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DICKINSARTELLA FAUNA FROM THE SAIWAN FORMATION (OMAN): A BIVALVE FAUNA TESTIFYING TO THE LATE SAKMARIAN (EARLY PERMIAN) CLIMATIC AMELIORATION ALONG THE NORTH-EASTERN GONDWANAN FRINGE

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Key words: Saiwan Formation, Oman, Gondwana, Sakmarian, Permian Deglaciation, Bivalvia, Cyrtodontidae, Permophoridae, shell microstructure.

Abstract. The transitional faunas of the Permian Huqf succession of Oman make it one of the key-sections for the intercalibration of Early to Middle Permian biostratigraphical scales.

The abundance of fossils improved the knowledge of some marine faunas which populated the North-Eastern Gondwanan fringe during times of climatic changes in the Permian.

A Sterlitamakian (upper Sakmarian, Lower Permian) bivalve fauna from the Saiwan Formation in the Huqf area, informally named "*Dickinsartella* Fauna", is described in the present paper. The specimens examined were collected from the "*Pachycyrtella* Bed" (Auctorum), the basal bed of the Formation in its type locality.

The *Dickinsartella* Fauna can be identified for the presence of the new genus *Dickinsartella*, which dominates the bivalve thanatocoenosis with *D. pistacina* sp. n. (type species). The bivalve fauna from the *Pachycyrtella* Bed includes the new species *Stutchburia sangallii* and *Promytilus mazzolenii,* and also *Astartella obliqua* Dickins, 1963, *Nuculopsis* cf. *bangarraensis* Dickins, 1963,?*Oriocrassatella* sp., and indeterminable aviculopectinids.

This fauna shows a low taxonomic diversity. Nevertheless, some species are represented by a high number of generally well-preserved specimens, i.e. some specimens of *S. sangallii* sp. n. and *A. obliqua* show part of the ligament. The good preservation of the shells permitted the microstructural analysis of *D. pistacina* sp. n. and *S. sangallii* sp. n. The microstructure of *S. sangallii* sp. n. supports the close phylogenetical link between modiomorphids and crassatelloids recognized by some previous authors.

The new genus *Dickinsartella* includes the more recent species belonging to the important Paleozoic Order Cyrtodontida Scarlato & Starobogatov, 1971.

The discovery of *Dickinsartella* gen. n. and other taxa of the *Pachycyrtella* Bed, present also in the Sakmarian levels of the Carnarvon and Perth Basins in Western Australia, indicates a wider distribution of the *Dickinsartella* Fauna and confirms the correlation between Arabian and Australian series already remarked by previous authors.

The *Dickinsartella* Fauna is the first bivalve fauna testifying to the climatic amelioration gradually affecting the North-Eastern Gondwanan fringe at the end of the Early Permian glacial events.

This pioneer fauna spread out, probably in a cool-temperate climate, on the substrate provided by the mid-Sakmarian (basal Sterlitamakian) transgression, connected with the final stages of the Gondwanan deglaciation and/or with initial sea-floor spreading in the Neotethys.

In the present paper some remarks on the autecology of the new species from the *Pachycyrtella* Bed are also discussed.

Riassunto. La successione permiana dell'area di Huqf in Oman è considerata per le sue faune a carattere transizionale una delle sezioni chiave per il confronto tra le scale biostratigrafiche del Permiano Inferiore e Medio. L'abbondanza dei fossili consente di approfondire lo studio di alcune tra le faune marine che hanno popolato il margine nord-orientale gondwaniano durante i periodi di fluttuazioni climatiche permiane.

In questo lavoro viene descritta una fauna a bivalvi sterlitamakiana (Sakmariano superiore, Permiano Inferiore), qui informalmente chiamata Fauna a *Dickinsartella*, proveniente dalla Formazione di Saiwan nell'area di Huqf; gli esemplari esaminati sono stati raccolti nel "Banco a *Pachycyrtella*" (Auctorum), che è il livello basale della Formazione nella sua località tipo. La Fauna a *Dickinsartella* è riconoscibile per la presenza del nuovo genere *Dickinsartella*, che domina la tanatocenosi a bivalvi con la specie *D. pistacina* sp. n. (specie tipo del nuovo genere). La fauna a bivalvi del Banco a *Pachycyrtella* comprende anche le due nuove specie *Stutchburia sangallii* e *Promytilus mazzolenii* e inoltre *Astartella obliqua* Dickins, 1963, *Nuculopsis* cf. *bangarraensis* Dickins, 1963, ?*Oriocrassatella* sp. e aviculopectinidi indeterminabili.

Questa fauna presenta una bassa biodiversità, alcune specie sono tuttavia rappresentate da un alto numero di individui generalmente ben conservati, alcuni esemplari di *Stutchburia sangallii* sp. n. e di *Astartella obliqua* esibiscono infatti parte del legamento; il buon livello di conservazione dei gusci ha consentito l'analisi microstrutturale di *D. pistacina* sp. n. e di *S. sangallii* sp. n.; la microstruttura di *S. sangallii* n. sp. consente di inferire strette relazioni filogenetiche tra modiomorfoidi e crassatelloidi riconosciute da autori precedenti.

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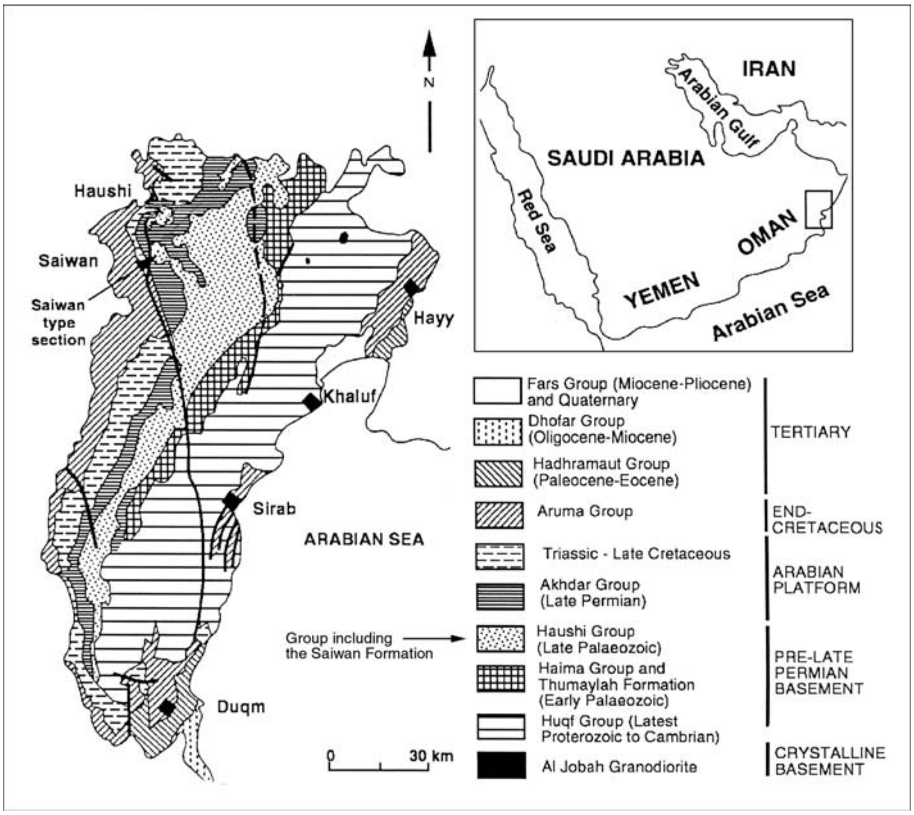

Fig. 1 - Geological sketch map of the Huqf area, southern Oman, showing the location of the Saiwan Formation type section, from Angiolini et al. (1997) modified.

Il nuovo genere *Dickinsartella* comprende apparentemente le ultime specie appartenenti all'importante Ordine paleozoico Cyrtodontida Scarlato & Starobogatov, 1971.

Il riconoscimento di *Dickinsartella* gen. n. e di altri taxa del Banco a *Pachycyrtella* anche in livelli Sakmariani dei bacini Carnarvon e Perth, in Australia Occidentale, permette di riconoscere una più ampia distribuzione della Fauna a *Dickinsartella*, confermando le correlazioni tra le serie arabiche e quelle australiane note in letteratura.

La Fauna a *Dickinsartella* è la prima fauna a bivalvi che testimonia il miglioramento climatico che ha gradualmente interessato la frangia nord-orientale gondwaniana al termine degli eventi glaciali del Permiano Inferiore. Questa fauna pionieristica si diffuse, probabilmente in un clima temperato-fresco, sul substrato prodotto dall'evento trasgressivo medio-sakmariano (Sterlitamakiano basale), legato agli stadi finali della deglaciazione gondwaniana e/o all'apertura della Neotetide.

Nel presente lavoro si discute inoltre l'autoecologia delle nuove specie riconosciute nel Banco a *Pachycyrtella*.

Introduction

The first discoveries of fossiliferous Lower Permian rocks from the Huqf area (Interior Oman) were made by the geologists of the Iraq Petroleum Company in 1955. The material collected was then studied by Hudson & Sudbury (1959). They described a brachiopod fauna from Lower Permian rocks, now named Saiwan Formation (Dubreuilh et al. 1992), and included in their paper a list of species of bivalves identified by L. R. Cox. Hudson & Sudbury's collection of bivalves was re-identified and discussed by Dickins & Shah (1977), who reported a list of species without a systematic description and pictures of the specimens. More recently, Dickins (1999) studied a bivalve fauna from the lower part of the Khuff Formation, regarded as not older than Wordian (Middle Permian) in age (Angiolini et al. 1998, 2003a), that consists of ten species from ten genera, of which six are newly established.

Among wider projects on the Permian Tethys (cfr.: Angiolini 2001c; Larghi 2002), recent investigations were made by researchers of the Università degli Studi di Milano (L. Angiolini, M. Balini, A. Nicora, and A. Tintori), and many specimens of bivalves were collected in the "*Pachycyrtella* Bed" (Angiolini et al. 2003b; "*Cyrtella* bed" of Angiolini et al. 2001), which represents the basal bed of the Saiwan Formation at Saiwan. Since specimens come only from a single layer, the number of species is lower than that reported by Hudson & Sudbury (1959) and Dickins & Shah (1977) for the whole Saiwan Formation, but the abundant material and the good preservation of the specimens resulted in significantly improved systematics. Some new taxa were recognised in the material collected, i.e a new genus of Cyrtodontidae Ulrich, 1894, a new species of Mytilidae Rafinesque, 1815, and a new species of Permophoridae Van de Poel, 1959, for which the names *Dickinsartella pistacina* gen. n. sp. n., *Promytilus mazzolenii* sp. n. and *Stutchburia sangallii* sp. n. were introduced, respectively. *Astartella obliqua* Dickins, 1963, *Nuculopsis* cf. *bangarraensis* Dickins, 1963, ?*Oriocrassatella* sp. and indeterminate aviculopectinids were also recovered (the last taxon, represented only by a few very poorly

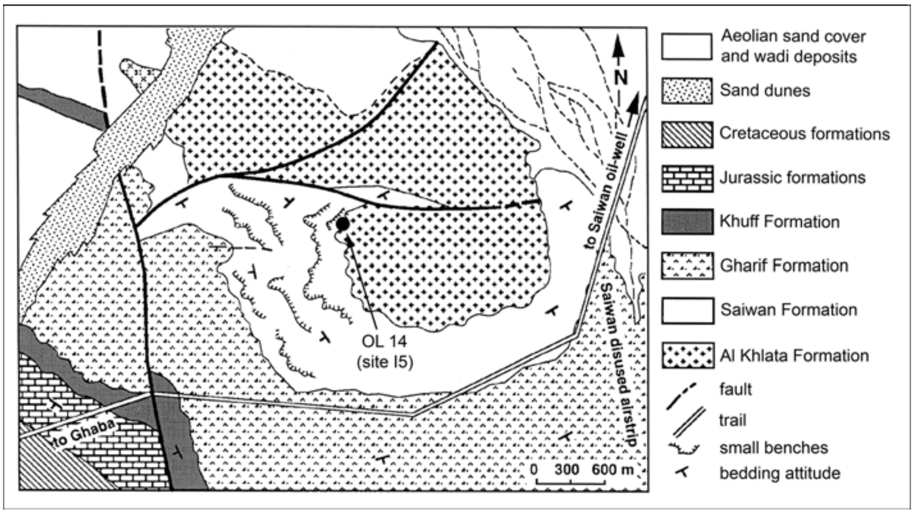

Fig. 2 - Detailed sketch map of the fossil locality I5, from Angiolini et al. (1997) modified.

preserved specimens, MPUM9025.1.x.3, is not discussed in the systematics).

