenley (1981) from the Major Mitchell Sandstone at Mt William, 40 km east-southeast of Mt Bepcha, as 'enigmatic structures', and identified as a possible alga belonging to the Phaeophyceae by Douglas (1981, 1983). At Mt William, they show spreite-like meniscate backfill (lacking at Mt Bepcha) and are certainly burrows (Figure 6d), and are here re-identified as *Taenidium barretti* (Figure 6c).

The burrows (Figure 6c) occur subhorizontally within dune cross-beds, and are large structures 20 cm to 2 m long, elliptical in cross-section with a long axis of 20 cm and a short axis of 10 cm, and thus fall within the size range reported for *T. barretti* (Keighley & Pickerill 1994). They have a convex upper surface and a flattened lower surface containing a median ridge extending the length of the burrow.

They are generally aligned subparallel to the primary current direction, as defined by dune cross-bedding; this is particularly evident at Mt William. At Mt Bepcha, these burrows plunge to the southeast at a shallow angle (Figure 7), meaning that the opening to the burrow faced northwest, that is, parallel to the current direction (described previously) and on the lee side of the channel-floor dunes. The convexity of the meniscate backfills at Mt William shows that the animal was burrowing down-current, probably keeping pace with the advance of the active dune face, and pushing sediment behind it as it burrowed through the substrate. These intrastratal burrows were probably formed by large burrowing arthropods that moved parallel to the flow of the current, and might have functioned as repichnia, fugichnia or equilibrium structures (Keighley & Pickerill 1994).

Large, sinuous *T. baretti* have been described by Bradshaw (1981), Woolfe (1990) and Wizevich (1997) from purely non-marine settings in the Devonian Taylor Group of Antarctica, and the constructors of the burrows were believed to be large myriapods. Bradshaw (1981) proposed that the burrows were formed by the same type of organism responsible for the arthropod trackways stratigraphically lower in the sequence. Draganits *et al.* (2001) described small diameter *T. barretti* from the Lower Devonian Muth Formation of India, and attributed them to either myriapods or arthropleurids.

Gierlowski-Kordesch (1991) described a similar ichnofacies with large burrows from the non-marine Jurassic East Berlin Formation in the Hartford Basin, USA. These burrows lack the meniscate backfill found at Mt William, are more irregularly shaped and contain large carbonate intraclasts. She proposed that burrowing vertebrates or decapods formed these burrows.

INTERPRETATION

The Scoyenia Ichnofacies is characteristic of non-marine environments (Seilacher 1967), and the Trough Cross-bedded Facies at Mt Bepcha is most easily interpreted as a fluvial deposit.

The trough cross-bedded component of this facies represents shallow scours up to 5 m wide that have basal lags, but lack epsilon cross-bedding. Such scours are typical of the numerous shallow, narrow avulsing channels of a braided river system and/or the distributary channels on a delta plain (Turner 1980). At present, such sandy or pebbly sequences occur predominantly in arid or Arctic areas, where there is very little vegetation to hold the coarser material in place. As vascular land plants are not known from before the mid- to Late Silurian (Kenrick & Crane 1997; Scheckler 2002), similar deposits are more common in the Early Palaeozoic. Without vegetation to increase infiltration and slow down run-off, stream flows following rainfall would be sporadic and high, resulting in more bed load, causing the avulsion of distributaries to be more common (Turner 1980). Trewin (1993) suggested that the ?Late Ordovician to Early Silurian fluvial succession of the Tumblagooda Sandstone of Western Australia was a sand-dominated fluvial system, also influenced by the lack of rooted vegetation that would have otherwise stabilised the sand-sized sediment.

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Figure 6 (a) *Daedalus* burrows (cross-section), plane-laminated sandstones of Trough Cross-bedded Facies, northern cliff of Mt Bepcha (602000E 5881500N); hammer (left) for scale. (b) *Scoyenia* burrow with prominent spreite, plane-laminated sandstones of Trough Cross-bedded Facies, northern cliff of Mt Bepcha (602000E 5881500N); coin is 24 mm in diameter. (c) Large *Taenidium barretti* lacking spreite, trough cross-beds of the Trough Cross-bedded Facies, northern cliff of Mt Bepcha (602000E 5881500N); hammer for scale (d) Large *Taenidium barretti* with prominent spreite, Mt William (642300E 5871500N); keys (right) are 13 cm across. (e) ?Fish trace fossil, Plane-laminated Sandstone Facies, slab at Glenisla Homestead (605500E 5877500N); pen for scale. (f) Arthropod trackways, Plane-laminated Sandstone Facies, Glenisla Quarry (603300E 5879700N); hammer for scale.

