# A Namurian brachiopod fauna from Meré (Province of Oviedo, Spain)

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An interesting brachiopod fauna from Namurian (Marsdenian?) deposits — provisionally named the Meré beds herein — is described. The fauna contains seven new species: Drahanorhynchus cantabricus, Anopliopsis? parva, Caenanoplia martinezi, Tornquistia scutiformis, Aseptella asturica, Kitakamithyris merensis, and Plicotorynifer lamellosus; and one new genus: Aseptella with the type species A. asturica. The material of a new productellid and a new ambocoeliid was too poor to give them formal names.

The special character of this fauna — only a much older fauna from the Chappel Limestone of Texas (U.S.A.) being closely comparable — indicates special environmental conditions: presumably a soft, muddy bottom.

The brachiopod fauna indicates a Namurian, probably Namurian B-C, age. This is in good agreement with the late Namurian B (Marsdenian) age found for the goniatites and with the stratigraphical position of the beds.

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| Introduction                               | 2  |
|--|----|
| Collections                                | 2  |
| Geological setting                         | 2  |
| The fauna of the Meré beds                 | 4  |
| Systematic descriptions of the brachiopods | 4  |
| Conclusions                                | 32 |
| Comparison                                 | 32 |
| Age of the Meré beds                       | 32 |
| Resumen                                    | 34 |
| References                                 | 35 |
| Plates                                     | 39 |
|  |    |

## Introduction

#### COLLECTIONS

Through the courtesy of Dr E. Martínez García, the second author (C.F.W.P.) received in the fall of 1970 a small brachiopod fauna, preserved as internal and external moulds, from a locality north of Meré, Province of Oviedo. This locality is situated opposite kilometre-post 8 along the road from Posada de Llanes to Ortiguero (coordinates 43°22' N, 4°55' W). The fauna was obtained from a variegated shale level slightly above the 'Caliza de Montaña' (Martínez García, 1971). A list of provisional identifications had been made available to Martínez García and was published by him (op. cit., p. 271, 274).

Since this fauna contained some interesting forms: Chonetipustula sp. nov. '= Aseptella asturica gen. et sp. nov.) and an unlisted phricodothyrid, than considered to be new (= Plicotorynifer lamellosus sp. nov.), and since a more detailed knowledge of the brachiopods might be useful for an exact dating of the 'Caliza de Montaña' in that area (compare Martínez García, 1971), it was considered useful to study the fauna in more detail.

It proved to be necessary to collect additional material, since from some species no internal moulds, or only brachial or pedicle valves, were found in the original collection. To this end, a short visit to the palaeontological department of the University of Oviedo in March 1972 was used to make a fieldtrip to Meré. The party existed of Professor J. Truyols, the first author (M.L.M.Ch.), her husband (L. Sánchez de Posada) and the second author (C.F.W.P.).

Altogether an interesting small brachiopod fauna was recovered which is described below. The material is partly stored in the Rijksmuseum van Geologie en Mineralogie (National Museum of Geology and Mineralogy: registered under the numbers RGM 130 030-130 099 and 143 556-143 774) and partly in the Department of Palaeontology of the University of Oviedo (registration numbers prefixed with DPO).

## Acknowledgements

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We thank Dr M. van den Boogaard (Rijksmuseum van Geologie en Mineralogie) for identifying some microfaunal remains.

## GEOLOGICAL SETTING

The Palaeozoic rocks in the area around Meré are found in thrust slices which form the north-eastern continuation of the Manto de Beleño (Julivert, 1967; Marcos, 1967).

The Carboniferous succession in this part of Asturias (Marcos, 1967; see also Wagner, Winkler Prins & Riding, 1972, for a detailed description of the formations) starts with a thin sandstone belonging to the Famennian to Lower Tournaisian Ermita Formation which lies disconformably on the Ordovician

Barrios Quarzite. The succession is generally continued with black shales of the Upper? Tournaisian Vegamián Formation and pink and grey griotte limestones and cherts of the Genicera Formation, also known as the Alba Formation or simply as the Griotte, and ranging in age from Late Tournaisian to Early Namurian (E2 Zone). Whether the Ermita Sandstone and Vegamián Black Shales are actually present in the thrust unit at Meré is questionable, since they are not indicated on the maps of Marcos (1967) and Martínez Garcia (1971, text-fig. 1). Also, the latter does not mention them and has drawn the stratigraphic column (op. cit., text-fig. 2) only from the griotte (Genicera Formation) onwards. It is not even sure that the Upper Tournaisian to Middle Viséan marly limestones (Gorgera Member) and shales and cherts (Lavandera Member) of the Genicera Formation are present, since the griotte indicated in the stratigraphic column appears to represent only the upper griotte limestone (Canalón Member) dated elsewhere as Late Viséan and Early Namurian (Pendleian and Arnsbergian) on goniatite and conodont evidence (see Wagner et al., 1972). It is quite probable that both formations and the lower members of the Genicera Formation are present but poorly exposed, as is often the case. Our short collecting trip did not permit us to look into this matter.

The Genicera Formation is conformably overlain by the 'Caliza de Montaña', which is the old name for the combined Barcaliente and Valdeteja formations. The dark, fetid, micritic limestones of the Barcaliente Formation, originally described as the Vegacervera Member of the Escapa Formation (Winkler Prins, 1968), start practically everywhere with the Chokierian and continue — at least in the Bernesga area — high into the Namurian B (Marsdenian). The base of the overlying Valdeteja Formation is at the type section considered to coincide practically with the Marsdenian/Yeadonian boundary. It is, however, uncertain whether this boundary is isochronous or (slightly) diachronous because the Barcaliente Formation and the lower part of the Valdeteja Formation are poor in fossils and cannot be exactly dated. The upper part of the Valdeteja Formation has been dated as Namurian C (Yeadonian) and also as early Bashkirian or late Morrowan (Moore et al., 1971, p. 341; Wagner et al., 1972, p. 638). In the section at Meré (Martínez García, 1971, text-fig. 2) the Barcaliente Formation is represented by c. 350 m of gray to black well-bedded, fine-grained limestones, a normal thickness for this formation, followed by only c. 15 m of light gray, coarse-grained, fossiliferous limestone, probably representing the lowermost part of the Valdeteja Formation.

The section continues with 40 m of siliceous shales with chert beds and with 45 m of reddish, yellowish and green soft shales with some siltstone beds. These latter shales are in part richly fossiliferous (see The fauna of the Meré beds). This whole sequence of 85 m seems to be rather condensed and rather different from the San Emiliano or Lena Formation usually found on top of the Valdeteja Formation. A much thinner sequence of similar variegated shales was called 'serie roja inferior' and 'serie abigarrada inferior' by Julivert (1960, p. 50, 61). The 85 m of shales near Meré are here informally called Meré beds, since a detailed study of the section is beyond the scope of this paper and since a detailed comparison with the comparable Ricacabiello Formation of Sjerp (1967, p. 82) seems necessary. The Meré beds are considered to be a lateral equivalent of the Valdeteja Formation, at least in part, and its Namurian (Marsdenian?) age will be discussed below (see chapter Age).

The overlying sequence of shales and sandstones contains rather abundant

plant debris and is obviously deposited under quite different environmental conditions. They can be provisionally assigned to the Beleño Formation of van Ginkel (1965, p. 190).

#### THE FAUNA OF THE MERÉ BEDS

The comparatively rich fauna found in the Meré beds consists — apart from the brachiopods described below — of abundant ostracodes, sponge spicules, some trilobites, cephalopods, bivalves, gastropods, and fucoids, and rare crinoid ossicles, foraminifera, conodonts and anthozoa.

The foraminifera are represented by indeterminable moulds and *Cornuspira*-like specimens; the siliceous sponge spicules are indeterminable, just as the crinoids, the fucoids and the coral.

The conodonts are preserved as moulds and as small fragments; Dr M. van den Boogaard could only identify *Hindeodella* sp. and *Ozarkodina* sp.

A provisional list of the tribolites was given by Dr J. Gandl (in Martínez García 1971, p. 274) and they will be described by him together with other Namurian and lower Westphalian trilobites from the Cantabrian Mountains. The ostracodes have been studied by Dr L. Sánchez de Posada who will publish his results shortly as part of his Doctor's thesis.

The gastropods, being moulds, are indeterminable and some bivalves could be identified by one of us (C.F.W.P.) as Aviculopectinidae indet., *Leptodesma?* sp., *Nuculopsis* sp., and *Parallelodon* sp. The cephalopods are represented by orthocones and goniatites. The latter were described by Mrs C. H. T. Wagner-Gentis (in Moore, Neves, Wagner & Wagner-Gentis, 1971; see also Martínez García, 1971, p. 271) as *Retites semiretia* McCaleb, 1964 and *Retites merensis* sp. nov.

# Systematic descriptions of the brachiopods

The classification and terminology of the 'Treatise' (Moore, 1965) has been followed, unless otherwise stated.

Class Inarticulata Huxley, 1869 Order Acrotretida Kuhn, 1949 Suborder Craniidina Waagen, 1885 Superfamily Craniacea Menke, 1828 Family Craniidae Menke, 1828 Genus Crania Retzius, 1781

Crania? quadrata (M'Coy, 1844) sensu Brunton, 1968 Pl. 1, fig. 1; Pl. 2, fig. 1; Text-fig. 1.

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    1926 Crania pertenuis sp. nov. — Girty, p. 25, pl. 5, figs. 1-3.
    1963 Crania cf. quadrata (McCoy) — Sokolskaja, in Sarytcheva, Sokolskaja,
        Besnossova & Maksimova, p. 66, pl. 1, fig. 8; text-fig. 21.
    1968 Crania quadrata (M'Coy) — Brunton, p. 5, pl. 1, figs. 1-9 (with synonymy).
    1970 Crania quadrata (M'Coy) — Kalashnikov, p. 10, pl. 1, figs. 8-9.
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Diagnosis — Outline irregular, rounded to subquadrate with gently folded margin; ventral valve fixed, dorsal valve subconical, beak closer to the posterior margin; ornamentation of concentric growth lines and scattered spinules; dorsal valve interior with anterior adductor scars close to apex, posterior adductor scars close to valve margin.

