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Living in the shadow of brachiopods: bivalves from upper Visean (Mississippian) mud mounds of Derbyshire, UK

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ABSTRACT - Few studies have been conducted on Carboniferous marine bivalves in the British Isles and Ireland since pioneering studies performed during the 19th century. Herein, we examine from a systematic, taphonomic and palaeoecological point of view, the bivalve fauna occurring as a minor component of brachiopod-dominated fossil assemblages in upper Visean (upper Brigantian) mud mounds in the southern Peak District, Derbyshire (UK). Our results show moderate bivalve diversity, with the fauna being composed of eight genera, representing eight families in four orders (Nuculida, Arcida, Ostreida, Pectinida) and one superorder (Anomalodesmata). Sulcatopinna flabelliformis *(Martin, 1809),* Aviculopecten planoradiatus *M'Coy, 1851, and* Cosmomya variabilis *(M'Coy, 1851) are herein re-described. Taphonomic bias related to the early dissolution of the aragonitic shell of seminfaunal and infaunal taxa cannot account alone for the scarcity of bimineralic epifaunal pectinids. Indeed, the scarcity of bivalves is also likely due to the presence of the diverse brachiopod community, acting as competitive dominant and ecosystem engineer, well-adapted to the low-turbidity and mesotrophic environment of the mud mound.*

INTRODUCTION

Upper Palaeozoic bivalves have received relatively little attention in recent years, especially when compared to other marine invertebrate groups such as brachiopods, corals, and bryozoans. This is because they are usually not recorded in high numbers, particularly in limestone units, hampering their usefulness as tools for biostratigraphy, palaeoecology and palaeogeographic reconstructions. Analyses of diversity and dominance in late Palaeozoic ecosystems –both at the local (Watkins, 1973; Phelps, 2004) and global scales (Sepkoski, 1981; Clapham et al., 2006; Fraiser & Bottjer, 2007)– indicate that bivalves were generally less abundant and less diversified than other marine benthic organisms, such as brachiopods. However, the poor preservation potential of the aragonitic shell of many bivalve taxa in limestone successions may lead to an underestimation of their real distribution and abundance (Cherns & Wright, 2000, 2009). Furthermore, bivalves usually have greater biomass and higher metabolic rates than brachiopods (Ballanti et al., 2012), meaning that, even if they were not dominant in terms of abundance and diversity, they were playing a significant role in the energy flow of marine ecosystems since the Carboniferous (Payne et al., 2014; Hsieh et al., 2019). Thus, the study of the fossil record of upper Palaeozoic bivalves –even if limited and incomplete– is fundamental for reconstructing the palaeoecology of upper Palaeozoic seas and for better understanding the taxonomy and evolution of this group.

The Carboniferous successions of the British Isles and Ireland yield numerous and diverse marine bivalve fossils. A plethora of pioneering geological and palaeontological publications in the 19th century described their systematics and stratigraphic distributions, the most notable contributions being the ones by Phillips (1836) for central England and M'Coy (1844) for Ireland. All these works were summarised and reviewed in the monographs by Wheelton Hind, whose work focused first on bivalves from the ironstones and shales of the Coal Measures (Pennsylvanian; Hind, 1894, 1895, 1896a), and later extended the study to the material collected from every Carboniferous unit in the British Isles and Ireland (Hind, 1896b, 1897, 1898, 1899, 1900, 1901, 1903, 1904, 1905).

Hind presented the descriptions and figures of 340 bivalve species of 50 genera, of which 55 species were newly defined. Although valuable, his work is now in need of a modern revision. Unfortunately, only a little work on the systematics of Carboniferous marine bivalves from the British Isles was performed afterwards, with two main contributions: one, by Morris et al. (1991), was focused on the species of the Anomalodesmata, previously assigned to *Sanguinolites* M'Coy, 1844 and *Allorisma* King, 1844, including the ancestors of most of post-Palaeozoic taxa, the other, by Fang & Morris (1999), was focused on the genus *Aviculopecten*, a common genus used as a waste basket for many upper Palaeozoic pectinid species (32 species assigned by Hind, 1903). Graham (1988) described a new pterioid species from Namurian (Serpukhovian-Bashkirian) units in Scotland.

Interestingly, most of the species described by W. Hind seem to occur in the early Carboniferous (Mississippian): 176 species occur in the Tournaisian-Visean of England alone. However, most of these taxa are found in shale and ironstone units: "[Limestone] English deposits do not appear to contain a fauna by any means rich in Lamellibranchs. […] The Brachiopoda are by far the

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most common fossils in the Carboniferous limestone of England and Wales, both as regards numbers and wideness of distribution" (Hind, 1986: p. 4). The scarcity of bivalve fossils in Mississippian limestone units is further confirmed by later regional palaeontological studies by Wolfenden (1958) and Mitchell (1971) in Derbyshire, Mundy (1980) and Brunton & Mundy (1988) in Yorkshire, Brunton (1987) in Ireland and Wilson (1989) in Scotland. The reasons for the low abundance of bivalves in the Mississippian limestone have never been investigated in detail. Given their scarcity, bivalves have never been the primary focus of palaeoecological works on the Mississippian limestone in the British Isles, but just few considerations on substrate relationships of genera reported in faunal lists were included in studies dedicated primarily to the palaeoecology of brachiopods (Mundy, 1980; Brunton, 1987; Gutteridge, 1990).

Here we present for the first time a detailed systematic, taphonomic and palaeoecological study of bivalve fossils collected from the Mississippian limestone in England, in particular from brachiopod-dominated upper Visean (Mississippian, Carboniferous) mud mounds in Derbyshire. Mud mounds, i.e., carbonate buildups lacking a skeletal framework built by metazoans and consisting of a substantial amount of carbonate mud (> 30%, Bridges et al., 1995; > 50%, Reitner et al., 1995), are a peculiar type of reef which was very common in the Mississippian (Wright & Faulkner, 1990; Webb, 2002; Yao et al., 2016), but has no modern analogues (Wood, 2001); thus, their palaeoecology remains elusive. Previous research on the mud mounds in Derbyshire focused on the systematic and palaeoecological study of their abundant brachiopod fauna (Carniti et al., 2022, 2023) but to achieve the best possible comprehension of the mud mound ecosystem the role of other groups should be evaluated as well.

Furthermore, we provide full modern redescriptions of three bivalve species from the mud mounds, *Sulcatopinna flabelliformis* (Martin, 1809), *Aviculopecten planoradiatus* M'Coy, 1851 and *Cosmomya variabilis* (M'Coy, 1851), supported by the study of conspecific material from a number of other Mississippian localities in the UK housed at the Natural History Museum in London, improving the data availability on Carboniferous marine bivalve taxonomy.

GEOLOGICAL SETTING

The mud mounds cropping out in the southern Peak District region, White Peak, of northwestern Derbyshire, England (UK; Fig. 1a), occur in the uppermost part of the Monsal Dale Limestone Formation, Peak Limestone Group (Fig. 1b-c; Gutteridge, 1991, 1995). The formation is part of the succession of the Derbyshire Carbonate Platform, developed on a structural high to the north of the Wales-Brabant High (Aitkenhead & Chisholm, 1982), in subtropical palaeolatitudes (Piper et al., 1991). The Monsal Dale Limestone Formation is Brigantian in age (upper Visean; Lucas et al., 2022) and shows a variety of lithofacies: in the platform interior the formation consists of shallowing upward 0.5-5.0 m thick cyclothems, whereas to the east, in an area interpreted as an intraplatform basin with an east-ward dipping ramp profile, the formation consists of a variety of carbonate units deposited in normal marine, poorly oxygenated, hypersaline and brackish environments (Gutteridge, 1989, 2024).

The mud mounds developed in various depositional environments, ranging from the platform interior to the intraplatform ramp and basin (Gutteridge, 1995), below fair-weather wave base (Nolan et al., 2017; Carniti et al., 2023; Carniti, 2024). These decametre-scale, lens-shape buildups, frequently accreted in mud mound complexes, are characterised by: 1) a bedded basal unit consisting of skeletal packstone to wackestone with brachiopods and bryozoans, mainly fenestellids, and associated crinoids, calcified siliceous sponge spicules, bivalves, ostracods and benthic foraminifers; 2) a lens-shape massive core dominated by carbonate mud with textures indicative of both an origin as detrital micrite or as microbially-mediated precipitates, associated with abundant early-marine fibrous calcite cement and a faunal association similar to the one in the basal unit (Fig. 2a); 3) inclined flank beds consisting of skeletal packstone where the fossil assemblage is dominated by brachiopods and fenestellid bryozoans in the upper part of flank beds, richer in crinoids towards the off-mud mound units (Carniti et al., 2023). Off-mud mound areas in the outer platform consist of brachiopod-rich packstone in the northern region of the platform, crinoid-rich packstone to grainstone in the southern region; in the intraplatform basin, the shallower off-mud mounds units consist of crinoidal packstone, whereas in deeper environments of cherty brachiopod-rich packstone (Carniti et al., 2023; Carniti, 2024).

The basal unit crops out only at Ricklow Quarry, whereas the base of the other investigated mud mounds is not exposed. Brachiopods are widespread in the three units forming the mud mounds and quite diverse: the fauna consists of 45 species belonging to 36 genera and seven orders (Productida, Orthotetida, Orthida, Rhynchonellida, Spiriferida, Spiriferinida, Terebratulida; Carniti et al., 2022).

The mud mounds are capped by a regional subaerial exposure surface corresponding with the boundary between the upper Monsal Dale Limestone Formation and the overlying Eyam Limestone Formation (Fig. 1b; Adams, 1980; Gutteridge, 1991, 1995; Nolan et al., 2017).

MATERIAL AND METHODS

Fossil molluscs and brachiopods were collected from four different upper Visean mud mounds cropping out in the Peak District, Derbyshire (UK; Fig. 1b): Linen Dale Mud Mound near the village of Eyam (53°17'18" N, 01°42'15" W), Ricklow Quarry Mud Mound Complex near Monyash (53°11'30" N, 01°45'17" W), Bradford Dale Mud Mound Complex near Youlgreave (53°10'35" N, 01°40'24" W), National Stone Centre Mud Mounds near Wirksworth (53°05'36" N, 01°34'25" W). The Linen Dale Mud Mound and National Stone Centre Mud Mounds developed in the outer platform to the north and south respectively, whereas the Ricklow Quarry Mud Mound Complex and Bradford Dale Mud Mound Complex developed in the intraplatform basin with ramp profile.

Several fossil assemblages were collected from the core and flank beds of each mud mound. Bivalves occur alongside brachiopods in the core of Ricklow Quarry Mud Mound Complex (assemblages RCC10, RCC12), in the core (assemblages CNW2-16, CNW2-17, CNW2-30, CNW2-39, CNW2-40, CNW2-41B, CNW2-42, CNW2-43, CNW2-44, CNW2-45, CNW3, CNW14, CNW20) and flank beds (assemblage CNW1) of Linen Dale Mud Mound, in the core (assemblages CRH1, CRH2-18, CRH2-46, CRH2-62, CRH2-63, CRH16) and flank beds (CRH2-47) of Bradford Dale Mud Mound Complex, in the core (assemblages CNSC10, CNSC24, CNSC41) and flank beds (assemblage CNT2-33) of mud mounds at the National Stone Centre. The collection of a standard volume of rock was not possible due to the stiffness of the rock matrix, therefore sampling continued until no new species were found in each assemblage.