Geological setting

The Saiwan Formation was introduced by Dubreuilh et al. (1992) to replace the informal Haushi Limestone of Hudson & Sudbury (1959).

The Saiwan Formation, with its age-diagnostic marine faunas, is intercalated between two non-marine formations: in southern Oman it overlays the glacial deposits (tillites) of the Al Khlata Formation (Upper Carboniferous to early Sakmarian, Osterloff et al. 2004) and is overlain unconformably by the transgressive shales and sands of the Gharif Formation (?Artinskian to?Wordian). The Gharif Formation is followed by the marine marls and limestones of the Wordian (Middle Permian) Khuff Formation (Angiolini et al. 1998, Angiolini et al. 2003a).

The Saiwan Formation comprises a terrigenous lower member, 10 m thick in the type section (probably corresponding to the "*Bellerophon* Limestone" of Hudson & Sudbury 1959) and a carbonate upper member, 40 m thick in the type section (probably the "*Metalegoceras* Limestone" of Hudson & Sudbury 1959). Both members yield rich and rather diversified marine assemblages composed of brachiopods, bivalves, gastropods, cephalopods, conularids, crinoids, asterozoans, barnacles, ostracods and bryozoans (Angiolini et al. 2001, 2003a). The brachiopod fauna was described by Angiolini et al. (1997), Angiolini (2001a, 2001b) and Angiolini et al. (2003b), who concluded that it is Sterlitamakian (late Sakmarian, Lower Permian) in age.

The type area of Saiwan

Most specimens of bivalves described were collected from the site I5 (20°52'19"N-57°36'24"E) of Angiolini et al. (2003a), in the type area of the Saiwan Formation at Saiwan (Huqf area, Interior Oman, Fig. 1, 2). This area (Fig. 1) is located near the Saiwan 1 oil well (Dubreuilh et al. 1992) and the section is reported by Angiolini et al. (1997, fig. 2, p. 381). All the specimens studied (L. Angiolini, pers. com.) were collected in the upper 28 cm of the *Pachycyrtella* Bed (bed OL14 in Angiolini et al. 1997), i.e. the basal bed of the lower member of the Saiwan Formation, biostratigraphically dated as early Sterlitamakian (late Sakmarian) by Angiolini et al. (2003a). A few specimens, not included in the type series of the new taxa, were collected from another site (field number OL130) of the *Pachycyrtella* Bed, near site I5 (A. Tintori, pers. com., Fig. 2).

The *Pachycyrtella* Bed, 40-60 cm thick, consists of cross-laminated bioclastic sandstones, passing upward to a level of burrowed red siltstones; at Saiwan it extends continuously N-S for at least 1 km. It contains many specimens of the syringothyrid brachiopod *Pachycyrtella omanensis* Angiolini, 2001, preserved in life position and dominating the palaeocommunity, especially in the lower part of the bed (Angiolini 2001b). In the upper 15 cm of the bed especially bivalves and gastropods can be collected, together with brachiopods such as *Derbya haribi* Angiolini, 1997, *Trigonotreta* sp., and many specimens of *Strophalosia* sp., while the dominance of *Pachycyrtella omanensis* is reduced (Angiolini et al. 2003a). The fossiliferous assemblage of the *Pachycyrtella* Bed represents a very short time-span, perhaps about 60 years for the deposition of the entire bed (Angiolini et al. 2001).

Climatic change in the Early Permian

It is largely accepted that during the Early Permian glaciations developed at high and middle latitudes of the South Hemisphere; nevertheless there is no large

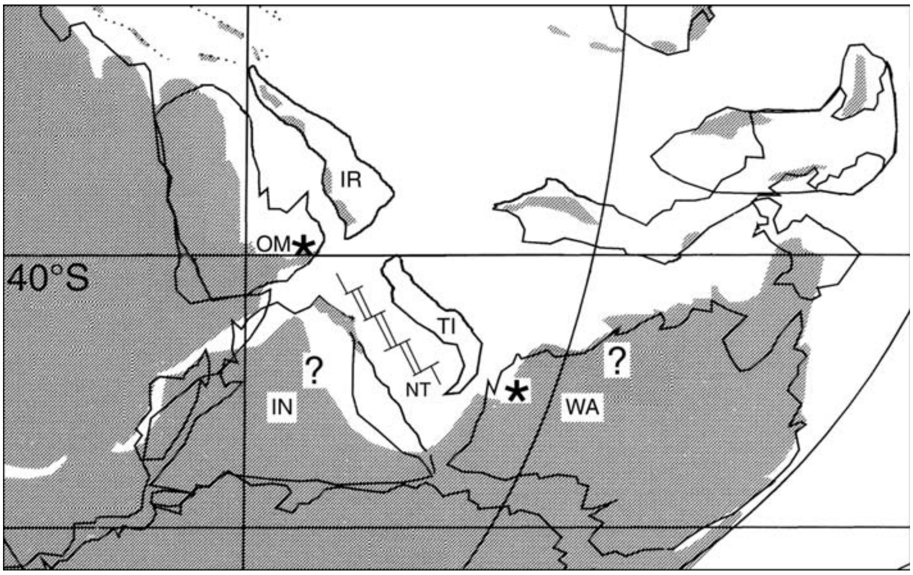

Fig. 3 - Palaeogeographical map of the North-Eastern Gondwanan fringe during the Sterlitamakian showing the diffusion of the *Dickinsartella* Fauna at a paleolatitude of about 40-50ºS, *:sure presence, ?:possible presence, IN: India, IR: Iran, NT: Neo-Tethys, OM: Oman, TI: Tibet, WE: Western Australia, in grey land areas, from Ziegler et al. (1996), modified.

consensus regarding the timing, number and character of the glacial events.

Australia represents a region where researchers most disagree. According to Eyles et al. (1998) Permian glaciations in Australia began in the Sakmarian and lasted, decreasing during the Artinskian and Kungurian, at least until the end of the Middle Permian or, according to Veevers et al. (1994), even to the "Tatarian". Instead, according to Dickins (1996) and Lindsay (1997), the glaciation in Australia was Asselian-early Sakmarian, and the ice covers did not exist after this period. Recent investigations in the Galilee and Bowen basins (Queensland, Eastern Australia) suggested to Jones & Fielding (2004) that, at least in this region, the late Paleozoic glaciers were of mountain or alpine-type and were restricted to discrete, short lived periods, in the Namurian, Westphalian and Sakmarian; the last glacial episode, in particular, seems to have been relatively short-lived in the early Sakmarian, between 293 and 289 Ma.

For Chumakov & Zharkov (2002) a glacial belt bordered the tropical arid belt in western Gondwana and the reduced temperate belt in the east during the initial Permian (Asselian-early Sakmarian). During the Asselian-early Sakmarian glacial maximum, the glaciers of Africa probably reached the Southern Arabian Peninsula (Levell et al. 1988; Alsharhan & Nairn 1995; Stephenson 1999). Thus, the northern boundary of the glacial belt in Africa was located near the 30º-40º S paleolatitudes (Chumakov & Zharkov 2002). In the late Sakmarian and/or initial Artinskian the glaciers retreated everywhere (icehouse-hothouse climatic transition?) and the hypothetical ice shield gradually approached the shape and the extension of a polar cap (cfr. Visser 1997; Visser et al. 1997; Dickins 1996; Chumakov & Zharkov 2002). Some glaciations centres, which sometimes grew in size due to different-rank climatic oscillations, could exist longer, up to the Kungurian (Visser & Young 1990; Visser 1994), but probably at the end of the Early Permian the cold temperate climate became prevalent in the polar areas of both hemispheres. Archbold (2001) suggested that glacial influence was strongest in the Asselian and early Tastubian (early Sakmarian), but absent in the Sterlitamakian (late Sakmarian), with the exception of eastern Australia.

The rate of global warming was probably high during the Sakmarian when glaciations terminated; the glacial maximum was probably followed in the Sakmarian by major fluctuations in climate from relatively cold, with seasonal ice, to periods as warm as subtropical or tropical (Dickins 1996).

According to Angiolini et al. (2005) there is a widespread signal of global warming at the beginning of Sterlitamakian and a consequent significant biotic change during the late Sakmarian, corresponding to an increase of diversity in the brachiopod faunas, both in northern Gondwana and its peripheral regions like Oman, Central Afghanistan, Peninsular India, Western Yunnan and Thailand. According to Angiolini et al. (2003a), the transgressive sharp base of the Saiwan Formation in Oman records the early Sterlitamakian deglaciation of the region and the consequent global sea-level rise, as indicated by reworked ferruginous pedogenetic concretions, phosphates and by paleoecologic analyses. The unconformity is also interpreted, on both biogeographical and petrographical grounds, to correspond with initial sea-floor spreading in the Neotethys Ocean (Angiolini et al. 2003b); according to Dickins (pers. com.) no glacial deposits were recognised in the Sterlitamakian, and the Sterlitamakian transgression should be tectonic in origin.

When the ice sheet collapsed and/or the valley glaciers disappeared in central South America and Southern Arabia, a narrow semiarid belt 5º-15º wide formed. In the late Sakmarian it considerably widened toward the middle latitudes between the paleolatitudes of 0°-15° and 40°-45° S.

Prevalently terrigenous units began to accumulate where land areas were formerly ice-covered (cfr. Chumakov & Zharkov 2002).

In the Haushi ring in Oman the Sterlitamakian bioclastic sandstones and sandy calcarenites of the lower member of the Saiwan Formation overlay the glacial deposits of the Upper Carboniferous- Tastubian Al-Khlata Formation. In Western Australia the limestones of the Fossil Cliff and Callytharra Formations overlay the diamictites of the Nangetty Formation and Lyons Group (Eyles et al. 2003).

Paleogeographical and paleoclimatical significance of the bivalve fauna

The bivalve fauna from the *Pachycyrtella* Bed at Saiwan can be correlated to coeval bivalve faunas from some Western Australian formations. *Dickinsartella* gen. n. is reported, together with *Astartella obliqua* Dickins, 1963 and *Nuculopsis bangarraensis* Dickins, 1963, also from the late Sakmarian levels (*P. pseudoreticulata* palynological zone, cfr. Eyles et al. 2003) of the Callytharra and Fossil Cliff Formations of the Western Australian Carnarvon and Perth Basins (Dickins 1963). There are also some similarities with bivalves from other Australian regions: *S. farleyensis* Etheridge, 1900 from the Lower Permian of Farley (Illawarra District, New South Wales) belongs to the same morphological group of *Stutchburia sangallii* sp. n., *Oriocrassatella queenslandica* Dickins, 1961 from the Sakmarian levels of Bowen Basin (Queensland), with the exception of an uncertain attribution, resembles ?*Oriocrassatella* sp. from the Saiwan Formation. These taxa form a low biodiversity bivalve fauna, here named informally "*Dickinsartella* Fauna", widespread in the post-glacial semiarid belt of the North-Eastern Gondwanan fringe during the Sterlitamakian (late Sakmarian, Early Permian) age of climatic amelioration after the Early Permian glaciations.

The whole Saiwan Formation yielded a rather diversified marine assemblage but lacks colonial corals, fusulinids, and other thermophilic forms. Nevertheless, because of the increment in biodiversity in the uppermost levels with the occurrence of specimens (as *Parallelodon* sp., unpublished data) suggesting milder or colder climates, and the information on the brachiopod fauna reported by Angiolini et al. (1997), Angiolini (2001a, 2001b) and Angiolini et al. (2003b), it is possible to infer a gradual climatic amelioration along the succession of the Saiwan Formation that starts with the *Pachycyrtella* Bed.

The *Dickinsartella* Fauna, dominated by the specimens of *Dickinsartella*, is thus interpreted as a cool-temperate low diversity fauna, which spread out at a middle southern paleolatitude (40°-50°S) along the North-Eastern Gondwanan fringe between the present-day Oman and Australia (Fig. 3).

The faunistic similarities between Oman and Western Australia were already noted by Hudson & Sudbury (1959), and later confirmed by Dickins & Shah (1977), who regarded the mollusc fauna from the Saiwan Formation (i. e. Haushi Formation) as equivalent to that of "Stage B" (Dickins 1963) of the Sakmarian of Western Australia. The faunistic Stage B of Fossil Cliff and Callytharra formations was considered by previous authors (Dickins 1984, 1996; Archbold & Dickins 1996) as a stage of climatic amelioration, which took place after the general Tastubian world-wide eustatic sea level rise, recognizable in South America, South Africa, India and Australia by the presence of the cold water *Eurydesma* Fauna (e.d. Dickins 1961).