Material — One external and three internal moulds of dorsal valves.

Description — All specimens are small but typical for the species, as described by Brunton (1968). The dorsal valve is moderately convex, subconical, and has an irregular quadrate outline with a gently folded margin. The umbo is excentrically placed. The surface is covered with thin concentric growth lines and rather widely spaced, thin spinules, becoming more numerous towards the margin. They are placed in irregular concentric rows.

The interior of the dorsal valve is smooth and no muscle scars could be observed. The small valves belonged probably to neanic individuals that had indistinct muscle scars in their valves. The imperfect preservation (as moulds) makes it impossible to distinguish these, even at rather high magnifications.

All specimens have a length and width of c. 2.5 mm, except one juvenile specimen (RGM 130 075) measuring only 0.5 x 0.6 mm.

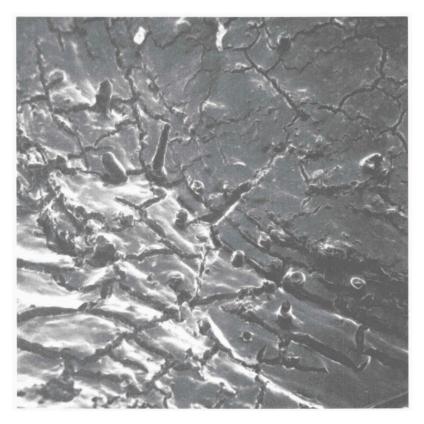


Fig. 1. Crania? quadrata (M'Coy, 1844) sensu Brunton, 1968, locality north of Meré, Namurian Meré beds. Detail of a latex cast of a brachial valve external mould (RGM 130 045; compare Pl. 2, fig. 1) showing the spinules. S.E.M. radiograph, x 100; cracks caused by the vacuum for gilding.

Discussion — The material is closely comparable to the material from Fermanagh (Brunton, 1968), especially to the smallest specimens. It is, however, not certain that the material from Fermanagh and Meré represents M'Coy's species, since Davidson's figures of the type specimen (1861, pl. 48, figs. 1, 2) do not show spinules, nor are they mentioned in his description (op. cit., p. 194), but the spinules are so small that they could easily have been overlooked. On the other hand, Graham (1970, p. 64) could be correct in placing Crania quadrata (M'Coy) into synonymy with Crania ryckholtiana (de Koninck, 1843); unfortunately, the type specimen of C. quadrata can apparently no longer be traced (Graham, 1970, p. 63). If Graham is right, the present species should in our opinion be renamed, since it can easily be distinguished from C. ryckholtiana by the presence of small, scattered spinules, by its less distinct muscle scars and its thinner shell. The fact that the spinules could be observed on the external mould of a dorsal valve from Meré (as pits, and as spinules on the latex cast of the mould: see Fig. 1) corroborates Brunton's opinion that they are not artifacts of the silicification process. If a new name should be given, several names could be available: Crania pertenuis Girty in Roundy, Girty & Goldman, 1926, appears to be similar, but the material was poorly preserved and no mention was made of spinules; the Permian species Crania? kirkbyi Davidson, 1858, appears to be closely related, although bearing more numerous spinules, and it should be restudied before one can decide whether or not C.? quadrata and C.? kirkbyi are conspecific (compare Brunton, 1968, p. 7).

Crania? quadrata (M'Coy) is a secondary homonym of Crania quadrata von Eichwald, 1829, the type species of Pseudolingula Mickwitz, 1909. According to article 59 of the International Code of Zoological Nomenclature (Stoll et al., 1964, see also Yochelson, 1973, p. 1010) M'Coy's name is available since it has never been rejected and both species are no longer considered congeneric.

We agree with Brunton (1968) that this species cannot be assigned to *Petrocrania*. We also agree that the ornamentation of scattered spinules is quite distinct from the spinose ornamentation of *Acanthocrania* and that the punctate shell of the latter also makes it impossible to assign this species to *Acanthocrania*. We are more reluctant, however, to assign this species to *Crania* — a genus based on the clearly distinct Cretaceous species *Anomia craniolaris* Linnaeus, 1758, which was recently revised by Kruytzer (1969) — and think that it should either belong to *Philhedrella* or, more likely, to a new genus. We agree with Brunton (1968) that this matter should be investigated, but our material is certainly too scanty and not well enough preserved to throw new light on this matter. For these reasons we referred this species questionably to the genus *Crania*.

Occurrence — Crania? quadrata (M'Coy) is known from the Lower Carboniferous of north-western Europe and the U.S.S.R., perhaps — when C. pertenuis Girty is considered conspecific — also from the Mississippian of the U.S.A., and now from the Namurian (Marsdenian?) of northern Spain.

Class Articulata Huxley, 1869
Order Orthida Schuchert & Cooper, 1932
Suborder Orthidina Schuchert & Cooper, 1932
Superfamily Enteletacea Waagen, 1884
Family Enteletidae Waagen, 1884
Subfamily Schizophoriinae Schuchert & LeVene, 1929
Genus Schizophoria King, 1850

Schizophoria sp. Pl. 1, fig. 2.

1971 Schizophoria sp. — Winkler Prins, in Martínez García, p. 272.

Material — Two fragmentary internal moulds of complete specimens and one nearly complete internal mould of a pedicle valve.

Description.— Ventri-biconvex shells with a subcircular outline. The ornamentation of fine costae could only be observed on a small fragment of the external mould of a pedicle valve (RGM 143 556).

The interior of the pedicle valve shows two stout dental plates almost parallel to a prominent median septum and only slightly shorter than it; the median septum is about two-fifth the length of the valve. A poorly preserved internal mould of a brachial valve showed the absence of a median septum.

The nearly complete internal mould of a pedicle valve (RGM 143 556) is 12.0 mm long, 12.8 mm wide, and 2.5 mm thick; the other specimens are too fragmentary to permit accurate measuring.

Discussion — Since the material is scanty and no adequate external moulds are present to show details of the ornamentation, no attempt has been made to identify the material specifically. The moderately developed dental plates and median septum in the pedicle valve, the absence of a median septum in the brachial valve, and the external ornamentation seen on the small fragment leave no doubt that this material belongs to the genus *Schizophoria*.

Order Strophomenida Öpik, 1934 Suborder Orthotetidina Cooper & Grant, 1974 Superfamily Orthotetacea Waagen, 1884 Family Schuchertellidae Williams, 1953 Subfamily Schuchertellinae Williams, 1953

Genus Drahanorhynchus Havlíček, 1967

Type species — by original designation Drahanorhychus drahanicus Havlíček, 1967.

Diagnosis — Small schuchertellids with an ornamentation of c. 10 primary costae with up to 3 secondary costae between each pair. Pedicle valve moderately convex to semi-conical with a high interarea and a strongly arched pseudodeltidium. Brachial valve practically flat (slightly concave) without an interarea. Pedicle valve interior without dental plates and a median septum, muscle field weakly developed. Brachial valve interior with long dentifers (= brachiophores) fused to a broad, bilobed cardinal process and diverging from it but usually soon recurving and running parallel to the hinge; in ephebic specimens well developed transmuscle septa are developed. The shell substance appears to be pseudopunctate to judge from the granular surface of the internal moulds, but this could not be ascertained since this genus is only known from moulds.

Discussion — The genus Drahanorhynchus belongs undoubtedly to the subfamily

Schuchertellinae — as it has been revised by Cooper & Grant (1974), although they have omitted it from their list of genera included in the subfamily — with Goniarina Cooper & Grant, 1969, as its closest relative. The revival of the superfamily Orthotetacea Waagen, 1884, by Cooper & Grant (1974) seems quite logical, but to give Waagen as the author of the suborder Orthotetidina (erroneously spelled Othotetidina by them) is in our opinion incorrect according to the rules of the Code (Stoll et al., 1964), since a suborder does not belong to the family-group and is therefore not of co-ordinate status. Accordingly, the suborder is considered a new taxon created by Cooper & Grant (1974).

The brachiophores (dentifers of Cooper & Grant, 1974) diverge from the cardinal process, but do not in our opinion always continue parallel to the hinge as Havlíček (1967, p. 204) states in his diagnosis of the genus. In the broad brachial valves of the type species this is a common feature, although one rather narrow specimen (op. cit. pl. 47, fig. 4) shows slightly diverging dentifers. Our narrower Spanish species — D. cantabricus — shows clearly diverging dentifers, but is nevertheless considered congeneric. The fine spinules on the costae mentioned by Havlíček (1967, p. 204) are hardly visible on his figures, but a cursory examination of the type material by one of us (C.F.W.P.) — kindly put at his disposal by Dr Havlíček during a short stay in Prague in connection with the Field and General Meeting of the Subcommission on Carboniferous Stratigraphy in 1973 — revealed the presence of the pits representing the spinules; these can also be seen on material of Drahanorhynchus paeckelmanni (Gallwitz, 1932) from Aprath (see Fig. 2). The absence of these pits from the moulds of D. cantabricus could perhaps be due to a less favourable conservation.

Apart from the type species — D. drahanicus — and our new species D. cantabricus, Streptorhychus (Schuchertella) paeckelmanni Gallwitz, 1932, is here also assigned to Drahanorhynchus, despite its moderate convexity. A study of the type material, kindly put at the disposal of one of us (C.F.W.P.) by the Director of the Museum für Naturkunde der Humboldt Universität (Berlin, German Democratic Republic), Dr H. Jaeger, and of material collected at the classical locality of Aprath by one of us (C.F.W.P.) during a short fieldtrip with Dr E. Paproth (Geologisches Landesamt Nordrhein-Westfalen, Krefeld) showed that this species has the ornamentation and internal structure typical for Drahanorhynchus (see Fig. 2). Streptorhynchus (Streptorhynchus) minimus Gallwitz, 1932, could possibly also belong to this genus, since it has the typical shape and ornamentation. The

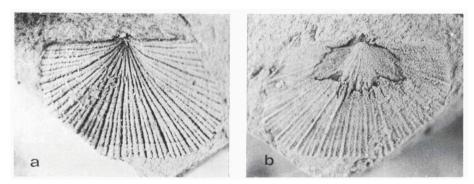


Fig. 2. Drahanorhynchus paeckelmanni (Gallwitz, 1932). Brachial valve from the late Viséan (Goniatites Zone α) Posidonia Shales of Aprath (German Federal Republic), RGM 143 968, x 10, coated with ammonium chloride; a: external mould; b: internal mould showing the well developed transmuscle septa, typical for Drahanorhynchus, and the granulose internal surface.

internal structure of the brachial valve could, however, not be observed on the type material, also kindly put at our disposal by Dr H. Jaeger, and no other material of this species was available to us.