Bivalve specimens were cleaned and prepared for the analysis with air drills in order to remove the embedding rock and reveal diagnostic morphological characters. The length and the height of each specimen were measured using calipers (to the nearest 0.1 mm). Each specimen was labelled with a field number corresponding to the locality acronym (CNW- Linen Dale Mud Mound; RCC- Ricklow Quarry Mud Mound Complex; CRH- Bradford Dale Mud Mound Complex; CNSC-, CNT- National Stone Center Mud Mounds) plus the number of the assemblage, and a progressive number for each specimen. Museum numbers were also assigned to the specimens when housed in the Museo di Paleontologia dell'Università degli Studi di Milano (MPUM13478-13518): a single museum number was given for each figured specimen, whereas non-figured bivalve fossils of the same type (e.g., right valve) and taxon, from the same locality, were housed under the same museum number.

Each specimen was identified at generic and specific level with the traditional methods of identification. The majority of the specimens were identified to the species level, or to genus level when the preservation of the specimens did not allow species determination. The systematic study follows the classification of Carter et al. (2011) and of the World Register of Marine Species (WoRMS, 2024); morphological nomenclature follows Carter et al. (2012).

The systematic study also involved specimens housed at the Natural History Museum (NHM), London, with the prefix L- (general fossil bivalve collection) and PL- (Palaeozoic bivalve collection). The specimens investigated belong to various collections from the Mississippian of the British Isles by palaeontologists and fossil collectors in the 19th and 20th centuries, then donated or acquired by the museum. The most notable are the collections by George Highfield Morton (1826-1900), a Liverpool businessman who studied the Carboniferous of North Wales (Morton, 1886), and Wheelton Hind (1860-1920).

As the number of specimens for each assemblage is low, the number of specimens for each taxon was calculated for each of the four investigated localities as a whole (Tab. 1) as follows: number of articulated specimens, plus number of disarticulated valves of the most common type (right, left), adding half of the number of the other valve type, rounding up (following standard palaeoecological sampling procedures as in Di Geronimo

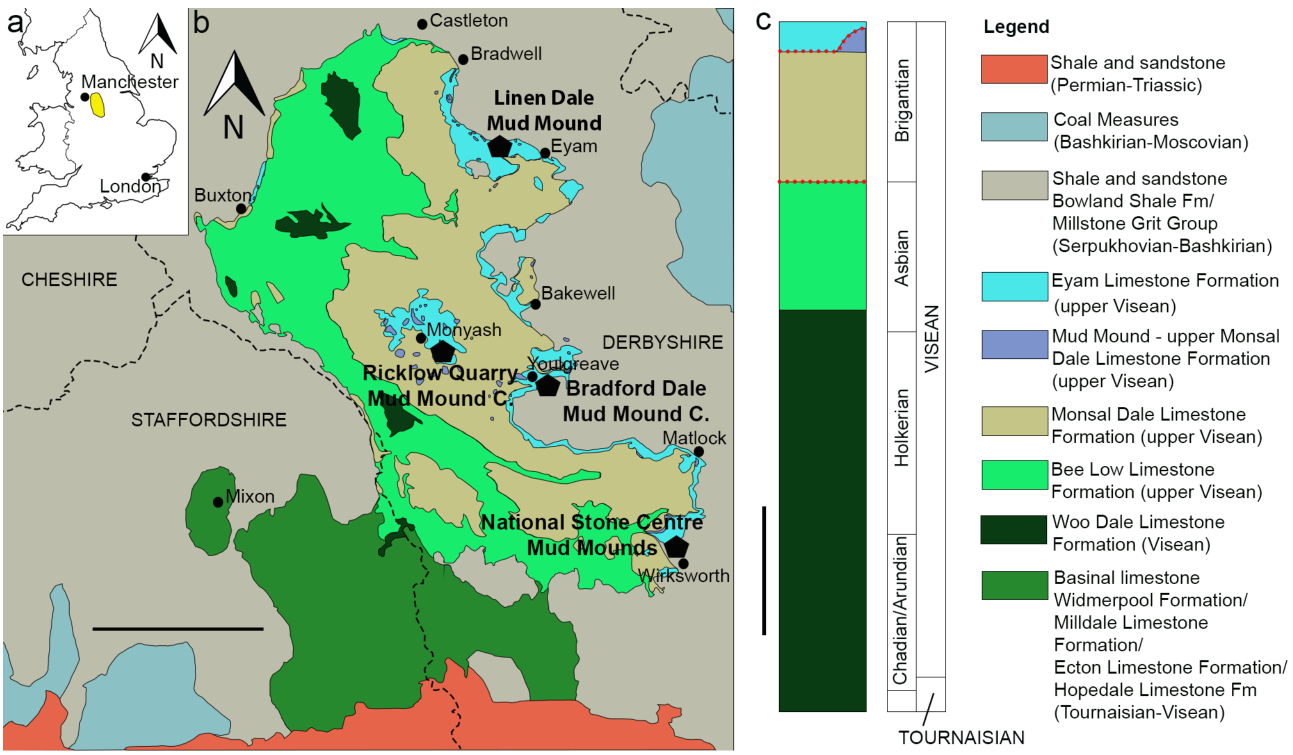


Fig. 1 - (color online) Geographical and geological setting of the upper Visean mud mounds in the southern Peak District, White Peak, Derbyshire (England, UK). a) Position of the Peak District in England (in yellow). b) Simplified geological map of the southern Peak District, White Peak, with the location of the studied sites. Modified after Aitkenhead & Chisholm (1982); Gutteridge (1987); Aitkenhead et al. (2002). Scale bar is 10 km. c) Stratigraphic column of the succession of the Derbyshire Carbonate Platform around the village of Monyash, based on data from Waters et al. (2009, 2011). Scale bar is 100 m.

Fig. 2 - (color online) Field photographs of upper Visean mud mounds in the southern Peak District, White Peak, Derbyshire (England, UK). a) Core of Linen Dale Mud Mound near Eyam. Scale bar is 1.5 m. b) Mud mound core at the National Stone Centre near Wirksworth, capped by bedded units of the Eyam Limestone Formation. Scale bar is 2 m. c) Specimen of *Aviculopecten planoradiatus* M'Coy, 1851, protruding from a mud mound core at the National Stone Centre. Scale bar is 10 cm. d) Specimen of *Sulcatopinna flabelliformis* (Martin, 1809) in the upper part of Bradford Dale Mud Mound Complex. Scale bar is 20 cm.

& Robba, 1976; Basso & Corselli, 2007). Recognition of valve type has proven to be difficult for *Sulcatopinna*, *Streblopteria* and ?*Limipecten*, thus for these taxa unidentified valves were all counted as single specimens.

BIVALVE FAUNA IN THE MUD MOUNDS

Bivalve macrofossils occur in the core and flank beds of the mud mounds in the Peak District of the UK, scattered among the widespread and abundant brachiopod specimens (bivalves account for 0.4 to 4.8% of specimens collected; Tab. 1), alongside a variable quantity of crinoid stems and ossicles and some fronds of fenestellid bryozoans. No bivalve specimens were found in the units lateral to the mud mounds. In petrographic thin sections from the core, the dominant skeletal components are shells of brachiopods and fenestellid bryozoan fronds, with a variable but usually minor abundance of crinoid ossicles, calcified siliceous sponge spicules, encrusting fistuliporid bryozoans, ramose bryozoans, bivalve and gastropod shells and fragments, in some cases represented by moulds filled by burial calcite cement, and rare foraminifers (endothyrids, tetrataxids, earlandiids, palaeotextulariids, tuberitinids, archeodiscides); the amount of crinoids, fistuliporid and encrusting bryozoans increases in the thin sections from the flank beds, though brachiopods and fenestellid bryozoans are still the most common skeletal grains (more details are given in Carniti et al., 2023).

Brachiopod and bivalve shells are commonly closely set in the micrite matrix and cement of the mud mound core and flank beds. The pectinids occur as left valves, but the corresponding right valve might be concealed below in the sediment; the other taxa occur mostly as moulds of articulated specimens. The high number of fragments in the collection is not a taphonomical effect, but rather the result of the difficulty of extracting entire specimens from the stiff limestone rock (Tab. 1). When preserved, the bivalve shells show only rare traces of corrasion, i.e., the combined effect of abrasion and dissolution (Brett & Baird, 1986); indeed, the external ornamentation is generally well preserved. The associated brachiopods

	Linen Dale Mud Mound	**Ricklow Quarry Mud Mound C.**	**Bradford Dale Mud Mound C.**	**National Stone Centre Mud Mounds**
?*Nuculopsis* sp.	0	0	3 (1AS, 1RV, 1UV)	0
?*Parallelodon* sp.	1 (1LV)	1 (1RV)	0	0
Leptodesma (*Leptodesma*) sp.	2 (1LV, 1UV)	0	0	0
Sulcatopinna flabelliformis (Martin, 1809)	2 (2 UV)	0	3 (2AS, 1UV, 2FR)	1 (1UV)
Aviculopecten planoradiatus M'Coy, 1851	15 (15LV, 37FR)	?FR	5 (5LV, 4FR)	5 (5LV, 4FR)
Streblopteria sp.	0	0	1 (1UV)	2 (2UV)
?*Limipecten* sp.	0	1 (1UV)	1 (1UV)	0
Cosmomya variabilis (M'Coy, 1851)	0	0	2 (2AS)	0
Gastropods	9	0	3	0
Nautiloids	1	0	0	0
Brachiopods	415	490	605	233
% Nuculida	0%	0%	20.0%	0%
% Arcida	5.0%	50.0%	0%	0%
% Ostreida	20.0%	0%	20%	12.5%
% Pectinida	75.0%	50.0%	46.7%	87.5%
% Anomalodesmata	0%	0%	13.3%	0%
Ratio Mollusca/ Brachiopoda	0.048	0.004	0.025	0.034

Tab. 1 - Composition of the bivalve fauna in upper Visean mud mounds of the upper Monsal Dale Limestone Formation, southern Peak District, White Peak, Derbyshire (UK). Number of bivalve specimens calculated without considering the fragments. For bivalves the number of specimens in percentage in each of the four bivalve orders (Nuculida, Arcida, Ostreida, Pectinida) and one superorder (Anomalodesmata) in the faunas is also reported. Data for brachiopods are from Carniti et al. (2022) and Carniti (2024). AS: articulated specimen; LV: left valve; RV: right valve; UV: unidentified valve; FR: fragment.

are mostly articulated and the productide brachiopods are commonly found convex-down in life position in the core, less commonly so in the flank beds (Carniti et al., 2022).

The bivalve collection from the mud mounds consists of 45 complete specimens and several fragments belonging to three species of three genera, and five additional genera lacking specific identification, representing in total eight families of four orders: Nuculida (?*Nuculopsis* sp.), Arcida (?*Parallelodon* sp.), Ostreida (*Leptodesma* [*Leptodesma*] sp., *Sulcatopinna flabelliformis* [Martin, 1809]), Pectinida (*Aviculopecten planoradiatus* M'Coy, 1851, *Streblopteria* sp., ?*Limipecten* sp.), and one superorder: Anomalodesmata (= Pholadomyida, alternative representation) (*Cosmomya variabilis* [M'Coy, 1851]). Table 1 and Fig. 3 summarise the composition of the bivalve component of the fauna in each locality.

Bivalves of the Order Pectinida are the most common, with specimens of *Aviculopecten planoradiatus* M'Coy, 1851 (Family Aviculopectinidae Meek & Hayden, 1865) being the most recurrent species in the mud mound assemblages, both in mud mound core and flank beds (20/45 specimens; Pl. 1, figs 7-13; Pl. 2, figs 1-2; Tab. 1). Besides *A. planoradiatus*, three convex, possibly equilateral valves with faint radial ribs with narrow interspaces, restricted ventrally and crossed by filae swinging ventrally in the rib interspaces, were found in the core of Bradford Dale Mud Mound Complex and National Stone Centre Mud Mounds (Pl. 2, figs 3-4). They are close in dimensions, morphology and ornamentation to the left valves of *Imoella* Hoare, Heaney III & Mapes 1989, a genus defined on material from the Upper Mississippian of Arkansas which was later considered a synonym of the smooth pectinid *Streblopteria* M'Coy, 1851, a genus defined on material from the Mississippian of England (Newell & Boyd, 1995) (Family Deltopectinidae Dickins, 1957). Therefore, they are here assigned to *Streblopteria* sp. Furthermore, two unidentified valves from the core of Ricklow Quarry and Bradford Dale mud mound complexes, with a wide triangular outline, show a well-developed reticulate ornamentation (Pl. 2, fig. 5), which is a peculiar character of *Limipecten* Girty, 1904, a genus defined on material from the Pennsylvanian of North America, but common worldwide in the late Palaeozoic (cf., Hoare, 1993, 2007; Amler, 2006) (Family Limipectinidae Newell & Boyd, 1990).