Possibly, like many inter or postglacial faunas, the *Dickinsartella* Fauna spreading into more southern latitudes was heterochronous. According to the actual data, the distribution of the *Dickinsartella* Fauna should be limited to the late Sakmarian Westralian Province (partim), initially defined for the brachiopods in the Gondwanan Realm (Shi & Archbold 1993; Angiolini 2001a). Nevertheless, its real distribution in the low diversity Gondwanan Realm (e. d. Ziegler 1990; Shi & Grunt 2000) is probably underestimated at present. Closely comparable faunas probably include those of Badhaura, Peninsular India, Kashmir, Himalayan India, Tibet and Western Argentina (cfr. Dickins 1997). Stratophenetic systematics applied to newly sampled specimens from these localities is necessary to clarify the chronological and geographical distribution of the *Dickinsartella* Fauna. The revision of some late Paleozoic species, until now doubtfully attributed to *Cypricardinia* Hall, 1859 or to *Cardinia* Agassiz, 1841 (e.d.: Branson 1948), would be particularly important for this purpose.

Palaeoecological remarks

The specimens of bivalves were collected, with a volumetric method, by L. Angiolini and A. Tintori (University of Milan) from different levels of the *Pachycyrtella* Bed (indicated by the field numbers). The sampling data will be used in a work in progress more focused on statistical analysis. Nevertheless, at present it is possible to briefly discuss some aspects of synecology and autecology.

The main part of the Saiwan Formation consists of cross-laminated sandstones and sandy calcarenites deposited in shallow-marine shoals, under the influence of waves and tidal currents (Angiolini et al. 2003b).

The bivalve fauna is composed, in order of dominance, by: *Dickinsartella pistacina* gen. n., sp. n. (>85%

of specimens) and *Stutchburia sangallii* sp. n. (~10%); *Promytilus mazzolenii* sp. n., *Astartella obliqua* Dickins, 1963 and *Nuculopsis* cf. *bangarraensis* Dickins, 1963 are present with few specimens. Few very poorly preserved specimens of indeterminate aviculopectinids (not discussed in the Systematic Palaeontology) were also collected from the *Pachycyrtella* bed, and only one specimen of ?*Oriocrassatella* sp. was collected at the top of this bed (OL130 field number, L. Angiolini and A. Tintori, pers. com.).

The *Dickinsartella* Fauna from the *Pachycyrtella* Bed shows palaeoecological features similar to those of the brachiopod fauna, as described by Angiolini (2001b) and Angiolini et al. (2003b).

It was probably a pioneer community living in a cool and inorganic nutrient-rich environment, a new habitat developed after the mid-Sakmarian transgression above the glacial deposits of the Al-Khlata Formation. *D. pistacina* was probably an opportunistic species in this pioneer community, similar, in its ecological role, to the syringothyrid *Pachycyrtella omanensis*, which largely dominates the brachiopod thanatocenosis, particularly in the lower part of the bed (>85%, Angiolini 2001b). Dickins (1963) mentions a high percentage of specimens of *D. elegantula* (Dickins, 1963) from the Fossil Cliff Formation (Perth Basin), whereas in the others localities this species is rare. This could indicate that *Dickinsartella* achieved dominance only in favourable ecological condition, as a typical opportunistic species. The rarity of other taxa in the *Pachycyrtella* Bed, such as *Oriocrassatella* or *Nuculopsis,* probably depends on edaphic factors. *Nuculopsis* in particular, is generally associated by the authors with silt environments (e.d. Dickins 1999).

The bivalves examined show different conditions of preservation with articulated and disarticulated specimens. Some specimens of *Promytilus mazzolenii* and of *D. pistacina* are also encrusted by bryozoans. In *P. mazzolenii* the partial incrustation of bryozoans on the specimens (only in the posterior portion of the shell) and the rectilinear commissural plane suggest a semi-infaunal endobyssate life habit, with the commissural plane in vertical position (Stanley 1972; Savazzi 1984). These bivalves were attached bissally to coarse sediments particles and roughly one third of the shell surface was exposed and overgrown by encrusting organisms (Pl. 1, figs 2, 5). The streamlined and elongated shape of *P. mazzolenii* suggests also an adaptation to borrowing at a high angle to the sediment surface (Savazzi 1984).

The absence of encrusting organisms on all the specimens of *Stutchburia sangallii* suggests an infaunal life habit.

The articulated specimens of *D. pistacina* completely encrusted by bryozoans (Pl. 1, figs 22-24; Pl. 2, figs 6a, 6b) or by brachiopods (*Strophalosia* sp., Pl. 2, figs 6a, 6b) indicate an epifaunal life habit for this species. The quite variable shell surface encrusted by epibionts, without relation with the specimen dimensions, could suggest the original presence of soft bodied (non fossilized) encrusting organisms, competitive with the bryozoans. Parson et al. (1998) have in fact studied the growth of encrusting organisms on present-day bivalve shells experimentally deployed, for one or two years, along two transects in the Bahamas by the Shelf and Slope (from 15 m down to 267 m). The percent surface area covered by each species of encrusters was determined for each shell. Shells at shallow sites approached 100% cover by encrusters, but the percent cover by preservable organisms (attached epibionts with hard skeletons) alone reached 40%.

Conclusions

The study of a rich and well-preserved new collection of bivalves from the Sterlitamakian (late Sakmarian, Early Permian) *Pachycyrtella* Bed of the Saiwan Formation at Saiwan (Interior Oman) provided significant new informations on some Permian bivalves.

- New taxa were proposed: *Dickinsartella pistacina* gen. n., sp. n. (cyrtodontid), *Promytilus mazzolenii* sp. n. (mytilid) and *Stutchburia sangallii* sp. n. (permophorid). The new genus *Dickinsartella* includes some Permian species belonging to the most recent Cyrtodontida Scarlato & Starobogatov, 1971 and previously attributed to *Cypricardinia* Hall, 1859. The microstructure of *S. sangallii* sp. n. supports the hypothesis proposed by some authors about the close link between permophorids and crassatelloideans.
- The bivalve fauna from the *Pachycyrtella* Bed, here named informally *Dickinsartella* Fauna, like the brachiopod fauna (Angiolini et al. 2003b), was a pioneer community living in a new favourable habitat provided by the early Sterlitamakian (late Sakmarian) climatic amelioration which followed the last pulse of the late Paleozoic Gondwanan glaciations.
- The *Dickinsartella* Fauna spread out along the North-Eastern Gondwanan fringe and it is actually reported from Oman and western Australia, but its extension could be wider.
- Bivalves lived in the photic zone, just below the storm wave base and were dominated by the opportunistic species *Dickinsartella pistacina* gen. n., sp. n. The presence/absence parameter of encrusting organisms provides information on life habit and position in the substrate of the epifaunal *D. pistacina* gen. n., sp. n. and of the infaunal *Stutchburia sangallii* sp. n. The semi-infaunal *Promytilus mazzolenii* sp. n. was attached bissally to coarse sediments particles and roughly one third of the shell surface was exposed and overgrown by encrusting organisms.

Systematic Paleontology

All the specimens described are housed in the Palaeontological Museum of the University of Milan, Italy (MPUM-numbers). Field numbers of the single fossiliferous level of the *Pachycyrtella* Bed for the site I5 are reported along with catalogue numbers (first number after the full stop, e. d. 3 in MPUM9026.3.1). The dimensions in italics are uncertain, due to poor preservation of the specimens. The microstructural terminology is taken from Schneider & Carter (2001).

The terminology regarding Mytilacea is from Newell (1942); the term of "transitional ligament" is from Newell & Boyd (1987) (for details on its meaning: Malchus 2004).

Abbreviations: (L): left valve, (R): right valve, (B): articulated bivalved specimen, (CL): crossed lamellar, (CCL): complex crossed lamellar, (BCL): branching crossed lamellar, (ICCL): irregular complex crossed lamellar, (FP): fibrous prismatic, (ISP): irregular simple prismatic, (PB): pallial band. Angle α angle between the tangent to the umbonal ridge and the cardinal margin (measured at a mature stage), angle β angle between the posterior margin and the cardinal margin.

Class **Bivalvia** Linné, 1758 (Buonanni, 1681)
Subclass **Palaeotaxodonta** Korobkov, 1954
Order **Nuculoida** Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Nuculidae Gray, 1824
Genus *Nuculopsis* Girty, 1911

Type species: *Nuculopsis girtyi* Schenk, 1934 (p. 30)- replacement name for *Nucula ventricosa* Hall, 1858 (junior homonym of that of Fleming, 1828) proposed by Girty as type species.

Nuculopsis cf. **bangarraensis** Dickins, 1963

Pl. 1, figs 9-11

? 1959 *Nucula* sp. Hudson & Sudbury, pp. 22-23 (*nn*).

? 1977 *Nuculopsis* (*Nuculanella*) cf. *bangarraensis* Dickins. Dickins & Shah, pp. 32-33 (*nn*).

Material: three small articulated specimens showing the external features (MPUM 9025.1.11, -9025.2.3, -9025.3.4)

Description. Triangular in outline, very high, posterior part of shell projecting only slightly behind umbo. Distinct posterior and anterior ridges. Ornamentation of thin growth lines. No ligament nymphs are present externally.

Specimen		Dimensions (in mm).		
Number	Picture	Length	Height	Thickness
MPUM9025.1.11 (B)	Pl.1, fig. 9a,-c	7.5	9	5
MPUM9025.2.3 (B)	Pl.1, fig. 11	6.2	7.4	4.5
MPUM9025.3.4 (B)	Pl.1, fig. 10a,-b	5.8	6.8	3.5

Discussion. A doubtful attribution was preferred due to some differences with the holotype of *Nuculopsis bangarraensis* Dickins, 1963, particularly visible in one specimen (MPUM9025.1.11).

The specimens are similar to the holotype of *Nuculopsis bangarraensis* Dickins, 1963 in size, outline and ornamentation, but MPUM9025.1.11 differs in the most developed height (height of 9 mm compared with 8 mm of the holotype of *N. bangarraensis* at the same length of 7.5 mm).

The specimens described are similar to *Nuculopsis shumardana* (Hall, 1856) in their sub-cuneate form and the length/height ratio, but the latter exhibits gibbous umbones and a less inequilateral outline.

Remarks on synonymy. *Nuculopsis* (*Nuculanella*) cf. *bangarraensis* Dickins, 1963 was mentioned by Dickins & Shah (1977) from the *Metalegoceras* Limestone (Saiwan Formation p.p.); the synonymy is doubtful, though, because the specimens are not described and illustrated. The same holds true for *Nucula* sp. reported by Hudson & Sudbury (1959) from the *Bellerophon* and *Metalegoceras* Limestone (= Saiwan Formation).

Subclass **Pteriomorphia** Beurlen, 1944
Order **Mytiloida** Ferussac, 1822
Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Genus *Promytilus* Newell, 1942

Type species: *Promytilus annosus* Newell, 1942.

Promytilus mazzolenii sp. n.

Pl. 1, figs 1-8.

Etymology: in honour of Giulio Mazzoleni.

Type series. 11 specimens, holotype MPUM9026.1.1 (Pl. 1, Figs 1a-1b), paratypes (10 specimens) MPUM9026.1.2, -.7,.10, MPUM9026.2.1, MPUM9026.3.1, -.2 (Pl. 1, Figs 2-8).

Type horizon. "*Pachycyrtella* Bed" (bed OL14 in Angiolini et al. 1997), base of Saiwan Formation at Saiwan.

Type locality. Saiwan (Interior Oman).

Age. Sterlitamakian (late Sakmarian, Early Permian).

Specimen		Dimensions (in mm).		
Number	Picture	Length	Height	Thickness
MPUM 9026.1.1 (B)	Pl. 1, figs 1a-1b	19.2	12	6.2
MPUM9026.1.2 (B)	Pl. 1, fig. 6	15.7	9	
MPUM 9026.1.3 (B)	Pl. 1, fig. 8	17.4	9.2	6.2
MPUM9026.1.4 (B)	Pl. 1, fig. 2	15.2	8.7	5
MPUM9026.1.7 (B)	Pl. 1, fig. 7	24.8	12.6	
MPUM9026.3.1 (B)	not illustrated	20	11.9	8.3
MPUM9026.3.2 (B)	Pl. 1, figs 4a-4b	14.8	8.9	

Diagnosis. Shell elongated; angle β rather acute (nearly 40°). Posterior margin narrow and broadly rounded. Umbonal ridge well developed and rather straight, except in the umbonal region, where it is slightly arched; angle α increasing regularly from 25°-30°, at nearly 2.5 mm from the beaks, until the maximum value of 65°-70°. Anterior lobe small and slightly protruding. Ornamentation given by marked concentric growth lamellae.