Functional morphology — The large cardinal process is a logical adaptation to the almost conical pedicle valve; it was necessary both for articulation and for attachment of strong diductor muscles. Similarly, the transmuscle septa served for attachment of strong adductor muscles.

Range — Upper Devonian (?) and Lower Carboniferous of Germany and Czechoslovakia; Namurian (Marsdenian?) of northern Spain.

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Drahanorhynchus cantabricus sp. nov. Pl. 1, figs. 3-10; Pl. 2, fig. 2; Pl. 3, fig. 1.
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1971 Schuchertella aff. paeckelmanni Gall. — Winkler Prins, in Martínez García, p. 272.

Holotype — Internal mould of a brachial valve (RGM 143 559, Pl. 1, fig. 8).

Type locality — Locality opposite kilometre-post 8, north of Meré.

Type horizon — The Meré beds of Namurian (Marsdenian?) age.

Derivatio nominis — This species is named after the Cantabrian Mountains, where the type locality is situated.

Diagnosis — Rather small, subquadrate, nearly plano-convex species of Drahano-rhynchus with dentifers distinctly diverging from the hinge; pedicle valve moderately convex except for juvenile specimens that are semi-conical; ornamentation of c. 12 primary costae with up to 3 secondary costae in between, originated by branching on the pedicle valve and by intercalation on the brachial valve.

Material — Rather numerous (c. 50) external and internal moulds of both valves, including juveniles.

Description — The shell is small (see Table 1), subquadrate and practically plano-convex. The width of the hinge is only slightly less than the greatest width, that occurs near the middle of the shell. The pedicle valve is moderately convex, only juvenile specimens being semi-conical, the interarea is accordingly moderately high (1.7 mm in a specimen 4.0 mm long: RGM 143 578) and is practically catacline, except for some specimens obviously deformed by compaction. The ornamentation consists of c. 12 primary costae with up to 3 secondary costae branching off, so that a total of 46 costae can be counted at the anterior margin; no spinules were observed on the costae. The brachial valve is flat, or slightly concave, with a slightly convex umbonal part; an interarea is lacking. The ornamentation is similar to the one on the pedicle valve, but the secondary costae are intercalated.

The interior of the pedicle valve lacks a median septum and dental plates, the dental ridges are prominent and the lanceolate adductor scars in the umbonal part are usually weakly developed. The interior of the brachial valve has dentifers fused with the broad, bilobed cardinal process and markedly diverging from the hinge. Ephebic specimens have transmuscle septa consisting of a median ridge

| Specimen    | L p.v. | L b.v. | W   | W hinge |
|-------------|--------|--------|-----|---------|
| RGM 143 560 | 1.0    |        | 1.2 | 1.2     |
| RGM 143 582 | 2.3    |        | 3.4 | 3.4     |
| RGM 143 587 | 3.0    |        | 4.6 | 4.5     |
| RGM 143 568 | 3.0    |        | 5.0 | 4.5     |
| RGM 143 578 | 4.0    |        | 5.6 | 4.9     |
| RGM 143 562 | 6.5    |        | 9.0 | 8.2     |
| RGM 143 567 |        | 0.8    | 1.1 | 1.1     |
| RGM 143 582 |        | 1.3    | 1.5 | 1.4     |
| RGM 143 583 |        | 1.3    | 1.7 | 1.5     |
| RGM 143 559 |        | 2.8    | 3.3 | 3.0     |
| RGM 143 576 |        | 4.2    | 5.5 |         |
| RGM 143 581 |        | 4.5    | 6.5 | 5.4     |

Table 1. Measurements (in mm) of Drahanorhynchus cantabricus sp. nov.

and up to four accessory ridges at each side of the median ridge, the number on both sides not always being the same. No granules have been observed on the surface of the internal moulds.

Discussion — D. cantabricus differs from the type species of Drahanorhynchus in its less transverse shape, less conical pedicle valve, in the dentifers diverging markedly from the hinge, and in its more numerous primary costae. D. paeckelmanni (Gallwitz) is distinguished from our species by its larger size, its even less convex pedicle valve, the presence of a median sulcus bounded by two broad, low, rounded folds on the brachial valve, and the dentifers running nearly parallel to the hinge. Our species differs from both afore mentioned species by the absence of spinules on the costae and by the absence of pits on the interior surface, but this may be due to a less favourable preservation.

Occurrence — Drahanorhynchus cantabricus is sofar only known from its type locality and type horizon.

Suborder Chonetidina Muir-Wood, 1955 Superfamily Chonetacea Bronn, 1862 Family Anoplidae Muir-Wood, 1962 Subfamily Anoplinae Muir-Wood, 1962

Genus Anopliopsis Girty, 1938

Type species — by original designation Chonetina subcarinata Girty, 1926.

Diagnosis — Small, subtrigonal anopliid with greatest width at the hinge, very narrow interareas, smooth shell surface except for a few prominent growth lines, spines extending at high angle to hinge of pedicle valve. Pedicle valve interior with rather short median septum continued anteriorly as a ridge, radially aligned pustules that may coalesce in gerontic individuals to form radial ridges (see Discussion below); minute teeth. Brachial valve interior with rather long anderidia, without a median septum but with two diverging septa and several additional radial ridges developed from the radial rows of pustules; minute cardinal process, presumably bilobed and externally quadrilobed; short curved prosocket ridges along the hinge; comparatively large alveolus.

Discussion — The Anopliinae have been quite rightly raised to family level by Boucot & Harper (1968), after the numerical analysis of the Chonetacea by Rowell (1967) had already shown that this group is a major separate unit. No attempt has so far been made to subdivide this family although one could easily distinguish two or more separate groups that would merit a subfamily status. Since, however, the relation between the different genera is poorly understood at the moment, we preferred not to subdivide the family.

Anopliopsis is inadequately known since the type species still poses some questions. Material from the Boone Limestone (= Chappel Limestone, see Carter, 1967) of San Saba County, Texas, from the Moorefield Shale (= Mayes Formation) of Oklahoma, and from the Fort Payne Chert and Ridgetop Shale of Tennessee was originally described as Chonetina subcarinata, but it is doubtful whether all specimens really belong to one species (and even to one genus), since the internal structure of most of the material is inadequately known. The description of A. subcarinata is based on the Tennessee material, as is explicity stated by Girty (1926, p. 27; 1938, p. 281), and it would be logical to choose as the lectotype one of the original figured specimens from Tennessee (Girty, 1926, pl. 5, figs. 10-12). These specimens were described as pedicle valves, but two of them were reinterpreted as internal casts of pedicle valves (Muir-Wood, 1962, pl. 5, figs. 1, 3), which seems to be quite reasonable since they show clearly a narrow groove marking the median septum. They show no trace of additional radial ridges, only one internal mould (Girty, 1938, fig. 10) does. The latter specimen is also from the Fort Payne Chert of Tennessee and could either be an aberrant (gerontic?) specimen with the radially aligned pustules fused to ridges, or a distinct (costate?) species. The genus and its type species should be revised on topotype material from Tennessee, but until this has been done it seems wisest not to attach too much importance to the radial ridges in the pedicle valve. The brachial valve, on the other hand, does show several prominent additional ridges.

So far only the type species has been assigned to *Anopliopsis*. Our new species — A.? parva — is only tentatively assigned to this genus, because it has a distinct, though very narrow, median sulcus in the pedicle valve and because the additional radial ridges are not as well developed as in the type species, and not at all in the pedicle valve. It has not been assigned to the closely related *Chonetina* because it has only a weakly developed median sulcus and not such prominent growth lines; besides *Chonetina* is so far only known from the Permian.

Functional morphology — The Chonetidina were generally considered schizolophous, partly with a low spirolophe (see Muir-Wood, 1962; Muir-Wood, in Moore, 1965), but Grant (1972, p. 233) argued convincingly that the spirolophe was in fact a ptycholophe similar to the one found in the closely related Productidina.

The Chonetidae could have accomodated a schizolophous lophophore that developed into a slightly modified Falafer-type ptycholophe. The lophophore of the Anopliidae, on the other hand, had a somewhat different development. After an initial trocholophous stage — possibly longer continued in Caenanoplia — a different type of schizolophe was developed with two diverging lobes as can be inferred from the two diverging septa that developed instead of a median septum. The two diverging septa could have effectively separated the lateral (inhalant?) currents from the central (exhalant?) current.

In some anopliids (e.g. Anopliopsis) several additional septa were developed,

thus indicating a multilobed ptycholophe comparable to the one of *Chonetina* (see Grant, 1976, p. 65, fig. 11). In *Tornquistia* a median ridge is sometimes developed indicating that a median indentation of the schizolophe occurred. The aberrant *Caenanoplia* could have remained trocholophous throughout life, but the two more prominent radial rows of pustules sometimes found — suggesting the two diverging septa normally encountered in anopliids — may indicate a poorly developed schizolophe.

Range — Mississippian of the U.S.A., Lower Carboniferous of the U.S.S.R.; now probably also found in the Namurian (Marsdenian?) of Spain.

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Anopliopsis? parva sp. nov.
Pl. 2, fig. 3; Pl. 3, figs. 2-11; Pl. 4, figs. 1-2.
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Holotype — Internal and external mould of a brachial valve (RGM 143 684: Pl. 3, fig. 6). Type locality — Locality opposite kilometre-post 8, north of Meré. Type horizon — The Meré beds of Namurian (Marsdenian?) age. Derivatio nominis — From its small size (Latin: parvus = small).

Material — Many (c. 150) internal and external moulds of both valves.