The palaeocurrents obtained from the trough cross-beds (Figure 5a) do not show the typical narrow range of unidirectional current flow indicative of braided river and deltaic systems (Potter & Pettijohn 1977). The greater spread of palaeocurrents might be because the environment was a delta plain rather than a typical braided stream; if the gradient was low and there was a strongly indented shoreline nearby, channel avulsion would result in different distributaries taking different routes to the shoreline. The overall palaeocurrent trend of northwest represents the general flow direction of the river system.

The plane-laminated sandstones merge laterally into the trough cross-beds, and were probably formed by relatively constant upper flow regime overbank sheet flooding of sediment-rich waters into interdistributary environments of the unvegetated delta plain (Schumm 1968; Turner 1980). Evidence for this comes from the palaeocurrent data (Figure 5b) that show a current direction normal to that within the distributary channels. The trace fossils *Daedalus* and *Scoyenia* colonised the plane-laminated sediment formed by periodic overbank flooding, and the extensive lateral migration and horizontal movement exhibited by these burrows and trails suggests that the times of quiescence following flood deposition were relatively long-lasting. The areas near the distributary channels where this facies was deposited were probably continuously underwater. The lack of silt or mud deposition after flood events suggests that water continued to flow across the interdistributary flats, keeping the fine-grained sediment in suspension.

Thus, the Trough Cross-bedded Facies at Mt Bepcha was probably deposited in shallow low-sinuosity channels by overbank-flooding events, most likely on a delta plain. The change from the underlying Massive Sandstone Facies, interpreted to be a high-energy upper shoreface environment, represents continuing delta progradation.

Jenkin (1989) and Jones (1993) described comparable lithofacies, characterised by abundant trough cross-bedding, from the Grampians Group to the east of Mt Bepcha, and interpreted them similarly as a distal, low-relief braidplain in a braid delta system formed by low-sinuosity rivers.

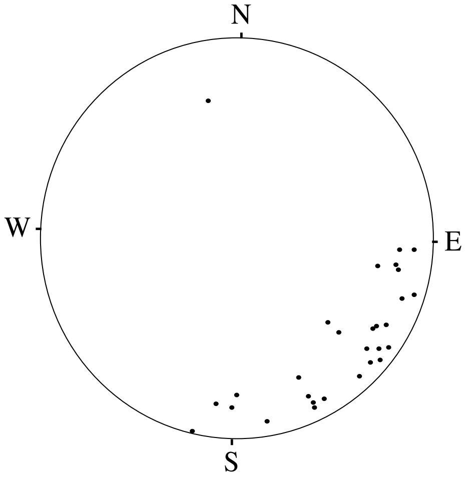

Figure 7 Equal-area stereoplot of orientation of large intrastratal burrows of the Trough Cross-bedded Facies, showing consistent dip towards the southeast (see text for discussion). Data corrected for dip of bedding.

Many authors have described similar fluvial facies comprising associated plane-laminated sandstone and trough cross-bedding, such as the conglomeratic Yadboro and Tallong units, and associated sandstones of the Shoalhaven Group of the Permian Sydney Basin (Tye *et al.* 1996). The Late Permian Bainmedart Coal Measures in the Northern Prince Charles Mountains of Antarctica contain sequences characterised by plane lamination and abundant large-scale trough cross-bedding with lags of pebble- to boulder-sized vein quartz clasts, deposited by low-sinuosity braided channels (Fielding & Webb 1996). The Tumblagooda Sandstone of Western Australia contains fluvial sandstones with erosional bases dominated by trough cross-beds, and less common tabular cross-bedding and plane-laminated sandstones (Trewin 1993).

Plane-laminated Sandstone Facies

LITHOFACIES

The Plane-laminated Sandstone Facies occurs only at Glenisla Quarry (Figure 1), where outcrop is limited (20 × 10 m). This facies is not in stratigraphic contact with the other facies at Mt Bepcha (Figure 1), but from its location and the strike and dip of the bedding, it can be shown to be the stratigraphically highest unit. It comprises a 10 m-thick sequence of thin, fining-upward, plane-laminated, current-lineated sandstones (Figure 2) with rare ripples and raindrop impressions, and common arthropod trackways.