The second order in terms of number of specimens and taxa in the mud mound bivalve collection is the Ostreida Férussac, 1822, which is represented by two strongly inequilateral small left valves with a strong, long posterior ear and an ornamentation of growth lamellae characterising species of *Leptodesma* (*Leptodesma*) Hall, 1883, a cosmopolitan genus first described in the

Devonian of North America (cf., Hind, 1901) (Family Pterineidae Meek, 1864), occurring in the core of Linen Dale Mud Mound (Pl. 1, fig. 4). In addition, six specimens and fragments of *Sulcatopinna flabelliformis* (Family Pinnidae Leach, 1819) occur in the core of Linen Dale Mud Mound, the core of National Stone Centre Mud Mounds and the core and flank beds of Bradford Dale Mud Mound Complex (Pl. 1, figs 5-6).

Specimens belonging to the orders Nuculida and Arcida and to the Superorder Anomalodesmata are less abundant. For the Nuculida, one articulated specimen and two valves from the core of Bradford Dale Mud Mound Complex (Pl. 1, fig. 1) are attributed to ?*Nuculopsis* Girty, 1911, a cosmopolitan Carboniferous genus (Family Nuculidae Gray, 1824), based on their orbicular morphology, opisthogyrate umbo and smooth valve surface (cf., Hoare & Sturgeon, 1975; Hoare et al., 1989). For the Arcida two poorly preserved elongated valves with a long posterior ear and faint posterior ribbing from the core of Linen Dale Mud Mound and Ricklow Quarry Mud Mound Complex (Pl. 1, figs 2-3) are attributed to ?*Parallelodon* sp. (cf., Amler, 1989; Friedel & Amler, 2024) (Family Parallelodontidae Dall, 1898). Finally, bivalves of the Anomalodesmata are represented by two specimens of *Cosmomya variabilis* (M'Coy, 1851) (Family Pholadomyidae Gray, 1847), collected near the top of the core of Bradford Dale Mud Mound Complex (Pl. 2, figs 6-7).

The few data available seem to support the absence of bivalve faunal differences among the core and flank beds of the mud mounds, as it is the case for brachiopods (Carniti et al., 2022). The flank beds yield *Aviculopecten planoradiatus* in all localities but Ricklow Quarry as well as *Sulcatopinna flabelliformis* in the flanks of Bradford Dale Mud Mound Complex. Both species occur in the core of mud mounds of all localities, associated with the few specimens of the other taxa (Tab. 1).

Based on the taxa here identified we can compare our data with the bivalve fauna provided by Gutteridge (1990) from the Ricklow Quarry Mud Mound Complex core. Gutteridge (1990) reported six species of six genera: 1) *Parallelodon* sp., which we also retrieved from Ricklow Quarry; 2) *Leiopteria* sp., corresponding to *Leptodesma* sp. which we found in the Linen Dale Mud Mound (*Leiopteria* is a subgenus of *Leptodesma* whose use is commonly restricted to the Devonian); 3) *Pinna* (= *Sulcatopinna*) *flabelliformis*, which we found in all localities but Ricklow Quarry; 4) *Aviculopinna mutica* (M'Coy, 1844), a smooth, small pinnid (possibly *Pteronites* sp., as *Aviculopinna* should be restricted to the Permian according to Yancey et al., 2022); 5) ?*Aviculopecten interstitialis* Phillips, 1836 and 6) *Girtypecten stellaris* (Phillips, 1836). The difference between the pectinids retrieved by Gutteridge

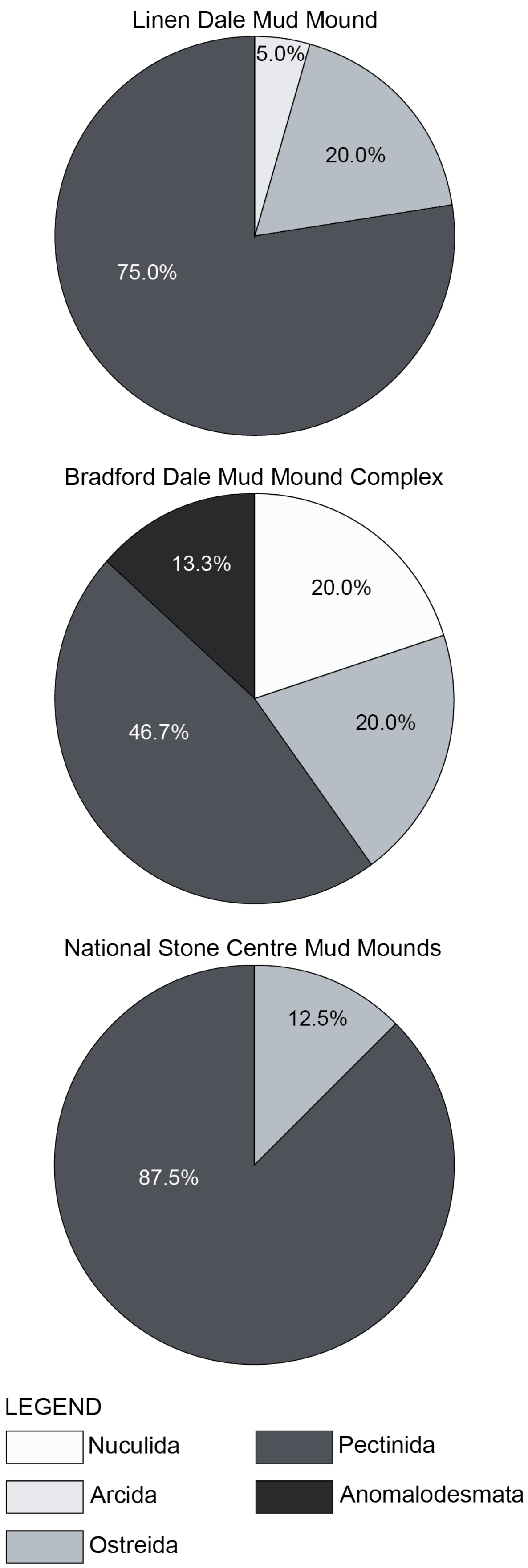


Fig. 3 - Pie diagrams showing the percentage in terms of number of specimens of each bivalve order (Nuculida, Arcida, Ostreida, Pectinida) and one superorder (Anomalodesmata) in the faunas collected in the upper Visean Linen Dale Mud Mound near Eyam, Bradford Dale Mud Mound Complex near Youlgreave, and National Stone Centre Mud Mounds near Wirksworth, Derbyshire (UK). The fauna collected in the Ricklow Quarry Mud Mound Complex near Monyash is not represented in this figure as only two specimens were collected from the site.

(1990) and this study is puzzling and is possibly due to a misidentification in that work, but as Gutteridge's material is lost and it was not figured or described, this hypothesis cannot be verified. Regardless of the specific identifications, Gutteridge's (1990) faunal list confirms that only a limited number of bivalve genera and species occur in the Derbyshire mud mounds, mostly with representatives of the Order Pectinida and Ostreida.

Comparable bivalve associations with *Aviculopecten*, *Sulcatopinna*, *Limipecten*, *Parallelodon*, *Leiopteria* (= *Leptodesma*) and representatives of the Anomalodesmata are recorded from the upper Tournaisian-lower Visean Waulsortian mud mounds in Belgium, Ireland and England (Lees & Miller, 1985), the upper Visean (Asbian) reefs in Yorkshire (Mundy, 1980) and the upper Visean (Brigantian) limestone units of Scotland (Wilson, 1989).

Aside from bivalves, small gastropods rarely occur in the mud mounds, including two specimens of *Naticopsis* (*Naticopsis*) sp. (cf., Gordon & Yochelson, 1983; Kues & Batten, 2001) from the core of Linen Dale Mud Mound and the upper core of Bradford Dale Mud Mound Complex (Pl. 2, figs 8-9) and a fusiform, high spired soliniscid from the core of Line Dale Mud Mound (Pl. 2, fig. 10). The cephalopods are represented by only one nautiloid specimen of *Liroceras* sp. of the Family Liroceratidae Miller & Youngquist, 1949 (identified by Dr. Xiang Fang, Nanjing Institute of Geology and Paleontology, CAS) (Pl. 2, fig. 11) from the core of Linen Dale Mud Mound, in the northern outer platform. Gutteridge (1990) also reported the rostroconch *Conocardium* sp., but no remains of rostroconchs were found during this study.

SUBSTRATE RELATIONSHIPS

The good preservation of the ornamentation of the pectinids, as well as the common articulation of the other taxa, indicate that the collected fossil molluscs suffered only limited or no transport: thus, they were living on the mud mound surface (Brenchley & Harper, 1998). This conclusion is also supported by the taphonomic analysis of the co-occurring brachiopod specimens, which are mostly articulated and in life position (Carniti et al., 2022).

Bivalves are benthic animals whose morphology can be indicative of their life habit and substrate relationship (e.g., Stanley, 1970, 1972, 2015). As bivalves are still ecologically dominant in the marine realm nowadays, most shell morphologies shown by Palaeozoic bivalves can be recognised among extant taxa, whose life habits and substrate relationships have been described by direct observation (e.g., Hoare et al., 1979; Stanley, 2015).

Based on the analysis of the bivalve morphotypes collected from the upper Visean mud mounds in Derbyshire, the examined fauna comprises both epifaunal, seminfaunal and infaunal suspension feeder taxa.

According to Stanley (1970, 1972), almost all pectinids are epifaunal. *Aviculopecten planoradiatus* has an inequivalve shell with a flattened right valve, unequal ears with larger posterior ear, byssal notch (Pl. 4, fig. 1) and tight umbonal angle, all characters indicative of a byssate epifaunal life habit (Kauffman, 1969; Stanley, 1972). According to Stanley (1972) aviculopectinids were possibly resting on the sea floor on the nearly flat right valve, but could reabsorb their byssus and swim with the aid to stabilisation of their wide ears. *Streblopteria* and *Limipecten* are also inequivalve shells with the right valve flatter than the left valve, tight umbonal angle, and unequal ears (Hertlein et al., 1969; Hoare et al., 1989; Newell & Boyd, 1995), so they likely had the same lifestyle of aviculopectinids.

Other epifaunal bivalves in the mud mounds were possibly species of *Leptodesma*. *Leptodesma* has a subrectangular, antero-posteriorly elongate morphology, well developed posterior ear and a strongly curved posterior margin, a morphology close to that of the modern byssate epifaunal bivalve *Pteria* (Stanley, 1970, 1972; Hoare et al., 1979). *Leptodesma* lived likely attached with the byssus to the substrate, the plane of commissure perpendicular to the substrate with the umbo down, the posterior ear directed towards the water current and acting like a helm in aligning the shell to it (Stanley, 1970; Hoare et al., 1979). Also, species of *Parallelodon* show a similar subrectangular morphology with a flattened posterior venter, in addition to a radial ornamentation and denticulation on the ventral margin, characters interpreted by Hoare et al. (1979) as indicative of a byssate epifaunal to seminfaunal shallow burrower lifestyle. We should also note that Mundy (1980) and Brunton (1987) considered *Parallelodon* as byssate seminfaunal/infaunal due to its morphological similarity to the burrowers in the Sanguinolitidae.