Diagnosis — Very small, rounded triangular, strongly concavo-convex species, presumably belonging to Anopliopsis, with a smooth surface except for a few growth lines; narrow median sulcus in the pedicle valve, interareas hardly perceptible. Pedicle valve interior with a prominent median septum continuing to the anterior margin as a high ridge, radially aligned pustules only in large (gerontic?) specimens, rather long teeth. Brachial valve interior with small prosocket ridges slightly diverging from the hinge, rather long anderidia, two prominent lateral septa starting in front of a deep and large alveolus and almost reaching the anterior margin, radial rows of pustules sometimes forming additional radial ridges anteriorly.

Description — Very small (see Table 2), strongly concavo-convex shells of rounded triangular to almost subquadrate shape with a thin body cavity; the interareas are very narrow, usually hardly perceptible. The pedicle valve is strongly convex with a very narrow median sulcus starting below the umbo, and with large flattened ears; the surface is smooth except for a few growth lines; there are at least two spines on each side of the umbo in the larger specimens, but they are unfortunately not well enough preserved to observe their angle with the hinge. The brachial valve is strongly concave with flat ears and a large, elongate oval notch posteriorly, sometimes a weak median fold is developed; the surface is smooth with a few indistinct growth lines.

The pedicle valve interior shows a short, prominent median septum continued as a broad ridge with pustules on it, corresponding with the median sulcus, usually reaching the anterior margin; the teeth are relatively long and diverge slightly from the hinge; the internal surface of the small specimens is apparently smooth, occasionally with a few scattered pustules, the large specimens on the contrary show prominent, radially aligned pustules except along the median ridge where lanceolate muscle scars can be seen (Pl. 3, fig. 11). The brachial valve interior shows small prosocket ridges slightly diverging from the hinge; it has

| Specimen    | L p.v. | L b.v. | W    |  |
|-------------|--------|--------|------|--|
| RGM 143 685 | 0.7    |        | 1.0  |  |
| RGM 143 666 | 0.8    |        | 1.4  |  |
| RGM 143 597 | 0.9    |        | 1.0  |  |
| RGM 143 689 | 1.0    |        | 1.6  |  |
| RGM 143 686 | 1.2    |        | 1.4  |  |
| RGM 143 687 | 1.2    |        | 1.7  |  |
| RGM 143 683 | 1.4    |        | 1.8  |  |
| RGM 143 670 | 2.3    |        | 3.4  |  |
| RGM 143 654 | 2.8    |        | 3.5  |  |
| RGM 143 680 |        | 0.6    | 0.8  |  |
| RGM 143 666 |        | 0.7    | 1.0  |  |
| RGM 143 595 |        | 0.8    | 0.9  |  |
| RGM 143 658 |        | 1.0    | >1.2 |  |
| RGM 143 684 |        | 1.1    | 1.4  |  |
| RGM 143 687 |        | 1.1    | 1.5  |  |
| RGM 143 690 |        | 1.3    | 1.4  |  |

Table 2. Measurements (in mm) of Anopliopsis? parva sp. nov.

prominent anderidia of about one-third the valve length, a minute cardinal process that is bilobate and externally quadrilobate, and minute chilidial plates; two long diverging lateral septa start in front of a deep and large alveolus and some radial rows of pustules often coalesce to form additional ridges on the anterior part of the valve; a few large pustules are found on the ears.

Discussion — From the type species of Anopliopsis our species can be easily distinguished by its small size and by the narrow sulcus in the pedicle valve; besides, it has less well developed radial ridges in the brachial valve and none at all in the pedicle valve (see also the Discussion of Anopliopsis). From Tornquistia? schmiereri Paeckelmann, 1930, a poorly known species that may belong to Anopliopsis, our species can easily be distinguished by its much narrower median sulcus in the pedicle valve.

Occurrence — Anopliopsis? parva is only known from its type locality and type horizon.

Genus Caenanoplia Carter, 1968

Caenanoplia martinezi sp. nov. Pl. 5, figs. 1-5; Pl. 6, figs. 1-2; Pl. 14, fig. 6.

E.P. 1971 Tornquistia polita McCoy — Winkler Prins, in Martínez Gracía, p. 271. 1971 Rugosochonetes sp. — Winkler Prins, in Martínez García, p. 271.

Holotype — Internal and external mould of a brachial valve (RGM 143 655: Pl. 6, fig. 2).

Type locality — Locality opposite kilometre-post 8, north of Meré.

Type horizon — The Meré beds of Namurian (Marsdenian?) age.

Derivatio nominis — This species is named in honour of Dr Enrique Martínez García who discovered the locality and provided one of us (C.F.W.P.) with the initial collection (see p. 2).

Material — Nearly one hundred internal and external moulds of both valves.

Diagnosis — Medium sized, rather weakly to moderately concavo-convex species

of Caenanoplia with a transversely subquadrate outline; usually ornamented by up to 20 low, broad costae, sometimes practically smooth, with radially aligned spicules forming an irregular quincunx, costae crossed by numerous growth lines; interareas of medium height; 2-4 spines on each side of the pedicle valve umbo at high angle to hinge. Pedicle valve interior with a short median septum, small teeth, pustules in radial rows except where the muscle scars are; brachial valve interior without lateral septa or a median septum, with small anderidia, pustules in radial rows, sometimes two more prominent rows suggest two lateral septa; without brachial ridges.

Description — The shells are medium sized (see Table 3), transversely rectangular with the greatest width at or near the hinge, the cardinal angles being approximately rectangular. The ornamentation consists on both valves of weakly developed, broad, rounded, simple costae that may be practically imperceptible and are absent from the ears; radial rows of spicules occur on the costae and form an irregular quincunx; the costae are crossed by numerous growth lines that are especially prominent on the ears. The pedicle valve is moderately or weakly convex, somewhat flattened on the venter; it has medium sized, well demarcated, slightly convex ears; the interarea is of medium height, apsacline, with a small pseudo-deltidium in the apex of the delthyrium; 2-4 pairs of spines extend at a high angle to the hinge and are symmetrically placed on each side of the umbo. The brachial valve is moderately concave to almost flat, leaving a narrow body cavity, the ears are flattened; the interarea is as high as the one of the pedicle valve, it is hypercline; the chilidial plates are small.

The pedicle valve interior has a short median septum and narrow teeth, the muscle scars are weakly developed and posteriorly bounded by a small, faint ridge; the internal surface is usually weakly costate, especially near its anterior margin, and covered by radial rows of pustules — except where the muscle scars are — being large on the flanks and becoming small and sometimes obsolete on the ears. The brachial valve interior has a small, quadrilobate cardinal process, supported by strong prosocket ridges that diverge slightly from the hinge, the external socket ridges are narrow, the alveolus is deep and rather large, and the anderidia are small; the internal surface is covered by radial rows of pustules except on the ears which are smooth; two rows in the central part may be slightly more prominent thus suggesting the lateral septa generally found in the Anopliidae.

| Specimen    | L p.v. | L b.v. | W   | W hinge |
|-------------|--------|--------|-----|---------|
| RGM 143 639 | 2.5    |        | 3.3 | 3.3     |
| RGM 143 658 | 3.2    |        | 4.5 | 4.2     |
| RGM 143 623 | 3.3    |        | 6.0 | 5.2     |
| RGM 143 643 | 3.8    |        | 6.5 | 5.6     |
| RGM 143 656 | 4.2    |        | 6.0 | 5.5     |
| RGM 143 694 | >4.0   |        | 7.3 | 6.9     |
| RGM 143 624 |        | 3.0    | 4.8 | 3.9     |
| RGM 143 752 |        | 3.7    | 6.0 | 6.0     |
| RGM 143 655 |        | 3.8    | 6.1 | 5.6     |
| RGM 143 624 |        | 5.0    | 8.6 | 8.6     |
| RGM 143 693 |        | 5.8    | 9.2 | 9.2     |

RGM 143 654

Discussion — Despite the absence of true lateral septa, we fully agree with

6.2

7.6

8.4

Carter (1968) that *Caenanoplia* is an anopliid, the two slightly more prominent radial rows of pustules occasionally found unmistakingly point in that direction (see also the paragraph Functional morphology of the description of *Anopliopsis*).

Our species has been assigned to Caenanoplia because it shows the typical external and internal features, such as the weak costation and the lack of septa in the brachial valve. It differs, however, from the type species — Caenanoplia burlingtonensis Carter, 1968 — in its less tumid pedicle valve, in the short median septum of the pedicle valve, and in the absence of brachial ridges from the brachial valve interior; besides, our species is almost rectangular instead of rounded triangular, weakly concavo-convex, and not lamellose. C. gibberula (Carter, 1967) differs from our species by its more extended hinge, its strongly concavo-convex shell, and its less numerous spines. C. logani (Norwood & Pratten, 1855) is distinguished by its strongly concavo-convex shell and by its larger size.

A few small, subquadrate, weakly concavo-convex specimens with up to 40 prominent costae are also assigned to this species (see Pl. 5, fig. 1). These are the specimens provisionally identified as *Rugosochonetes* sp. by Winkler Prins (in Martínez García, 1967, p. 271).

Occurrence — Caenanoplia martinezi has only been found at the type locality in the type horizon. This genus has thus far only been described from the Mississippian of the U.S.A.

Genus Tornquistia Paeckelmann, 1930

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Tornquistia cf. T. polita (M'Coy, 1852)
Pl. 6, figs. 3-5.
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E.P. 1930 Chonetes (Tornquistia) politus M'Coy — Paeckelmann, p. 227, pl. 15, figs. 11, 12.
E.P. 1962 Tornquistia polita (McCoy) — Muir-Wood, p. 61, pl. 5, figs. 18, 19, 22; text-fig. 12.
1968 Tornquistia polita (McCoy) — Winkler Prins, p. 112 (with synonymy).
1970 Tornquistia cf. polita (McCoy) — Brand, p. 96, pl. 8, figs. 4-6 (with synonymy).
E.P. 1971 Tornquistia polita (McCoy) — Winkler Prins, in Martínez García, p. 271.
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Material — Several (c. 15) internal and external moulds of both valves, usually lying together.

Description — The shells are weakly to moderately concavo-convex, rounded rectangular to somewhat triangular in outline, the surface is smooth, no growth lines were observed due to the poor preservation. The pedicle valve has a somewhat tumid venter; the interarea is broad triangular, rather narrow, and generally fragmentary preserved; 3-4 pairs of spines extend at a large angle to the hinge and are symmetrically placed on each side of the umbo. The brachial valve is weakly to moderately concave, only remnants of an interarea were observed.