Description. Shell small, maximum dimension less than 25 mm, strongly prosocline. Cardinal and anteroventral margin rectilinear. Slightly inequivalve, with the left valve slightly more convex than the right. The angle α increases regularly (corresponding to a curve in the growth vector) at nearly 2.5 mm from the beaks (at 3 mm in MPUM 9026.1.1, 2 mm in MPUM9026.1.2 or 2.5 mm in MPUM9026.3.2) from nearly 25°-30° until the maximum value of nearly 65°-70° (at 20 mm in MPUM 9026.1.1). Rather defined sulcus, which extends from the beaks backward to the ventral margin, where it coincides with a broad, clearly marked sinus in the shell margin; anterior lobe poorly defined. Ligament area almost narrow, hinge and muscle scars unknown.

Discussion. *Promytilus mazzolenii* sp. n. differs from *P. vetulus* Newell, 1942, from the "Wolfcampian" (lowermost Permian) of Kansas, in the more curved body of the shell, the more rounded posterior margin and the more developed concentric lamellae; it differs from *P. annosus* Newell, 1942, from the middle and upper "Missourian" (lower Upper Pennsylvanian) of Kansas, in the less protruding anterior lobe and the more developed concentric rugae. *P. mazzolenii* sp. n. differs from *P. swallovi* (McChesney, 1860) from the lower "Missourian" levels near Richmond, Mo., in the less incised ventral sinus and less developed anterior lobe, and from *P. priscus* Newell, 1942, from the middle and upper "Virgilian" (uppermost Pennsylvanian) of the Mid-Continent area, in the less obliquely elongate outline. *P. mazzolenii* sp. n. differs from *P. patagonicus* González, 1975 from the locality of El Molle, Chubut province (Argentina) in the more triangular outline and the more curved body of the shell.

Myalinella Newell, 1942 shows some similarities with *Promytilus* Newell, 1942; nevertheless, the former exhibits a more triangular outline, with a more acute umbo, and lacks the broad sulcus of the shell, from beak to ventral sinuosity, present in *Promytilus*. Similarly, some authors (González 1975) expressed doubts about the generic position of some species attributed to *Promitylus*, but also similar to "*Myalina*" (s. l.); therefore, the comparison of *P. mazzolenii* sp. n. with some species of *Myalinella* seems appropriate.

P. mazzolenii sp. n. is similar to *Myalinella acutirostris* (Newell & Burma, 1941), from the Middle Permian of northern Texas, in the development of the umbonal ridge and to *Myalinella cuneiformis* (Gurley, 1883), from the Pennsylvanian of Colorado, in the elongated outline. However, it differs from both species in the longer and narrower outline with a narrower posterior margin and a longer cardinal margin. Its outline is somehow similar to that of *Myalinella amosi* González, 1980 from the Huentelauquen Formation (upper Paleozoic) of Chile, but *Promytilus mazzolenii* sp. n. shows a more oblique and curved body of the shell.

P. mazzolenii sp. n. is distinguishable from *Modiolus konecki* Dickins, 1963 for the much less developed anterior lobe.

Occurrence and range. *Pachycyrtella* Bed (sensu Angiolini et al. 2003b) of the Saiwan Formation (Sterlitamakian, late Sakmarian, Interior Oman).

Order **Cyrtodontida** Scarlato & Starobogatov (in Nevesskaya et al. 1971), emend. Cope, 1996

Superfamily Cyrtodontoidea Ulrich, 1894

Family Cyrtodontidae Ulrich, 1894

Discussion. Cyrtodontida are Paleozoic bivalves, mainly widespread during the early Paleozoic, which are often regarded as the earliest pteriomorphians (Cope 1997).

Whereas important information on the Ordovician and Silurian species were supplied also in recent papers by Carter (1990), Cope (1996, 1997, 1999) and Zong-Jie & Cope (2004), whose useful diagnosis and discussions are considered in this paper, until now information on the late Paleozoic members, particularly Permian, were scant.

New information provided by late Palaeozoic forms are important for the common good preservation of the shells, since early Paleozoic shells are frequently affected by strong diagenesis which hampers the microstructural analysis. Taylor et al. (1973) reported in a late Ordovician ambonychiid a dubitative prismatic calcite outer layer, and according to Cope (1997) there are no other known Ordovician pteriomorphs with preserved shell microstructure. Carter (1990) provided new information on *Ptychodesma knappianum* Hall & Whitfield, 1872, but the shell microstructure of many other cyrtodontids is unknown.

Genus *Dickinsartella* gen. n.

Type species: *Dickinsartella pistacina* sp. n.

Etymology: in honour of the late James MacGregor Dickins.

Diagnosis. Equivalve, inflated, strongly inequilateral, from subrectangular to slightly modioliform in outline, posterior margin wider than anterior. Ligament transitional, opisthodetic. Hinge on the left valve with one small pseudocardinal tooth, two anterior teeth and two or three long laminar posterior teeth; right valve with one pseudocardinal tooth, one anterior tooth and two or three long laminar posterior teeth; edentulous sub-umbonal area poorly developed. Ornamentation given by imbricated concentric lamellae; uncertain presence of faint radial ribs in some species.

Composition of Genus. The genus is composed by the type species *Dickinsartella pistacina* sp. n. from the upper Sakmarian (Lower Permian) Saiwan Formation (Interior Oman), by *Cypricardinia ?elegantula* Dickins, 1963 from the Sakmarian Fossil Cliff and Callytharra Formations (Perth and Carnarvon Basins, Western Australia) and, doubtfully, by *Pleurophorus gregarius* Etheridge, 1900 from the Lower Permian of Farley (Sidney Basin, New South Wales). Relatively abundant species, tentatively attributed to the genus *Cypricardinia* Hall, 1859, show more similarities with the species of *Dickinsartella* gen. n., but without any information on the internal characters it is not possible to reach a definite generic attribution. *Cypricardinia* aff. *elegantula* reported by González (1972) from the Westphalian (Middle Pennsylvanian) Las Salinas Formation (Argentina) exhibits evident radial ribs suggesting a genus different from *Dickinsartella*.

Discussion. *Dickinsartella* differs from *Cipricardinia* Hall, 1859 in shape, hinge, ligament and ornamentation. *Cypricardinia*, unlike *Dickinsartella* is inequivalve. *Dickinsartella* exhibits a cyrtodontoid dentition with an edentulous sub-umbonal area, arched anterior teeth, pseudocardinal and anterior teeth more anteriorly placed than in *Cypricardinia* (for details about the dentition of *Cypricardinia*: Haffer 1959). *Cypricardinia* has a well-developed external ligament, whereas *Dickinsartella* shows a transitional one (sensu Newell & Boyd 1987). *Cypricardinia* exhibits ornamentation with equally spaced lamellae showing a more undulated and less imbricated pattern than *Dickinsartella*.

Essentially, *Dickinsartella* differs from *Cyrtodonta* Billings, 1858 in the general shell shape and hinge. *Dickinsartella* shows an inter-umbonal growth less developed than *Cyrtodonta* with a resulting narrower ligament area. *Dickinsartella* exhibits anterior teeth different in number (nevertheless this is a character rather variable in *Cyrtodonta*) and shape in comparison with those of *Cyrtodonta*; it exhibits also a narrower edentulous sub-umbonal area on the hinge-plate and posterior lamellar teeth longer than *Cyrtodonta* and originating from nearly the middle of the hinge-plate.

Others similar genera like *Edmondia* De Koninck, 1841 and *Permartella* Yancey, 1985 show important and noticeable differences in dentition and ligament.

Occurrence. Sterlitamakian *Pachycyrtella* Bed of the Saiwan Formation (Interior Oman) and Sakmarian (?Sterlitamakian) levels of the Fossil Cliff and Callytharra Formations (Western Australia).

Dickinsartella pistacina sp. n.

Plate 1, figs 22-24; Plate 2, figs 1-26; Plate 3, figs 1-8.

? 1959 *Stuchburia pallasi* (de Verneuil). Hudson & Sudbury, p. 23 (*n.n.*)

? 1977 *Cypricardinia*? sp. Dickins & Shah, pp. 32-33 (*n.n.*)

Etymology: name derived from the similarities of the shell with a pistachio, *pistacium* in latin.

Material: type series (28 specimens) from site I5 plus 7 specimens (MPUM9031.1.X.a, -g) from site I5 used in microstructural analysis and one specimen (MPUM9032.X.1) from OL130,

Type series: holotype: MPUM9030 (Pl. 2, figs 2, 9a, -b) and 27 paratypes: MPUM9031.1.1, – 1.23, MPUM9031.5.1, MPUM9031.a, -.b, -.c (Pl. 1, fig. 22-24; Plate 2, fig. 1, 3-8, 10-26).

Type horizon: "*Pachycyrtella* Bed" (bed OL14 in Angiolini et al. 1997), base of the Saiwan Formation at Saiwan.

Type locality: Saiwan (Interior Oman).

Age: Sterlitamakian (late Sakmarian, Early Permian).

Diagnosis. Shell small, sub-rectangular in outline, anteriorly truncated, dorsal and ventral margins rectilinear and sub-parallel. Highly prosocline and inflated. Shallow, broad sinus in the anteroventral margin of the largest specimens. Hinge on the left valve with one small pseudo-cardinal tooth, two anterior teeth, the anteriorless of which rather strong, and two long laminar posterior teeth sub-parallel to the hinge margin; right valve with one pseudo-cardinal, one anterior tooth and two long laminar posterior teeth sub-parallel to the hinge margin. Ornamentation given by concentric imbricated lamellae.

Description. The shell is equivalve, rather inflated, the valves are strongly inequilateral, the umbones are at the first quarter of shell length from the anterior margin. The outline is from sub-rectangular to slightly modioliform, the dorsal and ventral margins are rather rectilinear and sub-parallel. The ventral margin exhibits a shallow, broad sinus, particularly visible in some specimens (Pl.2, fig.8, 15a); this sinus is the effect on the ventral margin of a shallow groove which crosses the umbo. Posterior border rounded. The lunula and the escutcheon are lacking.

In some specimens the two anterior teeth on the left valve could appear united along the lower margin of the hinge.

Specimen		Dimensions (in mm).		
Number	Picture	Length	Height	Thickness
MPUM9030 (R)	Pl.2, fig.2, 9a,-b	21.4	14.7	5.1
MPUM9031.1.1 (R)	Pl.2, fig.17	21.3	14.3	5.4*
MPUM9031.1.2 (B)	Pl.2, fig.8	26.9	16.8	
MPUM9031.1.3 (R)	Pl. 1 fig.23, Pl.2, fig.14	22.1	15.4	5.9*
MPUM9031.1.4 (L)	Pl.1, fig.24	15.2	10.8	4.3*
MPUM9031.1.5 (B)	Pl.2, fig.20a,-c	18	11.1	
MPUM9031.1.6 (B)	Pl.2, fig.15a,-b	20	13.1	11.4*
MPUM9031.1.7 (B)	Pl.2, fig.3	19.1		
MPUM9031.1.9 (L)	Pl.2, fig.4		14.3	5.1
MPUM9031.1.10 (L)	Pl.2, fig.1, 6a,-b		13.5	
MPUM9031.1.12 (B)	Pl.2, fig.7	11.2	8.3	4.7
MPUM9031.1.13 (B)	Pl.2, fig.11	10.2	6.6	4.3
MPUM9031.1.15 (R)	Pl.2, fig.21	14.3	9.8	3.9
MPUM9031.1.18 (B)	Pl.2, fig.18	7.9	5.2	
MPUM9031.1.22 (B)	not illustrated	20.3	13	11.8
MPUM9031.1.23 (L)	not illustrated	17	11.2	4.5
MPUM9031.5.1 (R)	Pl.2, fig.22	18.1	12.8	5.7*
MPUM9031.a (B)	Pl.2, fig.23a,-b	16.9		9.8
MPUM9031.b (L)	Pl.2, fig.12	15.5	11	
MPUM9031.c (B)	Pl.2, fig.5	18.3	13.6	
MPUM9032.X.1 (R)	Pl.2, fig.24	29	17.1	17.9*

*specimen encrusted by bryozoans

On the internal mould of many specimens a thin posterior umbonal ridge is present, starting on the umbo and ending on the ventral margin, and indistinguishable on the outer surface of the shell.

Integripalleate, isomyarian.

The ornamentation consists of concentric growth lamellae which become wider with maturity.

The presence of very thin radial lines on some specimens (Pl. 2, figs. 20a, 20c) is only the effect of weathering and corrosion of the outer shell layers.