Sulcatopinna flabelliformis most likely had the same seminfaunal life habit of modern species of *Pinna* Linné,1758, with the anterior half of its shell buried in the soft muddy substrate (Kauffman, 1969).

Finally, the infaunal bivalves in the mud mounds are represented by *Nuculopsis* and *Cosmomya*. *Nuculopsis* species have an inflate ovato-triangular morphology with opisthogyrate umbos similar to modern species of *Nucula*, which are free burrowers and deposit feeders (Kauffmann, 1969; Stanley, 1970; Hoare et al., 1979). *Cosmomya variabilis* has an antero-posteriorly elongated morphology with long cardinal margin and valve gape posteriorly for extrusion of the siphon (Pl. 2, fig. 6a). This morphology is close to that of *Wilkingia* Wilson, 1959, an upper Palaeozoic genus of the Sanguinolitidae Miller, 1877, interpreted based on its morphology and pallial sinus as an infaunal byssate species with siphon by Stanley (1972). Hoare et al. (1979) retrieved several specimens of *Wilkingia* crushed dorsoventrally on bedding planes in numerous shale, limestone and calcarenite units of the Pennsylvanian of Ohio, suggesting they lived shallow buried in the sediment with the commissure plane perpendicular to the sediment-water interface. Amler (2004) considered specimens of ?*Cosmomya* sp. from an upper Famennian core sample in Germany as a seminfaunal/infaunal, non-byssate.

The wide spectrum of life habits shown by the bivalve fauna of the mud mounds supports the hypothesis of the occurrence of a wide spectrum of soft to firm/hard substrates, as confirmed also by the study of the associated brachiopod fauna (Carniti et al., 2022). Soft muddy substrates were colonised by infaunal and seminfaunal bivalves, whereas firm substrates, provided by brachiopod shells, bryozoan fronds and in-situ precipitated micrite, were suitable for byssate epifaunal bivalves.

WHY FEW BIVALVE FOSSILS?

In this study, out of a collection of 2,000 fossil specimens, only 45 were bivalves. The abundance of bivalves is thus much less than that of brachiopods in the Derbyshire mud mounds, which accounts for 95-99% of the specimens collected from each locality (Tab. 1). Bivalves also show lower diversity, with only three species and eight genera versus the 45 brachiopod species of 36 genera (Carniti et al., 2022). Our data confirm previous reports on the low abundance and species richness of bivalves in the Mississippian limestones: only a total of 13 bivalve genera are reported from the upper Tournaisian-lower Visean Waulsortian mud mounds of Belgium, England and Ireland versus 39 brachiopod genera (Lees & Miller, 1985: fig. 29); 27 bivalve genera vs 81 brachiopod genera are reported from the upper Visean (Asbian) Cracoean reefs on the margin of the Askrigg Block in northern Yorkshire, with brachiopods accounting for 82.5% of collected specimens (Mundy, 1980; Brunton & Mundy, 1988); just two bivalve species of two genera versus 56 brachiopod species of 47 genera are recorded in a collection of silicified fossils of Asbian shelf limestone in County Fermanagh, Ireland (Brunton, 1987). From the Brigantian (upper Visean) limestone units in Scotland, Wilson (1989) listed 98 bivalve species of 35 genera, but most of these occur in the mudstone associated or intercalated within the limestone units, which are otherwise almost devoid of bivalve fossils.

One explanation for the scarcity of bivalves in limestone units is the low preservation potential of taxa with an aragonitic shell (Morse et al., 1985; Palmer & Wilson, 1988; Hendry et al., 1995; Casella et al., 2017). Aragonite shells dissolution should be a synsedimentary process and preferentially affecting the shallow infaunal and seminfaunal aragonitic taxa (Cherns & Wright, 2000; Wright et al., 2003), such as the Nuculidae (?*Nuculopsis* sp.), Arcidae (?*Parallelodon* sp.) and Pholadomyidae (*Cosmomya variabilis*) (Kennedy et al., 1969; Carter et al., 1998), which are in fact preserved as internal moulds in the Derbyshire mud mounds. This is because microbial-led oxidation of the decaying organic matter, leading to acidity, is higher and more impactful in the oxygen-rich upper part of the sediment column (Walter & Burton, 1990; Rude & Aller, 1991; Walter et al., 1993). As the process occurs while the sediment is still unconsolidated, the bivalve moulds are mostly lost during sediment compaction (Wright et al., 2003). The same process possibly explains the scarcity of gastropods (also predominantly aragonitic).

Early dissolution in the upper sediment column was possibly also affecting the bimineralic shells of the Pinnidae (*Sulcatopinna flabelliformis*), which have an outer calcitic layer and aragonitic middle and inner layers (Cox & Hertlein, 1969; Carter et al., 1998), also preserved as moulds in the mud mounds. However, this process should not have affected the epifaunal bimineralic taxa such as the pectinids, including the families Aviculopectinidae (*A. planoradiatus*), Streblochondridae (*Streblopteria* sp.) and Limipectinidae (?*Limipecten* sp.), and the Pterineidae (*Leptodesma* [*L.*] sp.) (Hertlein et al., 1969; Kennedy et al., 1969; Carter et al., 1998), which are in fact preserved with an intact shell in the Derbyshire mud mounds.

We consider the scarcity of fossils of epifaunal calcitic bivalves with higher preservation potential in the mud mounds as reflecting the minor role played by bivalves in the ecosystem. In fact, infaunal and seminfaunal bivalves, possibly underrepresented in the mud mounds due to taphonomical bias, should not have been abundant; indeed, they are usually not successfully coexisting with brachiopods (Olszewski & Patzkowsky, 2001; Tomašových, 2006) and the brachiopod-shell rich substrate was not suitable for them.

Brachiopods were thus the most probable ecological dominants (sensu Clapham et al., 2006) in the mud mounds, accessing to most of the food resources and thus governing the energy flow and trophic structure. Brachiopods, alongside fenestellid bryozoans, were also acting as ecosystem engineers (sensu Jones et al., 1994), as the abundance of their skeletal remains on the seafloor enhanced the stabilisation of the carbonate mud, derived from transport by currents and microbial precipitation in the sediment, and sustained cavities filled by early-marine fibrous calcite cement (Carniti et al., 2023). These processes allowed the vertical growth of the mud mounds with resulting relief of some meters of the buildup above the sea-floor, enhancing further colonisation by suspension feeders (brachiopods, bryozoans, epifaunal bivalves, siliceous sponges, crinoids). On the other hand, bivalves were likely only weak interactors (sensu Berlow, 1999): even if their metabolic and feeding rate was higher than those of brachiopods, they were few and it is unlikely they had any significant role in regulating the energy flux in the environment.

It is unclear if brachiopods were actively competing against bivalves or were simply better suited to the environment. Brachiopods and bivalves occupy similar niches (e.g., Miller & Sepkoski, 1988; Liow et al., 2015), but have different adaptations and tolerance to oxygen levels, water turbidity, and concentration of nutrients and food resources (Stanley, 1972; Tomašových, 2006).

Regarding oxygenation, brachiopods seem to be more tolerant to dysoxic conditions, alongside many epifaunal bivalves (Tomašových, 2006), compared to infaunal bivalves. However, the well-structured, diversified brachiopod-fauna in the mud mounds (Carniti et al., 2022), and the absence of chonetidines, in some cases reported as opportunistic taxa related to dysoxic environments (Racheboeuf, 2000), indicate a normal and stable oxygenation of the mud mound environment.

Regarding turbidity, Steele-Petrovic (1975) and Thayer (1986) suggested that brachiopods are more turbidity-tolerant than bivalves based on the fact that the lophophore is an open structure allowing the free flow of sediment particles in the exhalant current, opposed to the bivalve particle-trapping gill. However, other comparative studies on brachiopod versus bivalve tolerance to turbidity demonstrated that modern terebratulid brachiopods stop to feed at lower turbidity levels than bivalves (Rhodes & Thompson, 1993), and some modern epifaunal bivalves are capable of selecting trapped particles and survive in high-turbid environments (Beninger et al., 2004). Higher turbidity tolerance of bivalves with respect to brachiopods is supported by their higher abundance and diversity in siliciclastic units both in the Palaeozoic and Mesozoic, while brachiopods were more successful in carbonate environments (Miller, 1988; Wilson, 1989; Patzkowsky, 1995; Tomašových, 2006). Sedimentological and palaeoecological characters of the Derbyshire mud mounds (Carniti et al., 2023) suggest a low turbidity environment, possibly more suitable for the successful colonisation by brachiopods.

A major difference between brachiopods and bivalves lies in their metabolic requirements: most bivalves, especially the infaunal ones, have high-energy metabolism, a competitive advantage in environments with abundant food resources (Bambach, 1993; Tomašových, 2006). On the other hand, brachiopod metabolism is slow (LaBarbera, 1977, 1981; James et al., 1992; Peck, 1996). This difference is also reflected in the feeding rate, which is higher in bivalves, especially filibranchs (such as the pectinids), than in modern rhynchonellide and terebratulide brachiopods (Rhose & Thompson, 1993). In the Mesozoic, brachiopods are more successful than infaunal bivalves in environments with limited food supply, but epifaunal bivalves do not seem affected by this factor (Fürsich et al., 2001; Tomašových, 2006).

The diverse and structured community of filter feeders in the Derbyshire mud mounds, as well as the dominance in terms of abundance, species richness and biovolume of productide brachiopods are indicators of limited and scattered food resources (Carniti et al., 2022). The feeding apparatus of productides consists of cilia attached to the dorsal valve interior, considered as enabling access to food particles in a wide area around the shell, thus making productides more successful than brachiopods with a complex plectolophe and spirolophe lophophore (such as rhynchonellides and terebratulides) in environments with scattered and scarce food resources (Pérez-Huerta & Sheldon, 2006; Angiolini, 2007; Carniti et al., 2022). The success of productides might also be the key for the scarce abundance of epifaunal bivalves: the highly diverse brachiopod fauna in the mud mounds, dominated by the productides, was very well adapted to the environmental conditions of low food supply, and low turbidity, thus it was dominating the environment and preventing occupation by epifaunal bivalves. On the other hand, the environmental conditions of scarce and scattered food resources and the abundance of brachiopod shell accumulation in the mound sediment was preventing seminfaunal and infaunal bivalve occupation.

In conclusion, brachiopods were likely competitive dominants in the ecosystem (sensu Bruno et al., 2003), well adapted to the low-turbidity environment with limited and scattered food resources, and acting as ecosystem engineers. The scarcity of bivalves is not only the result of a taphonomical bias but also a consequence of the ecological success of brachiopods and the unsuitable trophic and substrate settings.

CONCLUSIONS

The study of bivalve specimens retrieved from brachiopod-rich fossil assemblages collected from upper Visean mud mounds in the Peak District of Derbyshire (UK) reveals a moderate diversity: three species representing eight genera, spanning eight families across four orders (Nuculida, Arcida, Ostreida, and Pectinida) and one superorder (Anomalodesmata). Although the recovered bivalve fauna is not abundant, it still provides valuable palaeoecological insights.

The bivalves are preserved in situ and exhibit different life styles, including epifaunal byssate, seminfaunal and infaunal byssate, free burrower. This is indicative of a wide array of firm to soft substrates in the mud mounds, as previously indicated by the study of brachiopods (Carniti et al., 2022). Early dissolution of aragonitic shells resulted likely in the loss of most infaunal and seminfaunal taxa, which are in fact recorded as internal moulds. However, the bimineralic shells of pectinids are preserved, as they were not affected by early dissolution, but are anyhow negligible in terms of abundance with respect to brachiopods.