The pedicle valve interior has a short median septum and rather strong teeth; the two septa of the brachial valve interior often show as fine slits in the internal mould of the pedicle valve indicating that the septa completely sealed off the central part when the valves were closed. The brachial valve interior has a small quadrilobate cardinal process, small chilidial plates, and a minute alveolus; prosocket ridges and anderidia were not observed due to the fragmentary preservation; two high diverging lateral septa start somewhat in front of the alveolus, they are about half the valve length; a median ridge may be developed or only

indicated by a row of pustules, and the radial rows of pustules may form faint ridges outside the two lateral septa. For a functional interpretation of the septa see the description of *Anopliopsis*.

A large specimen consisting of both valves spread open (RGM 143 653) has a valve length of 3.6 mm and a width of 5.6 mm. A juvenile pedicle valve (RGM 143 646) is 2.2 mm long and 4.2 mm wide.

Discussion — It is at the moment uncertain whether the more or less quadrate to transversely rectangular forms fall within the variability range of *T. polita*, whose type specimen is triangular (Brand, 1970, pl. 8, fig. 3), so we followed Brand's usage and referred to our specimens as *Tornquistia* cf. *T. polita* (M'Coy).

Range — Tornquistia cf. T. polita occurs all over Europe in the Lower Carboniferous and Namurian. Whether the specimens from the uppermost Devonian of Western Germany (Gallwitz, 1932, p. 113, pl. 8, figs. 8-9) should also be assigned to this species is doubtful.

Tornquistia scutiformis sp. nov. Pl. 7, figs. 1-10.

Holotype — Internal mould of a brachial valve (RGM 143 706: Pl. 7, fig. 10). Type locality — Locality opposite kilometre-post 8, north of Meré. Type horizon — The Meré beds of Namurian (Marsdenian?) age. Derivatio nominis — This species is named after its heraldic shield-shape.

Material — Several (c. 25) internal and external moulds of both valves.

Diagnosis — Small, scutiform, weakly concavo-convex species of Tornquistia; ornamentation of growth lines and occasionally a few costae, which are most prominent on the ears; interareas narrow. Pedicle valve interior with prominent median septum, c. one-third the valve length; brachial valve interior with a deep, elongate alveolus; two lateral septa start in front of the alveolus, few inconspicuous pustules in radial rows, anderidia not observed.

Description — The shell is small (see Table 4), scutiform. The pedicle valve is weakly convex, has a narrow interarea, and c. 3 spines on each side of the umbo; the ornamentation consists of growth lines and occasionally a few simple costae can be observed. The brachial valve is weakly concave, almost flat, has a narrow interarea, a small, presumably bilobed, cardinal process, and a prominent, elongate notch corresponding to the alveolus; the ornamentation is similar to the one of the pedicle valve; sometimes two splits are present in the external moulds of brachial valves, probably representing the lateral septa of the interior, crushed through the valve.

The pedicle valve interior has a prominent median septum about one-third the length of the valve, and minute teeth. Some specimens show a few simple costae, especially on the ears (see Pl. 7, fig. 7). The brachial valve interior has a comparatively deep, elongate alveolus. Two lateral septa (in juvenile specimens represented by two diverging rows of pustules) start well below the alveolus, a few inconspicuous additional pustules occur in radial rows. The cardinal process was

| Specimen    | L p.v. | L b.v. | W   |  |
|-------------|--------|--------|-----|--|
| RGM 143 701 | 1.2    |        | 1.5 |  |
| RGM 143 734 | 1.6    |        | 2.0 |  |
| RGM 143 696 | 1.8    |        | 1.8 |  |
| RGM 143 708 | 2.0    |        | 2.6 |  |
| RGM 130 053 |        | 1.0    | 1.4 |  |
| RGM 143 698 |        | 1.5    | 1.6 |  |
| RGM 143 704 |        | 1.5    | 2.0 |  |
| RGM 143 697 |        | 1.8    | 2.0 |  |

Table 4. Measurements (in mm) of Tornquistia scutiformis sp. nov.

not well preserved, it is presumably quadrilobed internally; anderidia were not observed. The holotype shows well developed prosocket ridges, slightly diverging from the hinge (see Pl. 7, fig. 10).

Discussion — These small specimens are considered a distinct species and not juveniles of *Tornquistia* cf. *T. polita* because the latter are much broader, more strongly concavo-convex, and they do not show an incipient costation. They can neither be juveniles of *Caenanoplia martinezi* because they have two distinct lateral septa in the brachial valve and the incipient costation is not-confined to the median part of the shell but on the contrary is most prominent on the ears.

T. scutiformis is easily distinguished from most other species of Tornquistia by its small size. From the small T. diminuta (Demanet, 1949), our new species is distinguished by its much less concavo-convex shape (cf. Winkler Prins, 1968, p. 112).

Occurrence — Tornquistia scutiformis is only known from its type locality and type horizon.

Suborder Productidina Waagen, 1883 Superfamily Productacea Gray, 1840 Family Productellidae Schuchert & LeVene, 1929 Subfamily Productellinae Schuchert & LeVene, 1929

Productellinarum gen. & sp. nov. Pl. 8, figs. 1-3.

Material — Five fragmentary internal moulds of pedicle valves and three external moulds of brachial valves.

Description — Almost plano-convex productellid with a broad transverse outline, the greatest width occurring at the hinge margin. The brachial valve is nearly flat and shows numerous, irregular rugae. The cardinal process is externally bilobate with widely diverging lobes.

The pedicle valve interior is practically smooth, apart from a few fragments of internal moulds of spines which are preserved close to the hinge. One mould of a spine in connection with a fragmentary internal mould of a pedicle valve shows that they can reach a great length in comparison to the size of the shell.

The largest pedicle valve (RGM 143 758) is 4.8 mm long and over 6 mm wide; the largest brachial valve (RGM 143 759) has a length of 3.4 mm and a width of 4.6 mm.

Discussion — The shape, ornamentation, and especially the widely diverging lobes of the cardinal process make us assign this species to the Productellidae, and the absence of teeth points more in particular to the Productellinae. The species is unlike any other species known to us and appears to belong to a new genus, but the material — lacking exteriors of the pedicle valve and interiors of the brachial valve — is obviously inadequate to establish a new genus and species. The material most closely resembles the genus *Chonetipustula*, from which it is distinguished by the absence of rugae on the internal moulds of the pedicle valve and the rather indistinct rugae on the external moulds of the brachial valve, indicating a poorly developed, superficial rugation.

Family LEIOPRODUCTIDAE Muir-Wood & Cooper, 1960 Subfamily LEIOPRODUCTINAE Muir-Wood & Cooper, 1960

Genus Aseptella gen. nov.

Type species — Aseptella asturica gen. & sp. nov.

Derivatio nominis — From the Latin: a = without, and septum = plate, ridge; in view of the absence in ephebic individuals of a median septum in the brachial valve.

Diagnosis — Rather small, concavo-convex, transversely rectangular productid with rugose ornamentation; ephebic specimens bearing a flange. Pedicle valve with few, large spines along hinge and in a row on both flanks; brachial valve without spines, but with a few dimples. Pedicle valve interior with spine openings, pustulose, with lanceolate adductor scars separated by a narrow myophragm and enclosed within large rather vague diductor scars; brachial valve interior pustulose, especially anteriorly, with poorly developed brachial ridges given off at an angle of c. 45°, with strong marginal ridges diverging from the hinge and sealing off the ears from the visceral disc, median septum generally absent, except in some juvenile specimens where it is developed as a short, narrow ridge, cardinal process internally bilobed, externally quadrilobate.

Discussion — Aseptella has an ornamentation of prominent rugae and regularly scattered spines as in Acanthoplecta, but it is smaller, less strongly geniculated, has a different spine arrangement, and lacks a median fold on the pedicle valve. Besides, the interior of the brachial valve of Acanthoplecta is quite different in having a well-developed median septum and in the marginal ridges being parallel to the hinge and not sealing off the ears. Another distinguishing feature is the flange around both valves in some large, ephebic or perhaps gerontic, specimens of A. asturica.

On the base of its ornamentation and part of its internal structure (e.g. the cardinal process) the genus is assigned to the Leioproductinae, although its internal structure might eventually warrant the erection of a separate subfamily.

No other species are assigned to Aseptella. Pustula inconspicua Girty, 1926, however, looks superficially similar and might prove to belong to this genus. It is distinguished from A. asturica by its smaller size, less convex pedicle valve and correspondingly less concave brachial valve, and its semicircular instead of rectangular outline; its internal structure is unknown and no spines were observed. Carter (1967, p. 267, 268) considers the specimens of Pustula inconspicua to be juveniles of an indeterminate productid and does not recognize the species; he

gives, however, no sound reasons for his opinion other than the small size of the specimens.

Range — Sofar, Aseptella is only known with certainty from the type locality in northern Spain, from strata of Namurian (Marsdenian?) age.

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Aseptella asturica gen. & sp. nov.
Pl. 4, fig. 3; Pl. 8, figs. 4-10; Pl. 9, figs. 1-9; Pl .14, fig. 6; text-fig. 3.
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1970 Chonetipustula sp. nov. — Winkler Prins, in Martínez García, p. 274.

Holotype — Incomplete internal mould of the brachial and pedicle valves and external mould of the pedicle valve of one and the same specimen (RGM 143 736: Pl. 9, fig. 2).

Type locality — Locality opposite kilometre-post 8, north of Meré.

Type horizon — The Meré beds of Namurian (Marsdenian?) age.

Derivatio nominis — Latin: Asturicus — Asturian, from the region Asturias, where the type locality is situated.

Diagnosis — See the diagnosis of the genus.

Material — Almost one hundred internal and external moulds of both valves.