Individual plane-laminated beds are 1 mm to 5 cm thick, and grade upwards from basal coarse quartz arenites to fine quartz wackes, and commonly show a strong current lineation. One piece of float at the quarry shows asymmetrical current ripple foresets truncated by an overlying massive sandstone, and straight, asymmetrical wave ripples are preserved on the slab of rock that contains the 'tetrapod' trackway (Warren *et al.* 1986). Raindrop impressions are also present on a paving stone at Glenisla Homestead.

PALAEOCURRENTS

Current lineations show mean directional vector trends towards 48° and/or 228°, with a circular variance of 0.0144 (Figure 5c), that is, either northeast or southwest, with very little variation in the direction of flow. Application of the Rayleigh Test resulted in the rejection of the null hypothesis that the flow directions were uniformly distributed, that is, random, using a critical value (α) of 5% and $P < 0.001$.

ICHNOFACIES

The ichnofossils found in this facies include a vertebrate (?fish) trace, arthropod trackways and a trackway previously attributed to a tetrapod (Warren *et al.* 1986). They are found both at Glenisla Quarry and on slabs in the courtyard of Glenisla Homestead.

The ?fish trace (Figure 6e) is preserved as a series of five epichnial ridges that each curve in a semi-sigmoid shape and taper to a point. The overall width is 6.5 cm but this represents only half of the trace fossil; the left side is not preserved. The fins of a fish probably made this track.

The trackways (Figure 6f) will be described in detail elsewhere, so only brief descriptions are given here. They are all very extensive, although few are preserved in their entirety. Most are biserial with individual tracks on either side coinciding, but others show a staggered footfall. All the trackways are straight, and represent the same type of behaviour, repichnia.

Up to five different ichnospecies of *Diplichnite*s are present; one of these, *Diplichnites cuithensis*, also occurs in the Namurian of Scotland, where it was interpreted by Briggs *et al.* (1979) to have been formed by *Arthropleura*, a giant myriapod. The other *Diplichnites* species at Mt Bepcha, including Warren *et al.*'s (1986) 'tetrapod' trackway, were probably formed by other arthropods, including perhaps scorpionids, eurypterids, euthycarcinoids and xiphosurids (Gouramanis 2000). The *Diplichnites* trackways are generally orientated parallel to the current lineations; the 'tetrapod' trackway runs at a high angle oblique to the crests of the asymmetrical wave ripples on the rock slab where it occurs.

This ichnofacies is typical of Seilacher's (1967) Scoyenia Ichnofacies, due to the presence of arthropod trackways produced subaerially. However, since Scoyenia is not present in this facies, it is here named the Arthropod Ichnofacies.

INTERPRETATION

This facies was deposited by periodic high-energy events, with currents reaching the upper flow regime, and depositing fining-upwards sequences as the current energy waned. By analogy with the depositional environment deduced for the underlying facies, the Plane-laminated Sandstone Facies was probably deposited during sheet flooding of the delta plain close to the distributary channels. Such flood events spread as sheets across adjacent areas (Schumm 1968).

The raindrop impressions were formed during a period of subaerial exposure, and the rare asymmetrical current and wave ripples were probably formed following floods, when shallow water temporarily covered the delta plain.

The palaeocurrent directions from current lineations are parallel to those from the plane-laminated sandstones of the Trough Cross-bedded Facies, and normal to the mean direction of the distributary channels in the latter facies. This implies that the Plane-laminated Sandstone Facies was formed by flood currents spreading sideways from the distributary channels.

Jenkin (1989) described a plane-laminated facies from the Red Man Bluff Formation of the Grampians Group, but the presence of *Skolithos* piperock in this facies indicates a different, probably shallow-marine depositional environment.

The trace–fossil association of this facies comprises both a ?fish trace and a number of arthropod trackways. The ?fish trace was probably formed during a sheet-flooding event, when the fish was forced out of a distributary channel and onto the flooded delta plain. As the floodwaters disappeared and exposed the delta plain, large arthropods were able to walk across the wet sand.

Mid-Palaeozoic arthropod trackways described from elsewhere are believed to have formed in similar environments. The Tumblagooda Sandstone of Western Australia contains a large number of biserial arthropod trackways, including several different forms of *Diplichnites*, formed by a variety of arthropods in subaerial aeolian–fluvial conditions (Trewin & McNamara 1995). Similarly, the large *Diplichnites* trackways (up to 250 mm in width) in the Devonian Taylor Group of Antarctica are believed to have been produced subaerially in an aeolian to fluvial environment (Woolfe 1990). Carboniferous *Diplichnites* trails from Scotland and Eastern Canada are from strata interpreted as fluvial overbank sheet-flood sandstones on deltas or alluvial fans (Briggs *et al.* 1979, 1984).