Based on our analysis bivalves were not abundant in the mud mounds and were probably playing a limited role in the environment, which was otherwise dominated by brachiopods, acting as ecological dominants and ecosystem engineers. Brachiopods were possibly more adapted to the low-turbidity environment with scarce food and nutrient supply, thus preventing the colonisation by bivalves.

Limited food and nutrient supply have been proposed to explain the lower abundance of bivalves versus brachiopods in Palaeozoic (Bambach, 1993) and Triassic (Tomašových, 2006) carbonate units, and seem to be a well suited explanation also for Mississippian limestone units in the British Isles and Ireland, possibly exacerbated by the ecological success of productides at the time (Brunton & Mundy, 1988). However, more dedicated studies to bivalve taxonomy, taphonomy and palaeoecology in limestone units are required to confirm this hypothesis and address more precisely local ecological factors.

SYSTEMATIC PALAEONTOLOGY

Specimen measures are provided in Tabs 2-4.

Class Bivalvia Linné, 1758 in 1758-1759
Subclass Autobranchia Grobben, 1894
Infraclass Pteriomorphia Beurlen, 1944
Order Ostreida Férussac, 1822 in 1821-1822
Superfamily Pinnoidea Leach, 1819
Family Pinnidae Leach, 1819

Genus *Sulcatopinna* Hyatt, 1892
Type species *Pinna flexicostata* M'Coy, 1844

Remarks - The genus *Sulcatopinna* includes Carboniferous pinnids characterised by an ornamentation of strong radial ribs (Easton, 1962). Cox & Hertlein (1969) considered *Sulcatopinna* as a junior synonym of *Pinna* but *Sulcatopinna* lacks a median ridge in both valves (Waller & Stanley, 2005; Ros-Franch et al., 2014; Shilekhin et al., 2023) and has usually a narrower apical angle. *Sulcatopinna* differs from *Aviculopinna* Meek, 1864 and *Meekopinna* Yancey, 1978 in being strongly ribbed and in having less prominent growth lines (cf., Yancey, 1978; Yancey et al., 2022). *Sulcatopinna* differs from *Pteronites* M'Coy, 1844 in being larger, in lacking an angular posterior wing and in being ribbed (cf., Yancey et al., 2022).

Sulcatopinna flabelliformis (Martin, 1809)
(Pl. 1, figs 5-6; Pl. 3, figs 1-3)

1809 CONCHYLIOLITHUS Pinnites (*flabelliformis*) Martin, Pl. 6, figs 1-2.
1809 CONCHYLIOLITHUS Pinnitae *nudus* Martin, p. 14.
1836 *Pinna costata* Phillips, p. 211, Pl. 6, fig. 2.
?1843 *Pinna flabelliformis* (Martin) - de Koninck, p. 124, Pl. 5, fig. 1.
1843 *Pinna flabelliformis* var. *inaequicostata* Portlock, p. 437.
1844 *Pinna flabelliformis* (Martin) - M'Coy, p. 85.
1844 *Pinna inaequicostata* (Portlock) - M'Coy, p. 86.
?1849 *Pinna flabelliformis* (Martin) - Brown, p. 169, Pl. 67, fig. 19.
1885 *Pinna flabelliformis* (Martin) - de Koninck, p. 164, Pl. 27, figs 1-2.
1892 *Sulcatopinna flabelliformis* (Martin) - Hyatt, p. 342.
1901 *Pinna flabelliformis* (Martin) - Hind, p. 1, Pl. 2, figs 2-5, non 1, non 6; Pl. 4, fig. 1.
1969 *Pinna* (*Pinna*) *costata* (Phillips) - Cox & Hertlein, Fig. C23-2c.

Material - Material collected in Derbyshire, UK: two articulated specimen external moulds: MPUM13478 (CRH2-47–102a); MPUM13479 (CRH2-63–23); four unidentified valve external moulds: MPUM13480 (CNW2-16–1; CNW2-43–9a); MPUM13481 (CRH2-62–20); MPUM13482 (CNSC24–26); two fragments of external mould: MPUM13483 (CRH2-62–27b; CRH2-62–30a). All come from mud mounds in uppermost Monsal Dale Limestone Formation, upper Visean (Brigantian).

Material housed in the Natural History Museum, London, from Mississippian localities in the British Isles: seven articulated specimens: L3596 (Visean of Clifton, Bristol), L43698 (Roscoe Collection), L6294 (Derbyshire), L13356 (Upper Black Limestone, Holywell, Flintshire), L23917 (Narrowdale, Staffordshire), L40782 (Carpel Burn, Ayrshire), L46022 (Narrowdale, Staffordshire, Hind Collection); one right valve: L47563 (Narrowdale, Staffordshire, Hind Collection); two fragments: L43699 (Hartington, Derbyshire, Roscoe Collection), L46023 (Elbolton, Yorkshire, Hind Collection).

Description - Large, biconvex, equivalve, inequilateral shell. Strongly elongate triangular outline with terminal umbo, apical angle 20°; dorsal margin straight, corresponding to hinge, ventral margin slightly curved. Valves becoming less elongate and convex posteriorly. A shallow groove lies near the hinge, 1.0-2.0 mm towards the interior, on one of the two valves, not always clearly visible.

Both valves ornamented by rounded plicae, with narrow rounded interspaces, starting at or near the umbo. The dorsal region is entirely plicate, whereas the venter is smooth anteriorly, plicate posteriorly as it is covered by the radiating plicae at a distance of 20.0-35.0 mm from the umbo. Posteriorly plicae and the interspaces are wider than near the umbo, straight to slightly flexuous, but become finer and less regular in width towards the dorsal and ventral regions. Plicae number seven to eight per 5.0 mm near the umbo, two to four per 5.0 mm near the commissure. The largest plicae might bifurcate or develop secondary costae on the plica consisting of two to three thinner rounded costae with narrow interspaces. Scattered spine bases might be present.

Both valves also covered by growth lamellae, subparallel to the ventral margin, than deflected anteriorly to become perpendicular to the dorsal margin.

Remarks - The specimens under examination are attributed to *Sulcatopinna* based on their strongly elongated morphology with inequilateral valves, terminal umbo, and well-developed coarse costae. Several species

EXPLANATION OF PLATE 1

Upper Visean (Brigantian) bivalves from mud mounds in the uppermost Monsal Dale Limestone Formation, Derbyshire (UK). Scale bars are 10 mm for 1x specimens, 5 mm for 2x specimens, 3.3 mm for 3x specimens.

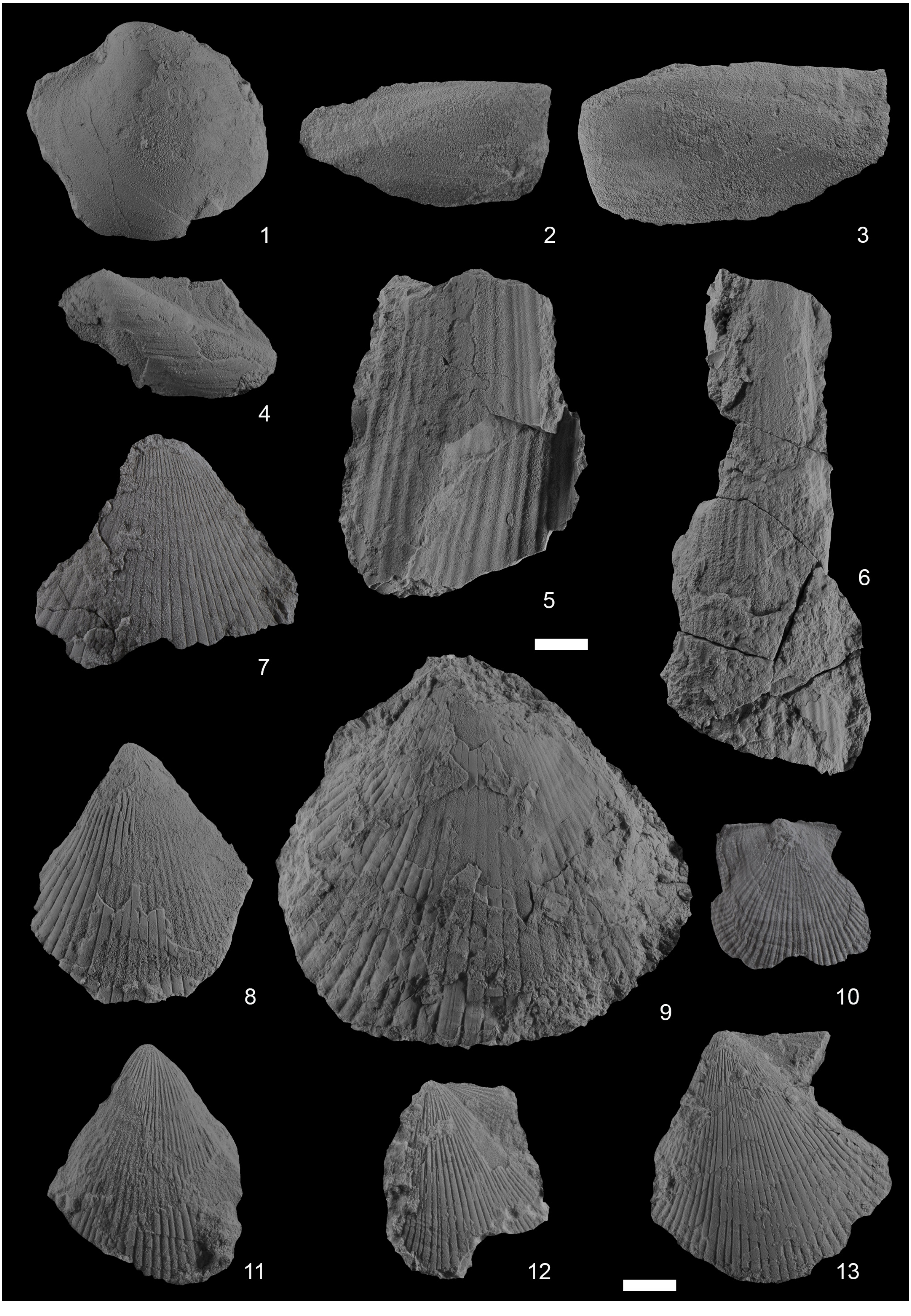
Fig. 1 - ?*Nuculopsis* sp. MPUM13503 (CRH1–8), right valve; 2x.

Figs 2-3 - ?*Parallelodon* sp.
2 - MPUM13506 (CNW2-45–31), right valve; 2x.
3 - MPUM13507 (RCC12–29), left valve; 2x.

Fig. 4 - *Leptodesma* (*Leptodesma*) sp. MPUM13508 (CNW2-45–31a), left valve; 3x.

Figs 5-6 - *Sulcatopinna flabelliformis* (Martin, 1809).
5 - MPUM13479 (CRH2-63–23), right valve; 1x.
6 - MPUM13478 (CRH2-47–102a), left valve; 1x.

Figs 7-13 - *Aviculopecten planoradiatus* M'Coy, 1851.
7 - MPUM13484 (CNW2–17), left valve, 2x.
8 - MPUM13486 (CNW2-40? –2), left valve; 2x.
9 - MPUM13488 (CNW2-43–1a), left valve; 1x.
10 - MPUM13494 (CNW2-44–12), left valve; 3x.
11 - MPUM13487 (CNW2-40–16), left valve; 3x.
12 - MPUM13489 (CNW3–49), left valve; 3x.
13 - MPUM13490 (CRH2-63–18a), left valve; 2x.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of *Sulcatopinna* are reported from the British Isles and Ireland, whose complex nomenclatural history needs to be revised: *Sulcatopinna flabelliformis*, *Sulcatopinna costata* (Phillips, 1836), *Sulcatopinna inaequicostata* (Portlock, 1843), and *Sulcatopinna flexicostata* (M'Coy, 1844).