Description — The shell is small (see Table 5), concavo-convex, transversely rectangular with the greatest width near mid length, cardinal extremities often rounded, nearly rectangular; the body cavity is normal for its size. The pedicle valve is strongly convex, the visceral disc has steep flanks and is well separated from the slightly convex ears, the umbo is incurved over the hinge; in large, ephebic or perhaps gerontic, specimens a smooth, flat flange borders the valve at a nearly right angle. The ornamentation consists of widely separated, prominent rugae up to 20 in number, nearly rectangular in shape like the outline of the shell, but anteriorly slightly incurved in a broad undulation at the middle; and long stout spines placed on the smooth band between the rugae in a row along the hinge and in a row on the flanks, the median portion of the visceral disc bearing no spines, their total number can exceed 12 (the often poor preservation of the external moulds makes it impossible to give an exact maximal number). The brachial valve is moderately concave with rather large flattened ears; it is rugose like the pedicle valve but the rugae are of course somewhat more crowded; it has no spines but shows a few dimples corresponding to the row of spines along the hinge of the pedicle valve.

The interior of the pedicle valve shows distinct, lanceolate, non-dendritic adductor scars separated by a thin but prominent myophragm, surrounded by large, indistinct diductor scars covered with taleolae; fragmentary internal moulds of the spines arise from the internal moulds proving that the spine openings were not sealed off from the interior. The interior of the brachial valve shows strong lateral ridges diverging from the hinge and forming prominent ear baffles which seal off the ears and terminate before reaching the anterior margin; a weakly developed median septum can only be seen in some juvenile specimens (Pl. 9, fig. 6: the groove representing the median septum is exaggerated in the picture) and is absent in the adults, probably embedded in callose material; the adductor scars are represented by two symmetrical areas

| Specimen    | L p.v. | L b.v. | W   |  |
|-------------|--------|--------|-----|--|
| RGM 143 737 | 1.8    |        | 2.6 |  |
| RGM 143 671 | 2.0    |        | 2.3 |  |
| RGM 143 723 | 2.0    |        | 2.8 |  |
| RGM 143 687 | 2.3    |        | 3.2 |  |
| RGM 143 728 | 3.3    |        | 5.5 |  |
| RGM 143 659 | 3.5    |        | 4.6 |  |
| RGM 143 741 | 5.0    |        | 7.3 |  |
| RGM 143 662 | 5.0    |        | 7.5 |  |
| RGM 143 688 |        | 1.4    | 2.4 |  |
| RGM 143 744 |        | 1.8    | 2.5 |  |
| RGM 143 663 |        | 3.2    | 4.5 |  |
| RGM 143 738 |        | 3.5    | 6.4 |  |
| RGM 143 736 |        | 4.3    | 5.5 |  |
| RGM 143 730 |        | 4.5    | 7.3 |  |
| RGM 143 742 |        | 4.8    | 6.5 |  |
| RGM 143 661 |        | 5.3    | 7.4 |  |

Table 5. Measurements (in mm) of Aseptella asturica gen. & sp. nov.

with prominent taleolae; the brachial ridges are indistinct, given off at an angle of c. 45°; the anterior border is covered with taleolae which reach in the anteromedian part between the adductor scars, the ears are smooth; the cardinal process is bilobed, externally quadrilobed (see Fig. 3).

Discussion — In the discussion of the genus a comparison is made with the inadequately known species *Pustula inconspicua* Girty, 1926; we do not know any other species comparable to ours which can easily be distinguished by its small size, its ornamentation, and the internal structure of the brachial valve.

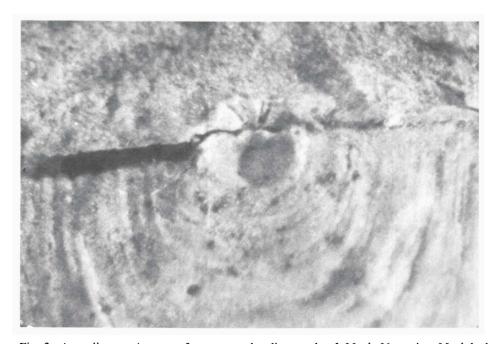


Fig. 3. Aseptella asturica gen. & sp. nov., locality north of Meré, Namurian Meré beds. Posterior part of the external mould of a brachial valve showing the quadrilobed cardinal process, RGM 143 732, x 11.

It is not clear whether the flange — a smooth, flat rim bordering the lateral and anterior margins of both valves and forming a large angle with the remainder of the valves (nearly a right angle in pedicle valves) — is of specific or even generic importance, or merely a gerontic feature. It seems to be a rather constant feature of large valves, although the preservation of the moulds does not always permit its observation. The function of a flange in general, and of the one of Kochiproductus coronus in particular, was discussed by Shiells (1968, p. 493), who apparently favoured the explanation of the flange as a support to prevent the shell from sinking in the soft mud and as a protection of the visceral cavity against fine detritic material. Both functions would have been of great advantage to Aseptella asturica since it is found in friable mudstones which were most probably an extremely soft mud at the time of deposition (compare the Conclusions).

Occurrence — Aseptella asturica is only known from its type locality and type horizon.

Order Rhynchonellida Kuhn, 1949 Superfamily Rhynchonellacea Gray, 1848 Family Camarotoechiidae Schuchert & LeVene, 1929 Subfamily Camarotoechiinae Schuchert & LeVene, 1929 Genus Leiorhynchus Hall, 1860

Leiorhynchus? sp. Pl. 9, figs. 10-12.

Material — Several poorly preserved external and internal moulds of both valves.

Description — The shells are small (see Table 6), weakly uniplicate, subcircular to elongate oval in outline; the hinge is short and the greatest width occurs near the anterior margin. The pedicle valve is slightly convex and has a weakly developed, wide median sulcus starting in front of the umbo. The sulcus and the flanks are covered with up to 20 rounded costae, separated by wide interspaces and starting anterior to the umbo; some bifurcations occur; the costae in the sulcus are larger than on the flanks; numerous concentric growth lines cross the costae. The brachial valve is slightly convex or flat and has a median fold and ornamentation similar to the pedicle valve.

The interior shows the reverse ornamentation of the exterior, the costae being pronounced. The pedicle valve has short dental plates diverging anteriorly at a large angle. The brachial valve has a low, weakly developed, short median septum; we have no specimens at hand in which the apical part of the brachial valve interior could be clearly observed.

Table 6. Measurements (in mm) of Leiorhynchus? sp.

| Specimen    | L p.v. | L b.v. | W   | N costae |
|-------------|--------|--------|-----|----------|
| DPO 5049    | 1.4    |        | 1.3 | 9        |
| DPO 5046    | 1.8    |        | 1.8 | 14       |
| DPO 5045    | 2.5    |        | 2.2 | 17       |
| DPO 5051    |        | 1.1    | 1.0 | 8        |
| RGM 143 766 |        | 1.5    | 1.5 | 16       |
| DPO 5047    |        | 1.7    | 1.7 | 18       |
| RGM 143 765 |        | 2.2    | 2.0 | 18       |

Discussion — The poorly preserved, scanty material makes specific identification impossible. Since the interior of the apical part of the brachial valve could not be observed, this form is only tentatively assigned to *Leiorhynchus*.

Superfamily STENOSCISMATACEA Oehlert, 1887 Family Atriboniidae Grant, 1965 Subfamily Atriboniinae Grant, 1965 Genus Camerisma Grant, 1965

Camerisma sp. Pl. 10, figs. 1-3.

Material — A few internal and external moulds of both valves, totalling some six specimens in all.

Description — The shell is strongly biconvex in its posterior region, flattened medianly.

The interior of the ventral valve shows a well-developed spondylium of pentagonal cross section in a plane parallel to the commissure; the spondylium is elevated on a low median septum which extends for a certain distance anterior to the spondylium. The dorsal valve interior has a high median septum carrying the camarophorium which is ventro-laterally directed and shows an intercamarophorial plate over all of its extent. The hinge plate is undivided, wider than long, slightly concave, and shorter than the camarophorium. A stout, posteriorly striated cardinal process with a rhomboid cross section is placed on the apex of the hinge plate.

The specimens are generally too incomplete to be measured accurately. The measurements of some internal structures (specimen DPO 5054) are: length of spondylium 2.5 mm and width 2.75 mm; median septum of pedicle valve 2.2 mm long; median septum of brachial valve, camarophorium, and intercamarophorial plate all 2.0 mm long; the hinge plate has a length of 1.25 mm and a width of 2.5 mm.

Discussion — The material is too poor to be identified at the species level, or even to decide whether it belongs to Camerisma (Camerisma) or to Camerisma (Callaiapsida). It has been assigned to Camerisma rather than to Coledium because the intercamarophorial plate extends to the end of the camarophorium.

Order Spiriferida Waagen, 1883 Suborder Delthyriddina Ivanova, 1972 Superfamily Martiniacea Waagen, 1883 Family Martiniidae Waagen, 1883 Subfamily Martiniinae Waagen, 1883 Genus Martinia M'Coy, 1844

Martinia aff. M. glabra (Sowerby, 1820) Pl. 11, figs. 1-6.

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1927 Martinia aff. glabra (Martin) — George, p. 111, figs. 3-11.
1938 Martinia aff. glabra (Martin) — Demanet, p. 103, pl. 9, figs. 24-29.
cf. 1963 Martinia glabra (Martin) — Nicolaus, p. 179, pl. 12, fig. 4.
1966 Martinia glabra (Sowerby) — Zakowa, p. 91, pl. 15, figs. 9a-f.
1971 Martinia sp. — Winkler Prins, in Martínez García, p. 274.
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Material — Several tens of external and internal moulds of both valves.

Description — The shell is medium-sized, ventri-biconvex, oval in outline, wider than long, strophic; the hinge is much less than the greatest width which occurs at mid length. The exterior is smooth, only ornamented with growth lines. The pedicle valve is strongly convex with the umbonal region inflated; a sulcus is absent in juvenile specimens and shallow in ephebic ones, occurring only at the anterior half of the valve. The high, triangular, concave interarea has a delthyrium with narrow deltidial plates. The brachial valve is subcircular and gently convex; the umbo is slightly more incurved than the lateral slopes; a median fold could not be observed. The interarea is very low.