Shell microstructure (Pl. 3). The microstructure of the outer shell layer in *Dickinsartella pistacina* sp. n. is not well preserved. It is likely that it was formed by a very thin ISP outer layer and a thick middle (?) layer, probably with a diffuse simple CL or BCL structure which thickened distally. The outer layers often show traces of burrowing organisms inside the test (Pl. 3, figs. 5, 6). The inner shell layer is composed by CL to CCL.

Discussion. *Dickinsartella pistacina* sp. n. differs from *Dickinsartella elegantula* (Dickins, 1963) in the outline, which is more sub-rectangular and with a rectilinear anterior margin; dorsal and ventral margins rectilinear and sub-parallel. There are also some slight differences in the hinge. Dickins (1963), in the original description of *D. elegantula*, mentions only two "cardinal teeth", but in the discussion he reports "two oblique cardinal teeth and possibly a third"; this uncertainty could result from poor preservation. In the specimens from Oman a small pseudo-cardinal tooth on the left valve could easily have been removed by abrasion. Nevertheless, the distance between the shell margin and the nearest anterior tooth in *D. elegantula* is very reduced and this tooth could be missing.

Dickinsartella? *gregaria* (Etheridge, 1900) is known only by few poorly preserved specimens which differ from *Dickinsartella pistacina* in the narrower hinge-plate.

Dickinsartella pistacina differs from *Cypricardinia*? *precordillerana* González, 1997 in its outline, less extended anteriorly, and in the large umbo.

Cypricardinia? *boliviana* Rocha, De Carvalho & Amos, 1977 and *Cypricardinia*? *boliviana* Licharew (Newell 1955) are similar in shape to *Dickinsartella pistacina* sp. n., but exhibit distinct radial ribs.

Remarks on synonymy. Dickins & Shah (1977) mentioned *Cypricardinia*? sp. from the *Bellerophon* Limestone (Saiwan Formation p.p.); according to them *Cypricardinia* ? sp. was listed by Cox as "*Stuchburia*" (as *Stuchburia pallasi* de Verneuil, in particular). Probably these specimens belong to *Dickinsartella pistacina* sp. n., because of the large abundance of specimens mentioned by Cox (in Hudson & Sudbury 1959), although the synonymy is doubtful for the absence of descriptions and figures of these specimens. The specimens of *D. pistacina* sp. n. studied in the present paper were attributed to *Cypricardinia*? sp. in Angiolini et al. (2003b).

Subclass **Heteroconchia** Hertwig, 1895

Order **Modiomorphoida** Newell, 1969

Superfamily Modiomorphoidea Miller, 1877

Family Permophoridae Van de Poel, 1959 (Dall, 1895)

Genus *Stutchburia* Etheridge, 1900

Type species: *S. costata* (Morris, 1845)

Discussion. Etheridge (1900) erected *Stutchburia* in order to include Permo-Carboniferous equivalve, transversely elongate shells, with an edentulous hinge. The author included in the genus five species rather different in the shape and ornamentation, such as the type species *S. costata* (Morris, 1845) or *S. farleyensis* Etheridge, 1900 from the Lower Permian levels of the Illawarra District (Australia).

S. costata exhibits a sub-quadrate to modioliform outline, generally posteriorly higher than anteriorly, radial ribs on the posterior part of the shell (also visible on the internal cast) and the anterior muscle scar on a buttress. On the contrary, *S. farleyensis* exhibits a subquadrate outline, anteriorly higher than posteriorly, without radial ribs, with anterior and pedal scars deeply incised but without buttress or myophoric ridge.

The already large generic diagnosis was modified and further enlarged by subsequent authors and at present *Stutchburia* includes forms different in shape, ornamentation and hinge. The hinge in particular, according to Logan (1967), exhibits poorly developed or absent cardinal teeth (2 and 3b), with the lateral PII of the left valve often present. Dickins (1963) considered the presence or absence of a postero-lateral tooth in the left valve as variable feature (opinion later accepted by Logan 1967).

Stutchburia probably should be revised and its meaning clarified, in order to verify the real intra-specific variability of characters which could be considered of generic rank.

Stutchburia could be narrowed to the morphological group represented by the type species *S. costata* and by the most similar species, with a sub-quadrate to modioliform outline and more or less developed radial ribs, whereas a new genus could be erected for *S. farleyensis* Etheridge, 1900 and similar species. In addition, the anterior adductor muscle scar of *S. costata* is posteriorly bounded by a well-developed myophoric ridge or buttress (Dickins 1963; Logan 1967); this seems typical of the Permophoridae, in which *Stutchburia* is placed with general agreement (e. g. Cox et al. 1969b: N548). The generic diagnosis, together with the diagnosis of the Myoconchinae Newell, 1957 and Permophoridae Van de Poel, 1959 (Dall, 1895), as proposed by Cox et al. (1969b), should be adequate to identify *Stutchburia*. Nevertheless, these topics require more in-depth investigation.

A revision of *Stutchburia* is largely beyond the purpose of this paper, thus the wide meaning of this genus was accepted.

Stutchburia sangallii sp. n.

Pl. 4, figs 1-22; Pl. 5, figs 1-10.

Etymology: in honour of Monica Sangalli.

Material: the type series (20 specimens) from site I5, 3 specimens (MPUM9035.1.X.a, -c) from the same site used in microstructural analysis and 1 specimen (MPUM9035.1) from site OL130.

Type series: holotype: MPUM9033.1, (Pl. 4, Figs 19, 21), paratypes: (19 specimens) MPUM9034.1.1, -1.14, MPUM9034.2.1, -2.3, MPUM9034.3.1, MPUM9034.5.1 (Pl. 4, Figs 1-18a, 20, 22)

Type horizon: "*Pachycyrtella* Bed" (bed OL14 in Angiolini et al. 1997), base of the Saiwan Formation at Saiwan.

Type locality: Saiwan (Interior Oman).

Age: Sterlitamakian (late Sakmarian, Early Permian).

Diagnosis. Shell small, equivalve, strongly inequilateral valve, long and narrow trigonally sub-oval in outline, anterior margin poorly developed and little protruding, beaks acute; lunula and escutcheon present, lunula deeply impressed, escutcheon flat. Ligament tubular opisthodetic placed in a deep ligament groove bordered by nymphs. Hinge edentelous or with a weak tooth-like protrusion under the umbo of the left valve. Integripalleate, sub-isomyarian, with adductor muscle scars deeply impressed. Ornamented only by strong, regularly widely spaced, concentric imbricated lamellae.

Description. Shell small (maximum size 20 mm), equivalve, valve strongly inequilateral and transversally oblong. The umbones are prominent, prosogyrate, the acute beaks are placed in the anterior half of the length. The escutcheon is rather impressed, whereas the deeply impressed lunula lies beneath the incurved beaks.

Hinge without well-defined cardinal and lateral teeth or in some specimens with only a weak tooth-like laminar protrusion under the umbo of the left valve parallel to the hinge margin (MPUM 9034.1.1, Pl.4, figs 5a, -b; MPUM9034.1.8, Pl.4, figs 6a, -6b).

A deep sunken ligamental nymph lies posteriorly to the beaks and develops on nearly 1/4 of the dorsal margin. Some specimens exhibit the preserved tubular opisthodetic ligament, lodged in a deep ligament groove, posteriorly to the beaks.

An entire pallial line is well displayed and it makes a regular curve from the anterior adductor, curving sharply back to meet the posterior one from a postero-ventral direction.

Sub-isomyarian, with the posterior adductor muscle scar slightly larger than the anterior; both adductor muscle scars are well impressed, with the anterior one most impressed.

The presence of other muscle scars over the adductors in *S. sangallii* sp. n. is questionable because of the preservation of the specimens; only one specimen (MPUM9034.1.1) shows a weak trace doubtfully attributable to a pedal muscle scar; this observation was not confirmed by other specimens, most of which are still articulated.

Ornamentation given by sharp concentric imbricated lamellae (nearly 10 in the largest specimens), distinctly marked at irregular intervals. Some specimens exhibit a weak posterior umbonal ridge (MPUM 9034.1.1, Pl. 4, figs. 5, 10), more visible on the internal mould (MPUM9034.2.3).

Specimen		Dimensions (in mm).		
Number	Picture	Length	Height	Thickness
MPUM 9033.1 (R)	Pl.4, fig.19, 21	15.8	9	3.6
MPUM 9034.1.1 (L)	Pl.4, fig.5a, -b	14.8	8.3	2.5
MPUM9034.1.2 (B)	Pl.4, fig. 10	12.9	7.2	4.4
MPUM9034.1.3 (L)	Pl.4, fig. 8a, -b		6.9	2
MPUM9034.1.4 (B)	Pl.4, fig. 15a, -b	9.4	6	4.2
MPUM9034.1.5 (B)	Pl.4, fig. 17	14.2	7	4.8
MPUM9034.1.6 (B)	Pl.4, fig. 18a, -b	15.7		5.2
MPUM9034.1.7 (B)	Pl.4, fig. 4	14	8.2	
MPUM9034.1.8 (L)	Pl.4, fig. 6a, -6b	12.1	7	2
MPUM9034.1.9 (L)	Pl.4, fig. 3a, -b	19.1	11.3	2.5
MPUM9034.1.10 (B)	Pl.4, fig. 12a, -b	13.1	8.1	4.5
MPUM9034.1.11 (B)	Pl.4, fig. 20	15.5	9	5.1
MPUM9034.1.12 (B)	not illustrated		7.8	4.9
MPUM9034.1.13 (B)	not illustrated	13.9	8.2	4.9
MPUM9034.1.14 (R)	Pl.4, fig.1	9.5	6.2	2
MPUM9034.2.1 (R)	Pl.4, fig. 11a, -b	10.2	6.6	2
MPUM9034.2.2 (R)	Pl.4, fig. 16		5.9	1.9
MPUM9034.3.1 (B)	Pl.4, fig.14	10.6	5.8	4.3
MPUM9034.5.1 (R)	Pl.4, fig. 7	13.1	7.9	2.2

Shell microstructure (Pl. 5). In acetate peels the outer prismatic layer is difficult to distinguish from the underlying thicker middle shell layer. The outer layer is probably composed of FP to ISP. The middle shell layer is composed of CL to BCL. The inner shell layer seems mainly ISP to ICCL. Some specimens exhibit the fibrous inner part of the ligament (Pl. 5, fig. 4).

Discussion. *Stutchburia sangallii* sp. n. differs from *S. muderongensis* Dickins, 1956 from the Coolkilya Greywacke (Kungurian) of the Carnavaron Basin (Western Australia), and from *S. variabilis* Dickins, 1957 from the top beds of Lyons Group of the Carnavaron Basin (Kungurian), in the more prominent umbo and the stronger, regularly spaced, growth lamellae; besides, no specimen of *S. sangallii* sp. n., sampled to date from the *Pachycyrtella* Bed, exceeds 20 mm of length, whereas *S. muderongensis* and *S. variabilis* may exceed 40 mm.

Among the species included by Etheridge (1900) in the original definition of *Stutchburia*, *S. sangallii* sp. n. shows more similarities with *S. farleyensis* Etheridge, 1900 than with *S. costata* (Morris, 1845), type-species of the genus. The type series of *S. farleyensis* is composed only by internal casts; *S. sangallii* sp. n. differs from this species in the outline more triangular and in the more impressed anterior adductor muscle scar.

S. sangallii sp. n. differs from *S. costata* (Morris, 1845) in outline, hinge and ornamentation. In *S. sangallii* sp. n. the outline, from sub-triangular to sub-oval, always shows the maximum height in correspondence of the beaks; the ornamentation is always without radial ribs and made only by growth lamellae, the hinge lacks lateral tooth. In *S. sangallii* sp. n. the anterior adductor scar is deeply impressed, nevertheless it does not exhibit a myophoric ridge.

S. sangallii sp. n. shows some resemblances with a few species of the Mesozoic *Cardinia* Agassiz, 1841, like C. *concinna* (Sowerby, 1819) or *C. attenuata* (Stutchbury, 1842), in its outline ("Concinnoids" by Palmer 1975 or "*Concinna* Group" by Hayami 1958), shape of the lunula and escutcheon, ornamentation and adductor muscle scars. Important differences are present in the dentition: the hinge of *S. sangallii* sp. n. is lacking the lateral teeth of the Cardiniidae Zittel, 1881. *S. sangallii* sp. n. differs from some species of the genus *Unionites* Wissmann, 1841 in the absence of lateral teeth and for its more developed and deeper lunula; it differs from the species of *Anodontophora* Cossmann, 1897 (placed in synonymy with *Unionites* by Cox et al. 1969b, N468) in the absence of lateral teeth and in its less developed cardinal plate.