Martin (1809) gave the first description of CONCHYLIOLITHUS Pinnites (*flabelliformis*) based on specimens from the Mississippian of the Peak District in Derbyshire and described its ornamentation as consisting of "sulci equal, and straight". He used his trinomial system of nomenclature, consisting of a first name supposed to be the genus (CONCHYLIOLITHUS), a second name supposed to be family name (Pinnites) and the species name (*flabelliformis*) (Ford, 2003). Martin's (1793, 1809) names and nomenclature system were considered invalid by the International Commission on Zoological Nomenclature (ICZN, 1954, Opinion 231). The species name *flabelliformis* is thus invalid.

Phillips (1836) renamed the same species as *Pinna costata*, thus this should be considered as the valid name. However, the species name *Pinna* (or *Sulcatopinna*) *flabelliformis* has been widely used by Carboniferous workers in Western Europe since the 19th century (e.g., de Koninck, 1843; Murchison et al., 1845; Hind, 1901; Wilson, 1989; Gutteridge, 1990), while *Pinna costata* has been used only by Cox & Hertlein (1969). It is thus the authors' opinion that the original species name *flabelliformis* should be retained for the species, based on its common use in the literature, and used with the combination *Sulcatopinna flabelliformis* as proposed by Hyatt (1892). Application for the validation of the name *Sulcatopinna flabelliformis* (Martin, 1809) to the ICZN is planned.

Sulcatopinna flabelliformis differs from *S. inaequicostata* as the latter has "ribs broader on one side than the other" (M'Coy, 1844, p. 86). However, the pattern of plication and secondary costae of *S. flabelliformis* seems to be more irregular than previously thought by early workers (Martin, 1809; Phillips, 1836; Portlock, 1843; M'Coy, 1844); no specimens with coarse ribs of the same width have been retrieved in the collection from Derbyshire and NHM, and specimens of *S. flabelliformis* figured by several authors clearly have ribs of various width and secondary costae posteriorly (e.g., de Koninck, 1843, 1885; Hind, 1901). *Sulcatopinna inaequicostata* can thus be considered a junior synonym of *S. flabelliformis*.

Sulcatopinna flabelliformis differs from *Sulcatopinna flexicostata* (M'Coy, 1844) in having a more restricted smooth ventral region anteriorly and a less strongly developed concentric ornamentation. A specimen housed in NHM from the Millstone Grit Group, Brandon Hill Quarry, Bristol, labelled as *Pinna flabelliformis*, bears the characters of *S. flexicostata* (longer than 61.5 mm, 30.0 mm high) (Pl. 3, fig. 4), and may be better placed in that species.

The specimens under examination differ from *Sulcatopinna ludlovi* (Whitfield, 1876) from the Upper Mississippian of Montana, USA, in showing less common secondary costae (cf., Easton, 1962), from *S. missouriensis* Swallow, 1863 from the Mississippian of Missouri, in having coarser ribs (cf., Hoare, 1993, 2007), from *S. inexpectens* Walcott, 1884, from the Upper Mississippian of Nevada, in having a larger apical angle and in having fewer spine bases on the valve surface (cf., Busanus & Hoare, 1991).

Distribution - *Sulcatopinna flabelliformis* occurs in numerous localities in the middle-upper Mississippian of England (e.g., Hind, 1901; Bond, 1950; Moore, 1958), Scotland (Wilson, 1989; Dean, 2017), Ireland, Isle of Man (Hind, 1901), Belgium (de Koninck, 1885). It is also reported from the Mississippian of Carinthia, Austria (Sieber, 1972), though it is not possible to confirm the determination for the lack of any illustration.

EXPLANATION OF PLATE 2

Upper Visean (Brigantian) bivalves, gastropods and nautiloids from mud mounds in the uppermost Monsal Dale Limestone Formation, Derbyshire (UK). Scale bars are 10 mm for 1x specimens, 5 mm for 2x specimens, 3.3 mm for 3x specimens.

Figs 1-2 - *Aviculopecten planoradiatus* M'Coy, 1851.
1 - MPUM13485 (CNW2-30–27a), left valve; 2x.
2 - MPUM13491 (CRH2-63–28a), left valve; 1x.

Figs 3-4 - *Streblopteria* sp.
3 - MPUM13510 (CNSC24–24), unidentified valve; 3x.
4 - MPUM13511 (CNSC24BIS–1), unidentified valve; 2x.

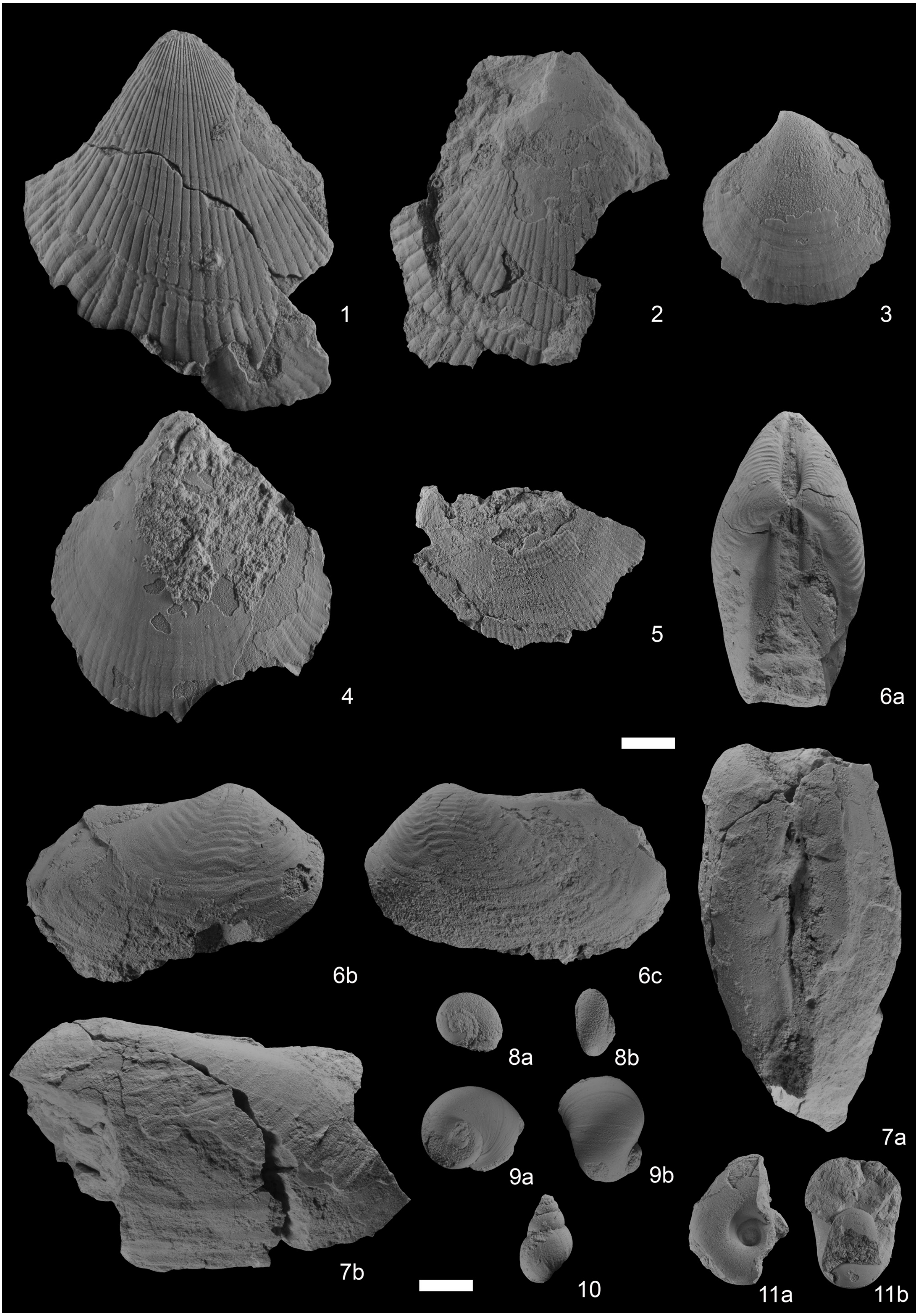
Fig. 5 - ?*Limipecten* sp. MPUM13513 (CRH1BIS–5a), unidentified valve; 1x.

Figs 6-7 - *Cosmomya variabilis* (M'Coy, 1851).
6 - MPUM13501 (CRH2-63–12), dorsal view (a), right valve (b), left valve (c); 1x.
7 - MPUM13502 (CRH2-63–28e), dorsal view (a), left valve (b); 1x.

Figs 8-9 - *Naticopsis* (*Naticopsis*) sp.
8 - MPUM13515 (CNW20–97), apical view (a), abapertural view (b); 2x.
9 - MPUM13516 (CRH2-63–14), apical view (a), abapertural view (b); 2x.

Fig. 10 - Soleniscidae gen. et sp. indet. MPUM13517 (CNW2-41B–60), abapertural view; 3x.

Fig. 11 - *Liroceras* sp. MPUM13518 (CNW2-41B–41), right lateral view (a), oral view (b); 1x.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6a
6b
6c
7a
8a
8b
9a
9b
7b
10
11a
11b

Specimen	Length (mm)	Height (mm)	Width (mm)
MPUM13478 (CRH2-47–102a)	115.0	42.0	/
MPUM13479 (CRH2-63–23)	/	40.0	/
L3596	113.0	> 32.0	6.0
L6294	105.0	25.0	/
L23917	/	23.0	/
L46022	/	27.5	4.7
L46023	/	55.0	4.5
L475b3	> 103.0	27.5	/

Tab. 2 - Measures of specimens of *Sulcatopinna flabelliformis* (Martin, 1809) in the fauna collected from the upper Visean mud mounds from the southern Peak District, White Peak, of Derbyshire housed at the Università degli Studi di Milano (MPUM-) and specimens housed at NHM in London (L-).

Order Pectinida Gray, 1854
Superfamily Aviculopectinoidea Meek & Hayden, 1865
Family Aviculopectinidae Meek & Hayden, 1865
Subfamily Aviculopectininae Meek & Hayden, 1865

Genus *Aviculopecten* M'Coy, 1851
Type species *Aviculopecten planoradiatus* M'Coy, 1851

Remarks - *Aviculopecten* was erected by M'Coy (1851) with *A. planoradiatus* as type species, a species known based on left valves only from Northumberland (see Newell, 1938, 1969 and Waterhouse, 1969, for further discussion). Newell (1938, 1969) re-described the genus based on North American Pennsylvanian and Permian forms (e.g., *A. exemplarius* Newell, 1938). He included acline to prosocline auriculate shells with a single oblique resilifer, with costae increasing by intercalation on the left valve and by bifurcation on the right valve, and with growth lines never swinging towards the ventral margin in interspaces. Newell & Boyd (1995) later restricted the diagnosis of the genus *Aviculopecten* to uniplicate, biconvex shells. Fang & Morris (1999) retrieved some articulated specimens and right valves of *A. planoradiatus* in the Natural History Museum of London, and re-described the species as having an inequiconvex shell with a nearly flat right valve, having simple plicae intercalating on both valves at early growth stages only, then only simple plicae ventrally, and growth lamellae slightly swinging towards the ventral margin in interspaces.