The interior of the pedicle valve lacks dental plates and a median septum, but has a thick apical callosity. The muscle field has inseparable adductor and diductor scars placed at the subumbonal region, deeply impressed in the floor; it has a narrow, elongate, rhombic form of variable length and is divided into two halves by a median slit of vascular origin, which runs longitudinally and extends to the front of the valve. The ovarian markings are well developed in some specimens and surround the muscle field. The vascular markings are deeply impressed, starting from the muscle field and radially extending towards the front which is not reached by all, generally simple, although some dichotomose, and not always symmetrical; they may be quite variable from one specimen to another. The interior of the brachial valve has long, deep sockets subparallel to the hinge, the inner socket ridges being strong and curved, the outer ones straight. A low, triangular, striated cardinal process is situated between the sockets. Crural plates and a median septum are lacking. The muscle field is weakly impressed and practically unperceivable in most of our brachial valves. There are generally three radially arranged vascular markings, which were only observed in some specimens and which are less distinct than those in the pedicle valve, one occurring in the middle and the other two placed symmetrically — one on each side — forming a different angle in different specimens; they all vanish before reaching the anterior margin.

A large pedicle valve is 14.7 mm long, 19.4 mm wide, and the hinge width is 7.4 mm. A small brachial valve is: L=7.0 mm, W=12.0 mm, W=12.0 mm, W hinge = 6.0 mm; whilst a large one is: L=15.7 mm, W=17.0 mm, W hinge = 10.8 mm.

Discussion — Our specimens seem to be rather different from the typical Martinia glabra because of the weakly developed median sulcus and the absence of a median fold. We do not want to create a new species on the present material, however, since the variability of M. glabra is poorly known. So we follow the general practice (George, 1927; Demanet, 1938) of identifying such specimens as Martinia aff. M. glabra.

The trivial name Conchyliolithus Anomites (glaber) of Martin, 1809, was ruled invalid by the International Commission on Zoological Nomenclature in 1948 and the species was referred to the first subsequent author, Sowerby, 1820, by Muir-Wood (1951, p. 109).

The revised subdivision of the Spiriferida by Ivanova (1972) has been adopted.

Occurrence — Martinia aff. M. glabra has often been encountered in the Lower

Carboniferous and Namurian of Europe, the present occurrence in Marsdenian (?) deposits from northern Spain being rather high in the Namurian.

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Family Ambocoellidae George, 1931
Genus Crurithyris George, 1931

Crurithyris cf. C. urii (Fleming, 1828)
Pl. 10, figs. 5-8.

cf. 1931 Crurithyris urei (Fleming) — George, p. 55, pl. 4, figs. 1-4.
cf. 1941 Ambocoelia urei (Fleming) — Sokolskaja, p. 85, pl. 8, figs. 1-10; pl. 9, figs. 7-11.
cf. 1941 Crurithyris urei (Fleming) — Demanet, p. 222, pl. 13, figs. 6-7.
1962 Crurithyris urei (Fleming) — Ferguson, p. 115ff, pl. 22, figs. 1-20.
cf. 1963 Crurithyris urei (Fleming) — Nicolaus, p. 178, pl. 12, fig. 5 (with extensive synonymy).
cf. 1965 Crurithyris urei (Fleming) — Pitrat, in Moore, p. H672, fig. 456,6.
1971 Crurithyris sp. — Winkler Prins, in Martínez García, p. 274.
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1972 Ambocoelia urei (Fleming) — Rehoř & Rehořova, p. 40, pl. 13, figs. 2-3.

Material — Several (c. 35) external and internal moulds of both valves.

Description — The shells are small (see Table 7), ventri-biconvex to almost plano-convex; the outline is rounded, approximately equidimensional; the hinge is brachythyrid, about half the width of the shell, the greatest width occurring almost at mid length. The surface of both valves is covered with very small, quincunxially arranged spines, 20 concentric rows are developed at 1 mm length and 15 spines occur at 1 mm on each row (specimen DPO 5071); an external mould of a pedicle valve (DPO 5068) shows — besides the imprints of these spines — those of others with a greater diameter occurring in a much smaller number and apparently irregularly arranged. The pedicle valve is convex with the umbo moderately inrolled; the interarea is triangular, well-developed, and concave; the delthyrium has not been observed. The brachial valve is slightly convex with the maximum curvature in the umbonal region; the interarea is low. Some specimens show a shallow and poorly defined median sulcus originating on the anterior half.

The interior of the pedicle valve shows no dental plates, an apical callosity is found in old specimens. The muscle field is impressed in the floor of the valve, it commences at the apex or in front of the callosity mentioned above, is linear, of variable length but normally short, and medianly divided by a weak septum which is not extended beyond the muscle field. The brachial valve has deep, divergent dental sockets, anteriorly bordered by curved internal plates and in its medio-posterior part by the crural plates which extend beyond the sockets. The crural plates are divergent, ventro-laterally directed, and from their anterior end subparallel and ventrally directed crura are originated. In the apex between the crural plates, a low, triangular cardinal process is situated. The adductor scars are slightly excavated in the floor of the valve at their posterior end; they initiate in front of the cardinal process between the crural plates, extending anteriorly of them; they are not divided by a septum and their anterior limits are indistinct.

Discussion — The name urii appears to be the original name (unfortunately we were unable to consult Fleming's original description of 1828) and is thus the

| Specimen    | L p.v. | L b.v. | w   | W hinge | L cr. | L ad. |
|-------------|--------|--------|-----|---------|-------|-------|
| DPO 5068    | 2.4    |        | 2.5 | 1.0     |       | 0.75  |
| RGM 143 765 | 2.5    |        | 2.7 | 1.5     |       | 0.8   |
| DPO 5054    | 2.7    |        | 3.0 | 2.0     |       | 1.1   |
| DPO 5058    | 3.0    |        | 3.0 | 2.0     |       | 1.25  |
| DPO 5072    | 3.7    |        | 3.3 | 2.1     |       | 1.7   |
| DPO 5059    | 4.2    |        | 4.5 | 2.5     |       |       |
| DPO 5062    |        | 1.1    | 0.9 | 0.5     | 0.15  |       |
| RGM 143 766 |        | 1.9    | 2.0 | 1.2     | 0.55  |       |
| DPO 5056    |        | 2.3    | 2.3 | 1.0     | 0.3   |       |
| DPO 5063    |        | 2.5    | 2.6 | 1.7     | 0.65  |       |
| DPO 5057    |        | 3.6    | 3.7 | 2.3     | 0.4   |       |
| DPO 5195    |        | 3.8    | 3.5 | 1.6     | 0.75  |       |
| DPO 5066    |        | 3.8    | 4.5 | 2.0     | 0.45  |       |
| DPO 5065    |        | 4.2    | 4.5 | 2.7     | 0.9   |       |

Table 7. Measurements (in mm) of Crurithyris cf. C. urii (Fleming, 1828).L cr. means length of the crural plates and L ad. means length of the ventral adductor scars.

correct name, although the species was named after D. Ure.

Our specimens show a shallow median sulcus and an ornamentation of small spines, occasionally with some larger ones, similar to the type material as redescribed by George (1931). They differ, however, in their smaller size and more elongate shape but this may be due to stunting because of less favourable ecological conditions. We preferred therefore to assign our material only tentatively to *Crurithyris urii*.

Occurrence — Crurithyris urii has been described from the Lower Carboniferous and Namurian of Europe and North Africa. The presently described specimens are from Namurian (Marsdenian?) beds of northern Spain.

Ambocoeliidarum gen. & sp. nov. Pl. 10, fig. 4.

Material — An external and internal mould of a brachial valve, a fragment of an external mould of a brachial valve, and another of an internal mould of a brachial valve. No pedicle valves were found.

Description — The brachial valve is medium sized, transverse, and has the greatest width at the hinge which is straight; the cardinal extremities are acute, approaching however 90°; the valve is gently convex with the greatest curvature at the umbo. The well-developed interarea is anacline. The ornamentation consists only of a few marked growth lines.

The interior of the brachial valve shows long, deep sockets, subparallel to the hinge, anteriorly bordered by thick plates; at their postero-lateral margins the sockets are bounded by short, concave, ventro-laterally divergent crural plates, subparallel in their dorsal insertion. Between them in the apex a stout, globose cardinal process is situated. In front of the cardinal process the mould shows three radial ridges, representing vascular grooves, which reach the anterior margin; they are separated by equal interspaces, the outer ridges making an angle of 30°.

The length of the complete brachial valve (DPO 5073) is 7.8 mm and its width 12.7 mm.

Discussion — The brachial valves suggest a member of the Ambocoeliidae, but they are unlike any genus known to us. The material is, however, obviously insufficient to base a new genus and species upon, lacking pedicle valves.

Occurrence — The material comes from the Namurian (Marsdenian?) Meré beds north of Meré.

Superfamily Reticulariacea Waagen, 1883 Family Elythidae Fredericks, 1924

Genus Kitakamithyris Minato, 1951

Type species — by original designation Torynifer (Kitakamithyris) tyoanjiensis Minato, 1951.

Diagnosis — Elythid with double-barreled spines in concentric rows and without intermediate pustules, no folding except for median sulcus and fold; pedicle valve interior with dental plates and a median septum, brachial valve interior generally with crural plates and a weakly developed median septum.

Discussion — Most species assigned to Kitakamithyris have a weak dorsal myophragm although some lack it; Weyer (1967) considers this not of generic value. Also, most species assigned to Kitakamithyris have crural plates but in some they are lacking.

The genus was amply discussed by Campbell (1955, 1961), Maxwell (1961), Pavlova (1969), Roberts (1965, 1971), Thomas (1970), and Weyer (1967). We accept the latter's diagnosis (op. cit., p. 437), because it seems to be the most precise. One should, however, bear in mind that the type species is insufficiently known and is based on poorly preserved material. As a result there is disagreement among the different authors about the generic characteristics. Eventually, several species will have to be ascribed to other (new) genera, when the type species of *Kitakamithyris* has been redescribed and its internal structure is better known.

Range — Kitakamithyris occurs from the Middle Devonian to Permian of Eurasia and Australia.

Kitakamithyris merensis sp. nov. Pl. 12, figs. 1-3.

Holotype — A slightly deformed, fragmentary internal mould of a pedicle valve (DPO 5075: Pl. 12, fig. 1).

Type locality — Locality opposite kilometre-post 8, north of Meré.

Type horizon — The Meré beds of Namurian (Marsdenian?) age.

Derivatio nominis — This species is named after the type locality, Meré.