Therefore, like the plane-laminated sandstones of the Trough Cross-bedded Facies, the Plane-laminated Sandstone Facies was probably deposited by overbank-flooding events from distributary channels on a delta plain. The lack of channel deposits most likely reflects the very limited outcrop of this facies.

The Plane-laminated Sandstone Facies has a different ichnocoenosis from the plane-laminated sandstones of the Trough Cross-bedded Facies. The latter occurs with large trough cross-beds, and represents distributary channels and nearby areas that might have been continuously underwater, even between flooding events, so that the *Daedalus* burrows and *Scoyenia* trails could form. In contrast, the Plane-laminated Sandstone Facies preserves overbank flooding distal from the distributary channels, deposited in an area subaerially exposed between floods. Hence, these differing niches would have been inhabited by different biotas.

COLONISATION OF THE LAND BY ARTHROPODS

Late Cambrian to Early Ordovician arthropod trackways described from an aeolian sandstone in southwest Ontario, Canada, are the oldest unequivocal terrestrial trackways yet described (MacNaughton *et al.* 2002). Arthropods continued to colonise the land during the Ordovician and Silurian, as shown by the trackways at Mt Bepcha and in the Tumblagooda Sandstone. The latter are probably the older of the two Australian examples, as the Tumblagooda Sandstone is directly overlain by Ludlovian limestones, and sandstones laterally equivalent to the Tumblagooda Sandstone are succeeded by the Ajana Formation, which has yielded Early Silurian conodonts (Iasky *et al.* 1998; McNamara & Trewin 2002). Previous studies regarded the Tumblagooda Sandstone as ?Late Silurian, because the upper part contains a palynoflora originally thought to be no older than Late Silurian (Playford *et al.* 1975; Hocking 1991).

Subaerial arthropod trackways also occur in the Devonian, for example, Taylor Group of Antarctica (Bradshaw 1981) and Muth Formation of Northern India (Draganits *et al.* 2001), both of which contain trackways comparable to those in the Tumblagooda and Major Mitchell Sandstones.

CONCLUSIONS

The sedimentary succession of the Major Mitchell Sandstone outcropping at Mt Bepcha was deposited in a prograding fluviodeltaic environment inhabited by abundant organisms that burrowed through the sediments to form the best-preserved evidence of the biological record of the time currently known from the Grampians Group.

The initial depositional environment was nearshore to middle shoreface on a low-energy delta front, below daily fairweather wave-base, and characterised by silt deposition and horizontal and vertical burrow systems. Minor tidal influences are evident. This environment was periodically inundated with sand from flooding events of the feeder river system (Interbedded Sandstone/Siltstone Facies). The degree of bioturbation decreases with increasing grainsize up the sequence, suggesting a progradation of the delta front and subsequent shallowing of sea-level.

The overlying Massive Sandstone Facies represents wave reworking of the delta-front sands in the high-energy, upper shoreface, river mouth environment. The characteristic, periodic sudden influxes of sandy sediment were probably caused by flooding events from the mouth of the nearby river. This environment was characterised by a high-abundance, low-diversity benthic biota, dominated by *Skolithos*.

Further progradation of the delta caused deposition of the braided distributary channels and interdistributary sandbanks (Trough Cross-bedded Sandstone Facies). The distributaries flowed, on average, northwest, and contained large *T. barretti* formed by animals burrowing downcurrent on the lee side of the channel-floor dunes. The plane-laminated interdistributary sandstones were deposited by overbank-flood currents flowing more or less perpendicular to the distributary channels and are characterised by trace fossils constructed by deposit-feeding organisms.

The uppermost facies, the Plane-laminated Sandstone Facies, was formed as graded overbank deposits during sheet flooding of the delta plain. The palaeocurrent directions are parallel to those of the interdistributary sandbanks in the underlying facies, indicating a similar mode of deposition. A ?fish trace formed during one period of inundation by flood waters, and many different arthropods crossed the delta plain during times of subaerial exposure.

The change from shoreface delta front to delta plain with distributary channels and sheet flooding of overbank deposits indicates a major marine regression. This regression probably reflects sediment accumulation accompanied by slow subsidence, and might have been accompanied by eustatic lowering of sea-level. There is no evidence of tectonic influence.

The arthropod trackways of the Plane-laminated Sandstone Facies, formed on the subaerially exposed surface of the periodically sheet-flooded delta plain, adds to the growing database of Early Palaeozoic terrestrial ichnofaunas.

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