Based on the revised description of the type species and genus by Fang & Morris (1999), *Aviculopecten* differs from *Hayasakapecten* Nakazawa & Newell, 1968 of the Hayasakapectininae Boyd & Newell, 2000, in being strongly inequivalve and lacking ventrally directed spines in the plicae interspaces (Waterhouse, 1969; Fang & Morris, 1999; Boyd & Newell, 2000), from *Spyridopecten* Campbell & McKelvey, 1972 of the Spyridopectininae Waterhouse, 2008 in being ornamented by few plicae of one rank only. *Aviculopecten* differs from *Heteropecten* Kegel & Costa, 1951, of the Heteropectinoidea Beurlen, 1954, in being plicate rather than multicostate and in lacking any rib bifurcation on the right valve, from *Acanthopecten* Girty, 1903 in having more quadrate plicae and in having a less strongly developed concentric ornamentation (cf., Newell & Boyd, 1995). *Aviculopecten* differs from *Etheripecten* Waterhouse, 1963, *Girtypecten* Newell, 1938 and *Limipecten* Girty, 1904, also of the Heteropectinoidea Beurlen, 1954 in not being multicostate and in having narrower interspaces between ribs (Newell & Boyd, 1990; Fang & Morris, 1999; Boyd & Newell, 2000). *Limipecten* has also a well-developed concentric ornamentation of erect growth lamellae (Newell & Boyd, 1990).

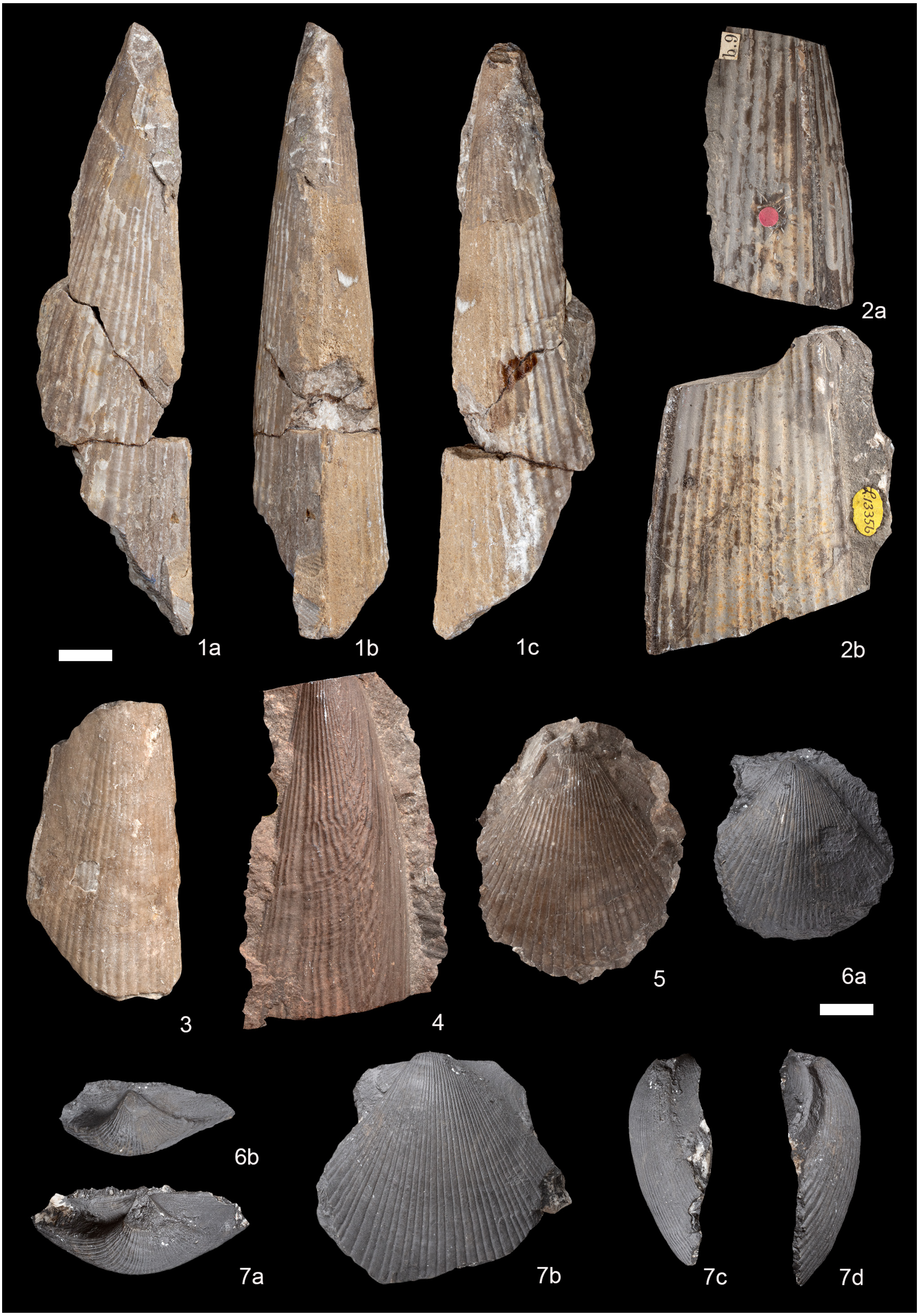
EXPLANATION OF PLATE 3

(color online) Mississippian bivalves from collections in the Natural History Museum, London (UK). Scale bars are 10 mm for 1x specimens, 5 mm for 2x specimens.

Figs 1-3 - *Sulcatopinna flabelliformis* (Martin, 1809).
1 - L6294, left valve (a), dorsal view (b), right valve (c); 1x. Derbyshire.
2 - L13356, left valve (a), right valve (b); 1x. Upper Black Limestone, Holywell, Flintshire, North Wales.
3 - L46022, left valve; 1x. Narrowdale, Staffordshire.

Fig. 4 - *Sulcatopinna flexicostata* (M'Coy, 1844). L26419, right valve; 1x. Millstone Grit Group (Serpukhovian-Bashkirian), Brandon Hill Quarry, Bristol.

Figs 5-7 - *Aviculopecten planoradiatus* M'Coy, 1851.
5 - L13403a, left valve; 2x. Middle White Limestone, Graig-faur, Flintshire, North Wales.
6 - L13403b, left valve (a), umbonal view (b); 1x. Middle White Limestone, Graig-faur, Flintshire North Wales.
7 - L43580, umbonal view (a), left valve (b), posterior view (c), anterior view (d); 1x. Narrowdale Hill, Hartington, Derbyshire.


1a
1b
1c
2a
2b
3
4
5
6a
6b
7a
7b
7c
7d

Hind (1903) included in *Aviculopecten* 32 species from the Carboniferous of the British Isles, but based on the redescription of the genus by Fang & Morris (1999) likely only *A. semicostatus* (Portlock, 1843), *A. pera* (M'Coy, 1844), *A. intermedius* (M'Coy, 1844), *A. knockonniensis* (M'Coy, 1844), *A. incrassatus* (M'Coy, 1844), and *A. carrolli* Hind, 1903 might be included in the genus, whereas the other species need to be revised and possibly assigned to other genera such as *Heteropecten, Etheripecten, Limipecten,* and *Euchondria* Meek, 1874.

Aviculopecten planoradiatus M'Coy, 1851
(Pl. 1, figs 7-13; Pl. 2, figs 1-2; Pl. 3, figs 5-7; Pl. 4, figs 1-4)

1851 *Aviculopecten planoradiatus* M'Coy, p. 171.
1855 *Aviculopecten planoradiatus* M'Coy - M'Coy, p. 489, Pl. 3E, fig. 8.
?1876 *Aviculopecten planoradiatus* M'Coy - Etheridge, p. 151.
1903 *Aviculopecten tabulatus* M'Coy - Hind, p. 67, Pl. 12, figs 1, 3-4, non 2.
1903 *Aviculopecten semicostatus* (Portlock) - Hind, p. 69 (pars), Pl. 13, fig. 13, non 9-12, non 14-15.
1938 *Aviculopecten planoradiatus* M'Coy - Newell, Pl. 5, figs 12-15.
1969 *Aviculopecten planoradiatus* M'Coy - Waterhouse, p. 1179, Text- fig. 1A-E.
1999 *Aviculopecten planoradiatus* M'Coy - Fang & Morris, Pl. 1, figs 1-9.

Material - Material collected from Derbyshire: 24 left valves: MPUM13484 (CNW2–17), MPUM13485 (CNW2-30–27a), MPUM13486 (CNW2-40?–2), MPUM13487 (CNW2-40–16), MPUM13488 (CNW2-43–1a), MPUM13489 (CNW3–49), MPUM13490 (CRH2-63–18a), MPUM13494 (CNW2-44–12), MPUM13491 (CRH2-63–28a), MPUM13492 (CNW2-40–10a; CNW14-1–9; CNW14-1–11b); MPUM13493 (CNSC24BIS–42; CNSC24BIS–46); MPUM13495 (CNW1–8a; CNW2-39–43a; CNW2-41B–87; CNW2-42–1; CNW20–8); MPUM13496 (CRH1BIS–20; CRH2-18–1); MPUM13497 (CNT2-33–9; CNSC10P–2; CNSC41–25); 46 fragments: MPUM13498 (CNW2-30–4; CNW2-30–14b; CNW2-30–15; CNW2-30–22; CNW2-30–24b; CNW2-30–27b; CNW2-30–32; CNW2-30–70b; CNW2-30–92b; CNW2-40–10b; CNW2-40–10c; CNW2-40–12; CNW2-40–13; CNW2-40–26; CNW2-40–34; CNW2-40–44; CNW2-40?–5d; CNW2-40?–10a; CNW2-40?–12a; CNW2-41B–88; CNW2-41B–89; CNW2-43–1c; CNW2-43–16; CNW2-43–18; CNW2-44–1; CNW2-44–2; CNW2-44–3; CNW20–11b; CNW20–11c; CNW20–22; CNW20–24; CNW20–25b; CNW20–27b; CNW20–73; CNW20–87; CNW20–104a; CNW20–104c); MPUM13499 (CRH1BIS–22c; CRH2-47–9; CRH2–53; CRH2-63–18c; CRH2-63–28d); MPUM13500 (CNSC41–28a; CNSC41–35; CNSC41–36; CNT2-33–10c). All come from mud mounds in uppermost Monsal Dale Limestone Formation, upper Visean (Brigantian).

Material housed in the Natural History Museum, London, from Mississippian localities in the British Isles: one articulated specimen: L13403a (Middle White Limestone, Graig-faur, Flintshire, Wales, Morton Collection); 22 left valves: L5243 (Visean, Elbolton, Yorkshire), L13403b, L13403c (Middle White Limestone, Graig-faur, Flintshire, Wales, Morton Collection), L43579, L43580, L43582, L43583, L43584, L43585 (Narrowdale Hill, Hartington, Derbyshire, Roscoe Collection), L43586, L43601, L43602 (Beresford Hall, Hartington, Derbyshire, Roscoe Collection), L45137, L45138, L45139 (Poolvash, Isle of Man, Hind Collection), L45218 (Visean, Elbolton, Yorkshire, Hind Collection), L45219 (Visean, Park Hill, Derbyshire, Hind Collection), L47618 (Visean, Elbolton, Yorkshire, Hind Collection), PL4411, PL4412, PL4413, PL4414 (Brigantian, upper Visean, Treak Cliff, Castleton, Derbyshire, Senior Collection); one right valve: L45141 (Poolvash, Isle of Man, Hind Collection).

Description - Medium to large sized, inequiconvex, inequilateral shell with sub-triangular bialate outline. Umbo orthogyrate to slightly prosogyrate; apical angle 50°. Left valve convex, more inflated anteriorly. Anterior submargin curved, posterior submargin straight. Anterior ear smaller and with deeper auricular sulcus than posterior ear. Right valve with poorly convex disc. Anterior ear smaller and with deeper auricular sulcus than posterior; anterior ear overhanging byssal notch (Pl. 4, fig. 1).