S. sangallii sp. n. shows similarities with "*Anodontophora*" *purdoni* Reed, 1944 and "*Cardinia*" *conjungens* Waagen, 1881 from the Wordian Amb Formation ("Lower *Productus* Limestone") of the Salt Range (Pakistan). "*Anodontophora*" *purdoni* shows a similar outline and ornamentation and exhibits an edentulous hinge; no information is available about the muscle scars. More doubtful is the position of "*Cardinia*" *conjungens*, which does not show internal characters; it was compared by Reed (1944) with "*Anodontophora*" *purdoni* and placed in the same genus. *S. sangallii* sp. n. differs from these species in its more developed trigonal outline, its more truncated anterior margin, the narrow umbo and its reduced size.

Remarks on microstructure. *S. sangallii* sp. n. shows many similarities in the microstructure of the three main shell layers and in the probable absence of nacre, with other permophorids like *Curionia gracilis* (Klipstein, 1848), *Permophorus* sp. and *Curionia paronai* (Bittner, 1895), according to the description of Carter (1990) and Schneider & Carter (2001).

There are also similarities with *Septocardia crenata* in the development and composition of the outer and middle shell layers; nevertheless, *S. crenata* exhibits a predominantly ICCL-CCL (the outer part) and matted (the inner part) inner shell layer, even if the ISP can be locally present (Schneider & Carter 2001). There are also some similarities with the microstructure of the post Devonian crassatelloideans, prevalently in the mostly inner ISP layer and in the absence of nacre (cfr. Schneider & Carter 2001). Schneider & Carter (2001) considered the absence of nacre as an important character to distinguish the Modiomorphidae Miller, 1877 from the Permophoridae inside the Superfamily Modiomorphoidea Miller, 1877.

According to these Authors the combined microstructural and morphological data set suggests that the modiomorphoideans are basal to the crassatelloideans. The new data provided by *S. sangallii* sp. n. support the hypothesis of a close link between permophorids and crassatelloideans.

Remarks on synonymy. The specimens of *S. sangallii* sp. n. from the *Pachycyrtella* Bed were attributed to *Stutchburia* sp. in Angiolini et al. (2003b).

Order **Veneroida**, H. Adams & A. Adams, 1856
Superfamily Crassatelloidea Férussac, 1822
Family Crassatellidae Férussac, 1822
Subfamily Crassatellinae Férussac, 1822
Genus *Oriocrassatella* Etheridge, Jr., 1907

?Oriocrassatella sp.

Pl. 1, fig. 15a, 15b

Material: only one articulated specimen MPUM9027, from site OL130.

Specimen		Dimensions (in mm)		
Number	Picture	Length	Height	Thickness
MPUM 9027 (B)	Pl. 1, fig. 15a,-b	13	9.6	4.3

Discussion. Only one specimen of a doubtful *Oriocrassatella* Etheridge, Jr., 1907 was collected from the *Pachycyrtella* Bed in the locality of Saiwan by L. Angiolini and A. Tintori during the field work of 2000. In spite of the poor preservation of the specimen, it is appropriate to shortly mention its discovery because of the palaeoecological and palaeogeografical importance of *Oriocrassatella* (Dickins 1996).

The preservation is not satisfactory for a specific and generic certain attribution because the surface is weathered and the concentric growth-lines are not preserved; nevertheless, the shape of the shell resembles that of the Sakmarian *Oriocrassatella queenslandica* Dickins, 1961 from the Bowen Basin in Queensland (Eastern Australia). The appearance of *Oriocrassatella* in this region is considered by Dickins (1996) as an indication of warmer conditions.

The rarity of this genus in the *Pachycyrtella* Bed at Saiwan could be related to palaeoecological reasons.

Family Astartidae d'Orbigny, 1844

Genus *Astartella* Hall, 1858

Type species (by monotypy, fide Nicol, 1955): *Astartella vera* (Hall, 1858)

Astartella obliqua Dickins, 1963

Pl. 1, figs 12-14, 16-21

? 1959 *Astartella permocarbonica* Hudson & Sudbury, p. 22, 23 (*nn*).

1963 *Astartella obliqua* Dickins, p. 105, pl. 16, fig. 2-9.

? 1977 *Astartella* cf. *obliqua* Dickins & Shah, p. 33 (*nn*).

Material: nine specimens, seven articulated, one left valve and one right valve, from site I5 (MPUM9028) and from site OL130 (MPUM9029).

Description. Shell equivalve, inequilateral valves, hinge with two cardinal teeth on each valve. The escutcheon is well developed while the lunula is poorly developed. Ligament small, tubular opisthodetic, lodged between the nymphae and the main part of the shell, posteriorly from beaks.

Crenulations consisting of pits present inside of shell margin.

Ornamentation given by concentric growth lines, distinctly marked at irregular intervals.

Specimen		Dimensions (in mm).		
Number	Picture	Length	Height	Thickness
MPUM9028.1-1 (L)	Pl.1, fig. 17a,-c	9.2	8.9	2.1
MPUM9028.1-2 (R)	Pl.1, fig. 21a,-b	9.4	9.3	2.7
MPUM9028.1-3 (B)	Pl.1, fig. 12	12.2	11.8	
MPUM9028.1-4 (B)	Pl.1, fig. 13	11.3	11.1	5.3
MPUM9029.X.1 (B)	Pl.1, fig. 20a,-b	8.8	8.1	4.1
MPUM9029.X.2 (B)	Pl.1, fig. 18a,-b	8.2	7.8	3.8
MPUM9029.X.3 (B)	Pl.1, fig. 19	8.1	7.8	4.1
MPUM9029.X.4 (B)	Pl.1, fig. 14	9.0	8.1	4.9
MPUM9029.X.5 (B)	Pl.1, fig. 16	8.2	8.0	4.7

Discussion. The specimens are very similar to the types of *Astartella obliqua* Dickins, 1963 and their characters coincide with the description of this author.

Remarks on synonymy. Hudson & Sudbury (1959) reported *Astartella permocarbonica* (Tschernyschew, 1885) from the Saiwan Formation (i.e. *Metalegoceras* and *Bellerophon* Limestones), and Dickins & Shah (1977) mentioned *Astartella* cf. *obliqua* from the *Bellerophon* Limestone; synonymy is doubtful because the authors neither describe nor illustrate the specimens.

Some particularly well-preserved specimens (Pl. 1, figs. 18a, 18b, 20a, 20b; OL130) show the preserved opisthodetic ligament, lodged between the nymphae and the principal part of the shell.

Occurrence and age. The species is widespread geographically in the Perth and Canning Basins of Western Australia and in the Saiwan Formation of Interior Oman. *Astartella obliqua* Dickins, 1963 is a typical Sakmarian form.

Acknowledgments. Few months have gone by since Dr James MacGregor Dickins prematurely left us; his publications represent a milestone in the field of Permian bivalves and I was honoured by his critical reviews and suggestions which much improved this paper.

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I am deeply indebted with Lucia Angiolini for the fruitful reviews that improved the manuscript. The financial support has been provided by the Peritethys Project.

PLATE 1

Figg. 1-8	- *Promytilus mazzolenii* sp. n.
Fig.1a, -b	- Holotype MPUM9026.1.1, articulated specimen x 2, a: left valve, b: right valve.
Fig. 2	- Paratype MPUM9026.1.4, articulated specimen x 2.3, right valve.
Fig. 3	- Paratype MPUM9026.1.5, articulated specimen x 2, right valve.
Fig. 4a, -b	- Paratype MPUM9026.3.2, articulated specimen x 2.6, a: left valve, b: right valve.
Fig. 5	- Paratype MPUM9026.1.10, articulated specimen x 2.2, right valve, external view.
Fig. 6	- Paratype MPUM9026.1.2, articulated specimen x 2, left valve.
Fig. 7	- Paratype MPUM9026.1.7, articulated specimen x 2.2, right valve, external view.
Fig. 8	- Paratype MPUM9026.1.3, articulated specimen x 3.75, internal mould, left valve.
Figg. 9-11	- *Nuculopsis* cf. *bangarraensis* Dickins, 1963:
Fig. 9a, c	- MPUM9025.1.11, articulated specimen x 3.3, a: right valve, b: posterior view, c: antero-dorsal view.
Fig. 10	- MPUM9025.3.4, articulated specimen x 3.5, a: right valve, b: anterior view.
Fig. 11	- MPUM9025.2.3, articulated specimen x 2.2, posterior view.
Figg. 12-14	- *Astartella obliqua* Dickins, 1963.
Fig. 12	- MPUM9028.1.3, articulated specimen x 2.5, left valve.
Fig. 13	- MPUM9028.1.4, articulated specimen x 2.7, left valve.
Fig. 14	- MPUM9029.X.4, articulated specimen x 2.7, left valve.

Fig. 15a, -b - ?*Oriocrassatella* sp., MPUM9027, articulated specimen x 2.5, a: left valve, b: right valve.
Figg. 16-21 - *Astartella obliqua* Dickins, 1963.
Fig. 16 - MPUM9029.X.5, articulated specimen x 2.9, right valve.
Fig. 17a, -c - MPUM9028.1.1, left valve, a: hinge x 6, b: external view x 2.7, c: internal view x 2.7.
Fig. 18a, -b - MPUM9029.X.2, articulated specimen, a: dorsal view x 3, b: ligament x 8.
Fig. 19 - MPUM9029.X.3, articulated specimen x 2.7, right valve.
Fig. 20a, -b - MPUM9029.X.1, articulated specimen, a: ligament x 9, b: dorsal view x 3.
Fig. 21a, -b - MPUM9028.1.2, right valve x 2.5, a: external view, b: internal view.
Figg. 22-24 - *Dickinsartella pistacina* gen. n. sp. n.
Fig. 22 - Paratype MPUM9031.1.19, articulatedd specimen x 2, encrusted by bryozoans.
Fig. 23 - Paratype MPUM9031.1.3, right valve x 2, encrusted by bryozoans.
Fig. 24 - Paratype MPUM9031.1.4, left valve x 2.3, encrusted by bryozoans.

PLATE 2

Figs. 1-26 - *Dickinsartella pistacina* gen. n. sp. n.
Fig. 1 - Paratype MPUM9031.1.10, left valve x 5, internal view of the cardinal plate (detail of Fig. 6a).
Fig. 2 - Holotype MPUM9030, right valve x 5, internal view of the cardinal plate (detail of Fig. 9b).
Fig. 3 - Paratype MPUM9031.1.7, articulated specimen x 2, anterior view.
Fig. 4 - Paratype MPUM9031.1.9, left valve x 1.75, external view.
Fig. 5 - Paratype MPUM9031.c, articulated specimen x 1.8, right valve, external view.
Fig. 6a, -b - Paratype MPUM9031.1.10, left valve x 1.75, a: internal view, b: external view.
Fig. 7 - Paratype MPUM9031.1.12, articulated specimen x 2.5, right valve, external view.
Fig. 8 - Paratype MPUM9031.1.2, articulated specimen x 1.5, left valve, external view.
Fig. 9a, -b - Holotype MPUM9030, right valve x 2, a: internal view, b: external view.
Fig. 10 - Paratype MPUM9031.1.20, articulated specimen x 1.7, anterior view.
Fig. 11 - Paratype MPUM9031.1.13, articulated specimen, left valve x 2, external view.
Fig. 12 - Paratype MPUM9031.c, left valve x 1.6, external view.
Fig. 13 - Paratype MPUM9031.1.16, left valve x 2, internal view.
Fig. 14 - Paratype MPUM9031.1.3, right valve x 2, internal view.
Fig. 15a, -b - Paratype MPUM9031.1.6, articulated specimen, a: anterior view, b: left valve x 2, external view.
Fig. 16 - Paratype MPUM9031.1.8, left valve x 1.8, internal view.
Fig. 17 - Paratype MPUM9031.1.1, right valve x 1.8, internal view.
Fig. 18 - Paratype MPUM9031.1.18, articulated specimen x 2.5, right valve, external view.
Fig. 19 - Paratype MPUM9031.1.17, right valve x 2.5, internal view.
Fig. 20a -b, -c - Paratype MPUM9031.1.5, articulated specimen, a: left valve, external view x 1.6, b: dorsal view x 1.6, c: particular of 20a x 3.5.
Fig. 21 - Paratype MPUM9031.1.15, right valve x 2, external view.
Fig. 22 - Paratype MPUM9031.5.1, right valve x 1.7, internal view.
Fig. 23a, -b - Paratype MPUM9031.a, articulated specimen x 1.8, a: dorsal view, b: anterior view.
Fig. 24 - MPUM9032.X.1, articulated specimen x 1.4, dorsal view.
Fig. 25 - Paratype MPUM9031.1.4, internal mould of a articulated specimen x 2, dorsal view.
Fig. 26 - Paratype MPUM9031.1.11, internal mould of a articulated specimen x 2.3, left valve.

PLATE 3

Figs. 1-9 - *Dickinsartella pistacina* gen. n. sp. n., acetate peels showing details of the microstructure.
Fig. 1 - MPUM9031.1.X.g, radial, dorsoventral section, a: detail in fig. 9, b: detail in fig. 3.
Fig. 2 - MPUM9031.1.X.f, vertical dorsoventral section, a: detail in fig. 4, 1: CL to CCL inner shell layer, 2: simple CL middle (?) shell layer.
Fig. 3 - MPUM9031.1.X.g, detail b of fig. 1, 1: CL to CCL inner shell layer, 2: simple CL middle (?) shell layer.
Fig. 4 - MPUM9031.1.X.f, detail a of fig. 2, PB: possible pallial band, 2: simple CL middle (?) shell layer.
Fig. 5 - MPUM9031.1.X.a, radial dorsoventral section, detail a of fig. 6, 1: CL to CCL inner shell layer, PB: possible pallial band, 2: simple CL middle (?) shell layer, the arrows indicate the traces of burrowing organisms inside the test.
Fig. 6 - MPUM9031.1.X.a, radial dorsoventral section through the inner and middle (?) shell layers, a: detail in fig. 5.
Fig. 7 - MPUM9031.1.X.f, vertical dorsoventral section near the ventral shell margin, 1: CL to CCL inner shell layer, 2: simple CL middle (?) shell layer, 3: possible ISP outer shell layer.
Fig. 8 - MPUM9031.1.X.f, vertical dorsoventral section, 1: CL to CCL inner shell layer, 2: simple CL middle (?) shell layer, 3: possible ISP outer shell layer.
Fig. 9 - MPUM9031.1.X.g, detail a of fig. 1, 1: CL to CCL inner shell layer, PB: possible pallial band, 2: simple CL middle (?) shell layer, 3: very thin possible ISP outer shell layer.

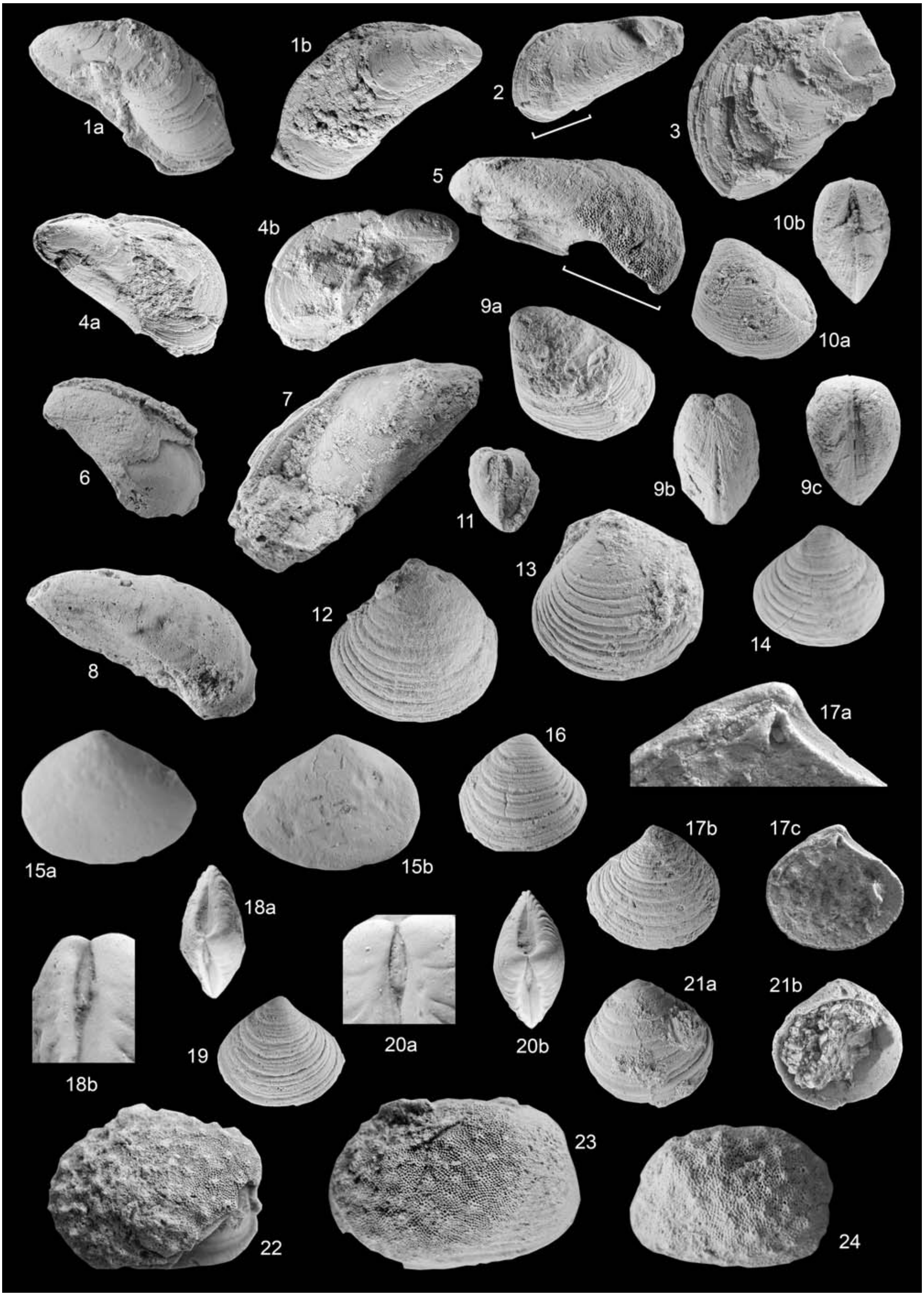
PLATE 4

Figs. 1-22 - *Stutchburia sangallii* sp. n.
Fig. 1 - Paratype MPUM9034.1.14, right valve x 2, external view.
Fig. 2 - MPUM9035.3, left valve x 2, external view.
Fig. 3a, -b - Paratype MPUM9034.1.9, left valve x 2, a: internal view, b: external view.
Fig. 4 - Paratype MPUM9034.1.7, articulated specimen x 2, left valve.
Fig. 5a, -b - Paratype MPUM 9034.1.1, left valve x 2.5, a: external view, b: internal view.

Fig. 6a, -b - Paratype MPUM9034.1.8, left valve x 3, a: internal view, b: external view.
Fig. 7 - Paratype MPUM9034.5.1, right valve x 2.5, external view.
Fig. 8a, -b - Paratype MPUM9034.1.3, left valve x 2.5, a: internal view, b: external view.
Fig. 9 - MPUM9035.2, articulated specimen x 2, left valve.
Fig. 10 - Paratype MPUM9034.1.2, articulated specimen x 2.6, left valve.
Fig. 11a, -b - Paratype MPUM9034.2.1, right valve x 3, a: external view, b: internal view.
Fig. 12a, -b - Paratype MPUM9034.1.10, articulated specimen x 2.8, a: right valve, b: anterior view.
Fig. 13 - MPUM9035.1, articulated specimen x 2.5, right valve.
Fig. 14 - Paratype MPUM9034.3.1, articulated specimen x 3, dorsal view.
Fig. 15a, -b - Paratype MPUM9034.1.4, articulated specimen x 3, a: right valve, b: anterior view.
Fig. 16 - Paratype MPUM9034.2.2, right valve x 3, internal view.
Fig. 17 - Paratype MPUM9034.1.5, articulated specimen x 2.7, right valve.
Fig. 18a, -b - Paratype MPUM9034.1.6, articulated specimen, a: dorsal view x 2.6, b: detail of ligament x 5.
Fig. 19 - Holotype MPUM 9033.1, left valve x 2.6, internal view.
Fig. 20 - Paratype MPUM9034.1.11, articulated specimen x 3, right valve.
Fig. 21 - Holotype MPUM 9033.1, detail of the cardinal margin x 6 (detail of Fig. 19).
Fig. 22 - Paratype MPUM9034.2.1, (fig. 12a, -b), right valve, detail of the cardinal margin x 8 (detail of Fig. 11b).