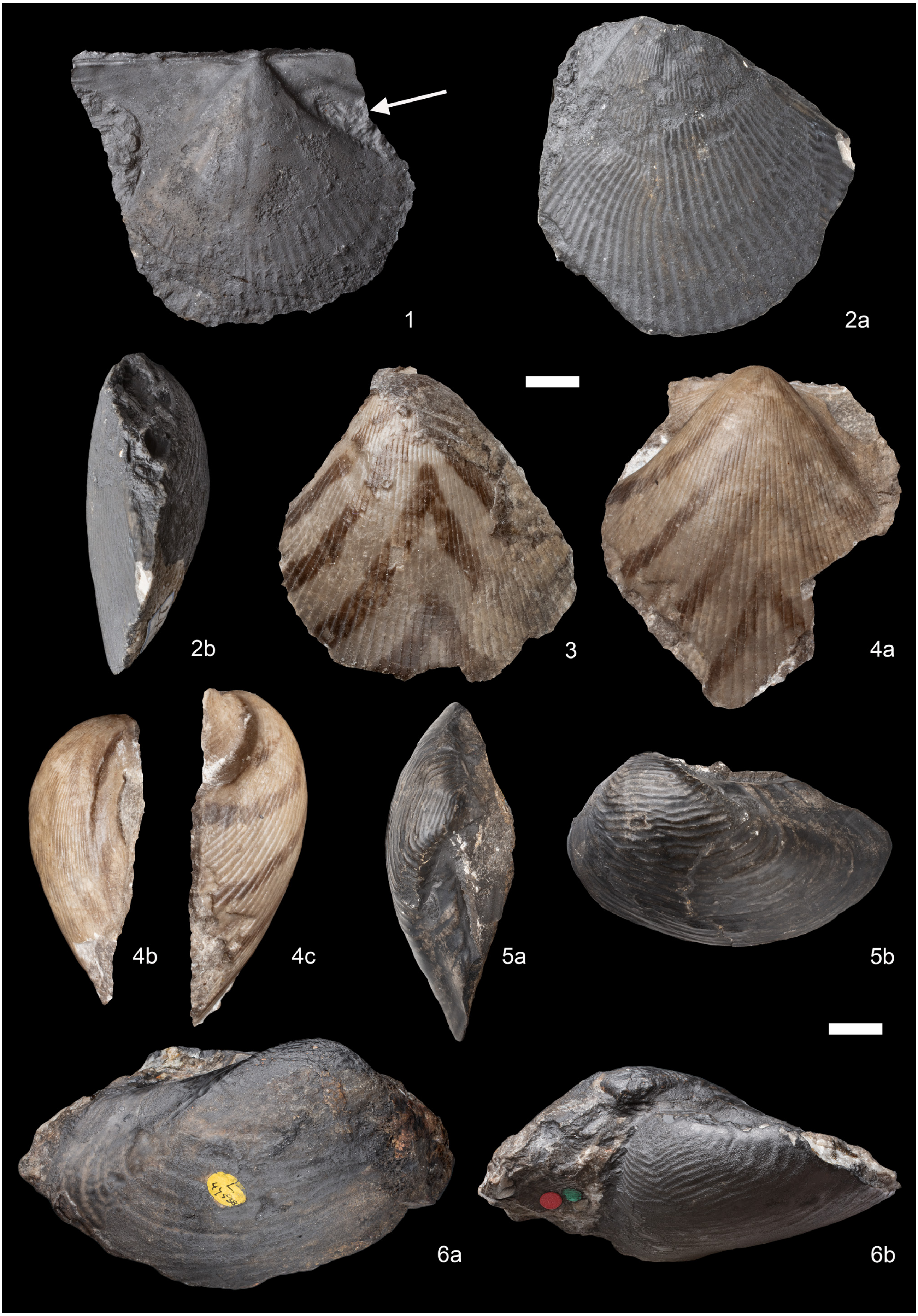
Both valves covered by radial plicae. Plicae subquadrate in cross-section with deep, subquadrate interspaces, narrower than plicae. Plicae increasing in number by frequent intercalation in early growth stages, resulting in distinctive ornamentation of plicae of two

EXPLANATION OF PLATE 4

(color online) Mississippian bivalves from collections in the Natural History Museum, London (UK). Scale bars are 10 mm for 1x specimens, 5 mm for 2x specimens.

Figs 1-4 - *Aviculopecten planoradiatus* M'Coy, 1851.
1 - L45141, right valve; 2x. Poolvash, Isle of Man (arrow indicates byssal notch).
2 - L13403c, right valve (a), posterior view (b); 2x. Middle White Limestone, Graig-faur, Flintshire, North Wales.
3 - PL4412, left valve; 2x. Brigantian (upper Visean), Treak Cliff, Castleton, Derbyshire.
4 - PL4411, left valve (a), posterior view (b), anterior view (c); 2x. Brigantian (upper Visean), Treak Cliff, Castleton, Derbyshire.

Figs 5-6 - *Cosmomya variabilis* (M'Coy, 1851).
5 - PL1598, dorsal view (a), left valve (b); 1x. Main Limestone, lowest Namurian (Serpukhovian), Stanhope, Weardale.
6 - L47538, right valve (a), dorsal view (b); 1x. Visean, Derbyshire.


1
2a
2b
3
4a
4b
4c
5a
5b
6a
6b

Specimen	Disc length (mm)	Disc height (mm)
MPUM13484 (CNW2–17)	22.0	> 25.0
MPUM13485 (CNW30–27a)	38.0	34.0
MPUM13486 (CNW2-40? –2)	26.0	24.0
MPUM13488 (CNW2-43–1a)	70.0	74.0
MPUM13490 (CRH2-63–18a)	25.0	24.0
MPUM13491 (CRH2-63–28a)	50.0	64.0
MPUM13492 (CNW14-1–9)	22.0	> 20.0
MPUM13492 (CNW14-1–11b)	15.0	14.0
L43579	54.0	67.0

Tab. 3 - Measures of specimens of *Aviculopecten planoradiatus* M'Coy, 1851 in the fauna collected from the upper Visean mud mounds from the southern Peak District, White Peak, of Derbyshire housed at the Università degli Studi di Milano (MPUM-) and specimens housed at NHM in London (L-).

orders. No or few intercalations occur after 4.0 mm from the umbo, where plicae become all of comparable width. Plicae straight below umbo, curved towards margins. They number five-six per 5.0 mm at a distance of 24.0 mm from the umbo; they are 0.8-1.8 mm wide at 30.0 mm from the umbo, up to 5.0 mm wide at 75.0 mm from the umbo. The radial ornamentation of the ears consists of low, rounded ribs with narrow interspaces, 7 per 5.0 mm, on the right and left valve anterior ears, and of fine, subcylindrical costae, with wide flat interspaces on the posterior ears, six-seven on the entire ear. Concentric growth lines poorly defined on left valve, stronger and more lamellose on right valve, spaced 0.2-1.0 mm, also extending on ears. Colour ornamentation consisting of v-shaped dark brownish-red band with the tip of the v at the umbo; additional v-shaped bands occur anteriorly every 3 mm.

Remarks - The specimens under examination clearly show the same morphology and ornamentation as previously published specimens of *A. planoradiatus*, with radial ornamentation characterised by intercalating costellae near the umbo, passing to regular ribs all of the same width towards the commissure.

The specimens differ from other species of *Aviculopecten* retrieved from the Visean of Castleton, Derbyshire (Hind, 1903): they differ from *A. semicostatus* in having more inequilateral shells and coarser ribs (cf., Hind, 1903, pl. 13, figs 9-12), from *A. carrolli* in being larger and in having all plicae of the same width ventrally (Hind, 1903, pl. 17, figs 24-27), from *A. incrassatus* in having a more inequilateral shell disc outline and plicae more quadrate in section (Hind, 1903, pl. 14, figs 12-15). They differ from *A. pera*, *A. intermedius* and *A. knockonniensis* in being larger with coarser ribs, from ?*Heteropecten tabulatus* in having ribs intercalating rather than bifurcating on the right valve.

Distribution - *Aviculopecten planoradiatus* is common in the Mississippian of the British Isles, possibly being restricted to the upper Visean (Asbian-Brigantian). It has been reported from Derbyshire (Hind, 1903; Newell, 1938; Waterhouse, 1969; Fang & Morris, 1999), Elbolton in Yorkshire, Poolvash in the Isle of Man (Fang & Morris, 1999) and Flintshire in North Wales (Morton, 1886; Fang & Morris, 1999).

Infraclass Heteroconchia Hertwig, 1895
Subterclass Euheterodonta Giribet & Distel, 2003
Superorder Anomalodesmata Dall, 1889
Superfamily Pholadomyoidea King, 1844
Family Pholadomyidae Gray, 1847

Genus *Cosmomya* Holdhaus, 1913
Type species *Cosmomya egraria* Holdhaus, 1913

Cosmomya variabilis (M'Coy, 1851)
(Pl. 2, figs 6-7; Pl. 4, figs 5-6)

1851 *Sanguinolites variabilis* M'Coy, p. 174 (pars).
1854 *Sanguinolites variabilis* (M'Coy) - Morris, p. 223.
1855 *Sanguinolites variabilis* (M'Coy) - M'Coy, p. 508, Pl. 3f, fig. 6a.
1900 *Allorisma variabilis* (M'Coy) - Hind, p. 424, Pl. 44, fig. 2.
1900 *Sanguinolites interruptus* Hind, p. 383, Pl. 42, figs 8-10; Pl. 49, fig. 10.
1991 *Cosmomya variabilis* (M'Coy) - Morris et al., p. 68, Fig. 17a-d.

Material - Material collected in Derbyshire: two articulated specimens: MPUM13501 (CRH2-63–12), MPUM13502 (CRH2-63–28e) from uppermost Monsal Dale Limestone Formation, upper Visean (Brigantian).

Material housed in the Natural History Museum, London, from Mississippian localities in the British Isles: two articulated specimens: L47538 (Visean of Derbyshire, UK), PL1598 (Main Limestone, lowest Namurian, Stanhope, Weardale, Northumberland).

Description - Large, biconvex, equivalve, strongly inequilateral shell with sub-elliptical outline. Dorso-ventral diameter markedly smaller than antero-posterior one. Anterior and posterior margin rounded; anterior area more convex than posterior. Umbo well developed, arched, slightly prosogyrate. Lunule obscure, longer than wide. Cardinal margin straight, posterior to umbo, long, with wide escutcheon, also longer than wide. Valves in contact for all cardinal margin, anterior margin and commissure, but diverging posteriorly to create a wide suboval opening, higher than wide (Pl. 2, fig. 6a).

Both valves covered by subrounded rugae with narrow interspaces. Near to the umbo rugae are regularly

Specimen	Length (mm)	Height (mm)	Thickness (mm)
MPUM13501 (CRH2-63–12)	57.0	33.0	25.0
MPUM13502 (CRH2-63–28e)	> 72.0	48.5	38.0

Tab. 4 - Measures of specimens of *Cosmomya variabilis* (M'Coy, 1851) in the fauna collected from the upper Visean mud mounds from the southern Peak District, White Peak, of Derbyshire housed at the Università degli Studi di Milano (MPUM-).

concentric, with convexity towards the commissure. In some specimens in the central part of the valves, the convexity of the rugae is deflected towards the umbo in the medial area of the disc, with a resulting characteristic w-shape; after mid-valve towards the ventral region rugae become more regularly concentric. Escutcheon smooth. Poorly developed concentric growth lines and lamellae, sometimes crossing rugae. Rugae number three-four per 5.0 mm.

Remarks - The specimens under examination possess the same morphology and characteristic w-shape concentric ornamentation shown by some specimens of *C. variabilis* illustrated by Morris et al. (1991, fig. 17a-b, d). They differ from *Cosmomya v-scripta* (Hind, 1900) in being more inequilateral and in the less developed posterior deflection of rugae.

Distribution - *Cosmomya variabilis* occurs in the Mississippian of Thorpe Cloud (lower Visean; Bridges & Chapman, 1988), Dovedale, and Castleton (upper Visean, Bunton & Tilsley, 1991) in Derbyshire, UK (Hind, 1900), and around Narrowdale, Staffordshire (Visean, Morris et al., 1991).

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