PLATE 5

Figg. 1-9 - *Stutchburia sangallii* sp. n., acetate peels showing details of the microstructure.
Fig. 1 - MPUM9035.1.X.b, radial dorsoventral section, a: detail in fig. 4, b: detail in fig. 2, c: detail in fig. 7.
Fig. 2 - MPUM9035.1.X.b (detail b of fig. 2), a: detail in fig. 3, b: detail in fig. 5.
Fig. 3 - MPUM9035.1.X.b, radial section through two imbricating growth lamellae (detail a of fig. 2), 1: ISP to ICCL inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.
Fig. 4 - MPUM9035.1.X.b, radial section immediately behind the umbones, PB: possible pallial band, L: ligament, 1: ISP inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.
Fig. 5 - MPUM9035.1.X.b, radial section through two imbricating growth lamellae (detail b of fig. 2), 1: ISP inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.
Fig. 6 - MPUM9035.1.X.a, vertical dorsoventral section, PB: possible pallial band, 1: ISP inner shell layer, 2: CL to BCL middle shell layer.
Fig. 7 - MPUM9035.1.X.b, detail c of fig. 2, 1: ISP to ICCL inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.
Fig. 8 - MPUM9035.1.X.b, radial section through two imbricating growth lamellae, 1: ISP to ICCL inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.
Fig. 9 - MPUM9035.1.X.b, radial dorsoventral section, 1: ISP to ICCL inner shell layer, 2: CL to BCL middle shell layer, 3: possible FP to ISP outer shell layer.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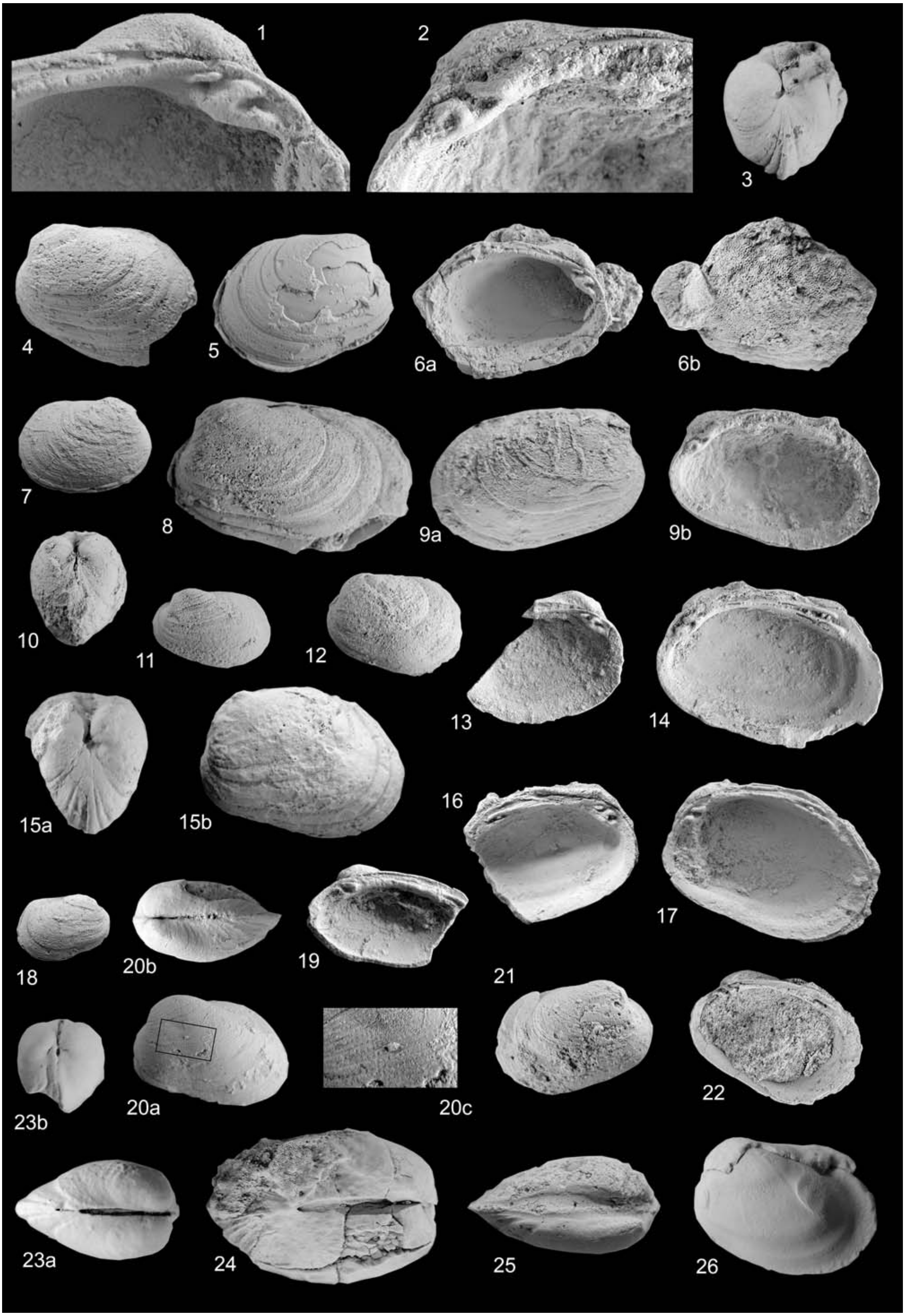
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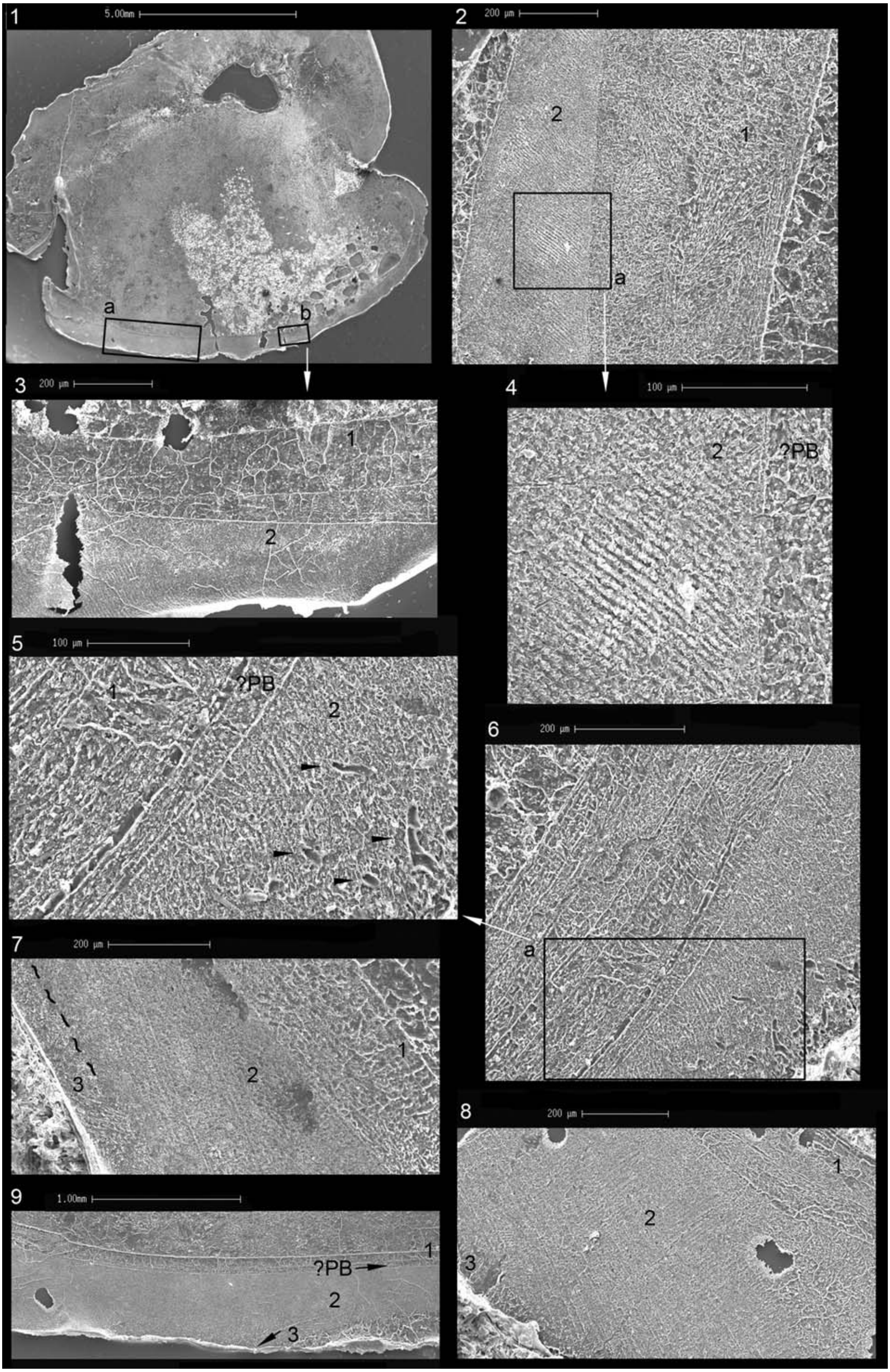
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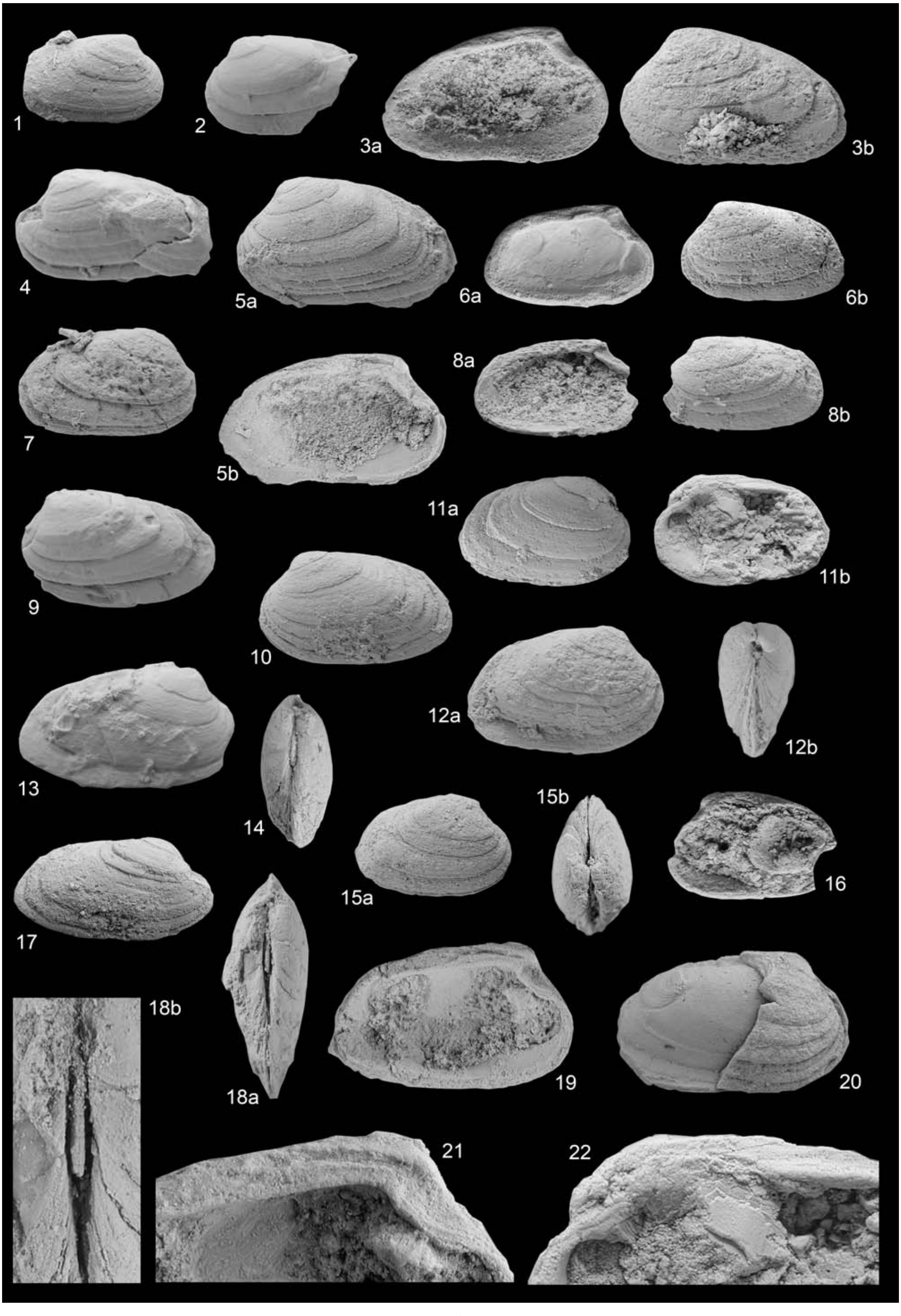
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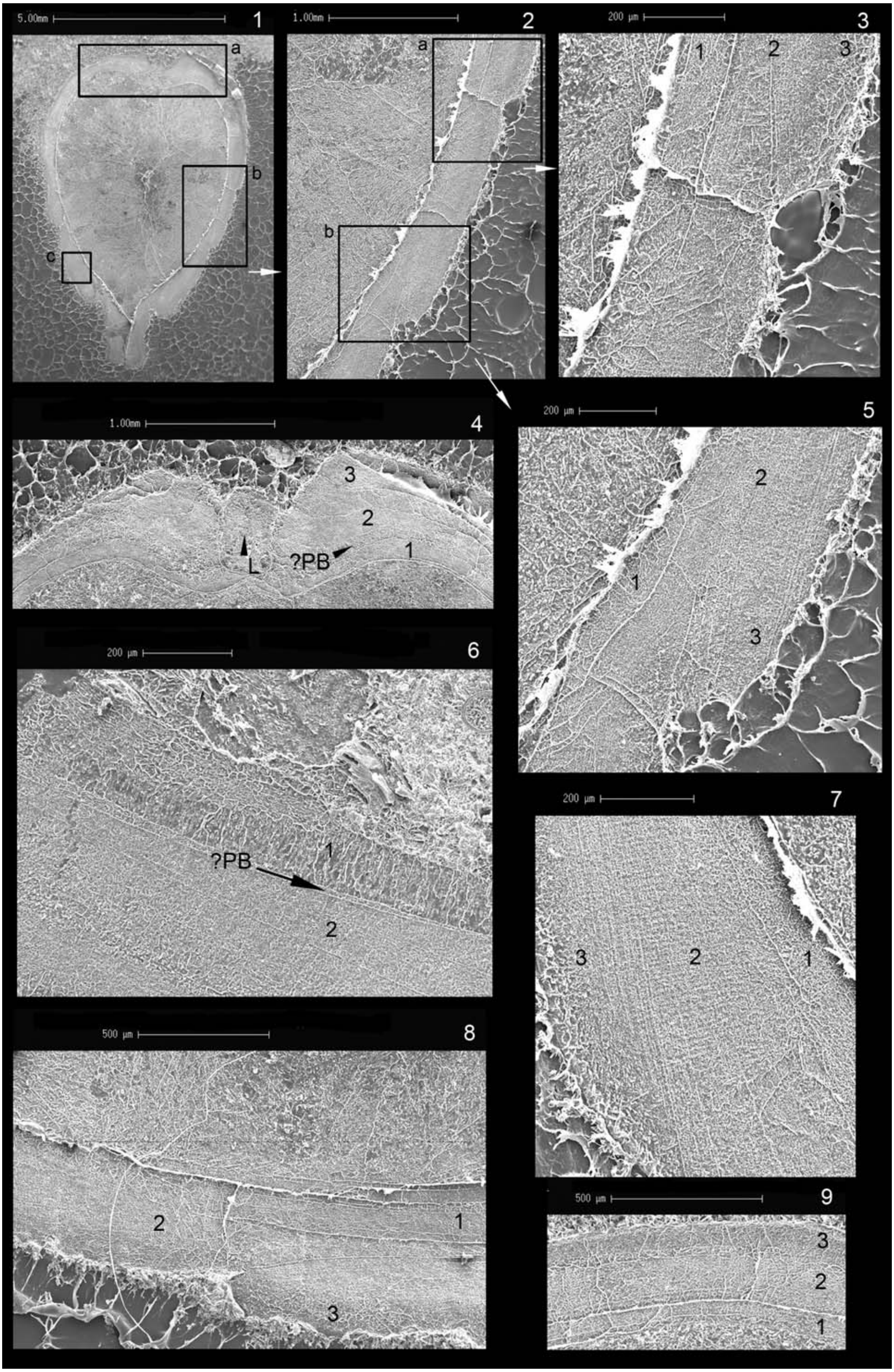
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PLATE 5

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