Material — A slightly deformed, fragmentary internal mould of a pedicle valve, an internal mould of a juvenile brachial valve, and fragments of the external moulds of both specimens and of another pedicle valve showing the ornamentation.

Description — The shell is ventri-biconvex, brachythyrid with a transversely

oval outline, widest near mid length. The ornamentation of both valves consists of concentric, imbricate lamellae, 5-6 occurring at 2 mm length near the anterior margin; the anterior edge of each lamella carries a row of double-barreled spines of variable diameter with a density of 5-7 in 2 mm on each row near the anterior margin; the spines also form radial rows. The pedicle valve is strongly convex with a prominent umbo and sloping flanks; as far as from our deformed specimen can be judged it has no median sulcus, but if it had it was very weak and started anteriorly of the umbo; the interarea is high, triangular, and concave; delthyrial plates could not be observed. The (juvenile) brachial valve is rounded, slightly wider than long, gently convex with the greatest convexity at the umbo, and without a median fold.

The pedicle valve interior has stout dental plates diverging at an angle of c. 30° and continuing as ridges bordering the muscle field, and a prominent median septum increasing in width and height towards the front as far as the end of the dental plates and afterwards it continues, broadening but decreasing in height, until it vanishes at the end of the muscle field; the septum has a thin longitudinal slit that ends approximately where the dental plates end, its origin could not be observed since the posterior part of the septum is not preserved. The adductor scars could not be observed in detail, they seem to be elongate and narrow, placed on both sides of the septum, and surrounded by the diductor scars which are lanceolate, striated, postero-laterally bordered by the dental plates, and continue to the end of the septum. Irregular radial grooves crossed by some concentric ones initiate from the muscle field where they are especially abundant and continue to the margins where they become obscure. The interior of the brachial valve has short sockets, subparallel to the hinge, and bordered by slender inner socket ridges and short highly divergent (c. 90°) crural plates. In the apex between the crural plates there is a small thickening corresponding to the cardinal process. In front of it a weak myophragm originates continuing a little less than half the valve length. The adductor scars lie along the myophragm and can be divided in a weakly impressed inner pair and a more strongly impressed, narrow, elongate outer pair; the muscle field is laterally bordered by two low ridges originating in front of the crural plates, parallel to the myophragm, and slightly longer than it.

The pedicle valve (holotype) has a length of c. 24 mm, a width of 36.4 mm, a 14.6 mm wide hinge, and the length of its median septum is 12.5 mm. The brachial valve (DPO 5076) is 5.8 mm long, 6.4 mm wide, its myophragm is 2.5 mm long, and the crural plates are 0.7 mm long.

Discussion — Externally Kitakamithyris merensis resembles K. moogooriensis Thomas, 1970, from the Tournaisian of the Carnarvon Basin (Australia) rather closely but it is distinguished by its much wider, higher, and shorter septum with a median slit in the pedicle valve.

Occurrence — Kitakamithyris merensis is only known from its type locality and type horizon.

Genus Plicotorynifer Abramov & Solomina in Abramov, 1970

Type species — by original designation Plicotorynifer simakovi Abramov & Solomina in Abramov, 1970. The same species was cited as Plicotorynifer snjatkovi

Abramov (in litt.) by Solomina (1970) due to a printers error (see Discussion below).

Diagnosis — Plicate elythid with dental plates and a median septum in the pedicle valve and crural plates and a median septum in the brachial valve.

Discussion — Plicotorynifer has been established by Abramov & Solomina in 1970, describing it twice as a new genus in two separate publications (Abramov, 1970; Solomina, 1970) with different names for the type species. Since both papers were published in the same year and were not exactly dated, they should officially be considered to have appeared at the end of 1970. In Abramov (1970, p. 153) the type species is cited as Plicotorynifer simakovi gen. et sp. nov., whereas the same authors in a chapter on brachiopods by Solomina (in Menner, Sarytcheva & Tschernjak, 1970, p. 111) established Plicotorynifer snjatkovi Abramov (in litt.) as the type species. One of us (C.F.W.P.) wrote to both Abramov and Solomina about this matter and Mrs R. V. Solomina answered that the work of Abramov was much earlier than hers, and that snjatkovi is a printer's error for simakovi (letter dated 30-10-1972). Consequently P. simakovi is considered the type species of Plicotorynifer Abramov & Solomina in Abramov, 1970, and P. snjatkovi Abramov in Solomina, 1970, is considered a lapsus calami for P. simakovi and thus a synonym of it.

To make a complicated matter even worse, Kotlyar & Popeko stated, as early as 1967, in a discussion of the subfamily Elythinae that the genus Plicotorynifer Abramov & Solomina is a synonym of Taimyrella Ustritsky in Ustritsky & Tschernjak, 1963. In the original description of Taimyrella it is stated that the genus is characterized by a plicate shell, dental and crural plates, and by the absence of a median septum from the pedicle valve. A restudy of the type species of Taimyrella — Martiniopsis(?) pseudodarwini Einor, 1946 — by Pavlova (1969) showed that there is a shallow median ridge in the pedicle valve; in the brachial valve no median septum or ridge was observed, presumably due to the absence of the umbonal point. Pavlova further considers - rightly in our opinion - the folding of the shell to be distinct from normal costation, as observed in Elytha, and concludes that Taimyrella will probably prove to be a synonym of Kitakamithyris Minato, 1951, an opinion which we cannot share, be it only for the plicate shell of Taimyrella. Also we do not find the evidence for the synonymy of Plicotorynifer and Taimyrella convincing, because there is at least a qualitative difference in the internal structure of both genera: Plicotorynifer has a stout median septum in the pedicle valve unlike the shallow ridge found in Taimyrella and the median septum seems to be truly absent in the brachial valve of Taimyrella since it should have been observed between the crural plates or in the specimen figured by Ustritsky & Tschernjak (1963, pl. 42, fig. 3b), if it was similar to the median septum found in Plicotorynifer. At the moment there seems to be therefore insufficient grounds to consider both genera synonymous, an opinion probably shared by Abramov and Solomina, or they would not have published the genus Plicotorynifer; unfortunately they did not discuss this matter in their publications.

Range — Originally *Plicotorynifer* was described from the Sette Daban area (U.S.S.R.). Abramov (1970) gives the range as Middle and Middle-Upper Carboniferous, which can probably best be interpreted as Bashkirian into Kasimovian. Solomina (1970), on the other hand, gives the range as Lower Carboniferous (Ovlachan Formation) and Middle Carboniferous, corresponding most probably

to the lower Namurian (Serpukhovian), Bashkirian, and Moscovian. Especially the latter range is in good agreement with the Spanish occurrence, which is from Namurian (Marsdenian?), or Serpukhovian to lower Bashkirian, deposits.

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Plicotorynifer lamellosus sp. nov. Pl. 12, fig. 4; Pl. 13, figs. 1-10; text-figs. 4-5.
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Holotype — Internal and external mould of a pedicle valve (DPO 5078: Pl. 13, fig. 1).

Type locality — Locality opposite kilometre-post 8, north of Meré.

Type horizon — The Meré beds of Namurian (Marsdenian?) age.

Derivatio nominis — This species is named after its highly lamellose ornamentation (Latin: lamellosus = lamellae bearing).

Diagnosis — A small, ventri-biconvex species of *Plicotorynifer* with numerous lamellae, up to two plicae on each side of the medium sulcus or fold, and spines of two diameters. Pedicle valve interior with a prominent median septum and short dental plates.

Material — Several tens of external and internal moulds of both valves.

Description — Small (see Table 8), ventri-biconvex, strophic submegathyrid shells with rounded cardinal extremities; the greatest width occurs somewhat anterior to the hinge. The outline is rounded, the juvenile specimens being elongate and the adults equidimensional or slightly wider than long. The anterior commissure is uniplicate, U-shaped. The lateral slopes are unfolded in juvenile specimens and become gently plicated in ephebic ones, showing maximal two plicae on each side of the sulcus or fold; they become more pronounced anteriorly. The whole surface is covered by concentric, imbricate, regularly spaced lamellae, 4-8 per 1 mm at the median frontal region, covered by thin, closely spaced, concentric growth lines. At the front of each lamella occurs a concentric row of radially arranged, double-barreled spines of two sizes; the two kinds of spines are apparently arranged alternatingly, the larger ones being inserted slightly more posteriorly. There are c. 20 spines per 1 mm on each lamella. The pedicle valve is strongly convex, with the greatest convexity at the umbo. It has a wide median sulcus with a smooth, rounded bottom bounded by two elevations, commencing at the apex and reaching the anterior margin, becoming wider and shallower anteriorly. The interarea is triangular, fairly high, and concave. The delthyrium is apparently without deltidial plates. The brachial valve is slightly convex, with a smooth, rounded median fold bordered by two lateral depressions corresponding to the sulcus of the pedicle valve, commencing at the apex and running to the anterior margin, where it is broader.

The interior of the pedicle valve has a high, narrow, edge-like median septum commencing at the apex and becoming progressively lower anteriorly, less than one-third the valve length; its posterior end is enclosed in an apical callosity in ephebic specimens. The dental plates are subparallel and short; a juvenile specimen shows stout dents which are not yet fused to the bottom of the valve. The muscle field is weakly impressed, practically imperceptible in most specimens. The adductor scars in the interior of the brachial valve are slightly elevated above the floor, short, obliquely striated, and clearly divided into two by the base of the cardinal process. The latter is high, striated, and has a lanceolate myophore. The long dental sockets are laterally directed, with rather strong,

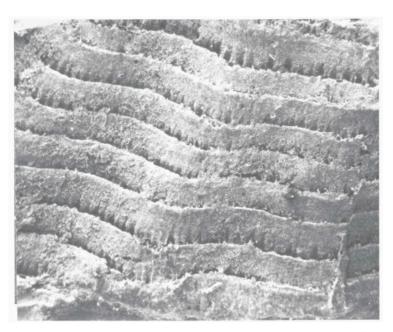


Fig. 4. Plicotorynifer lamellosus sp. nov., locality north of Meré, Namurian Meré beds. Fragment of an external mould of a pedicle valve, RGM 130 029, S.E.M. radiograph, x 60, gilded.

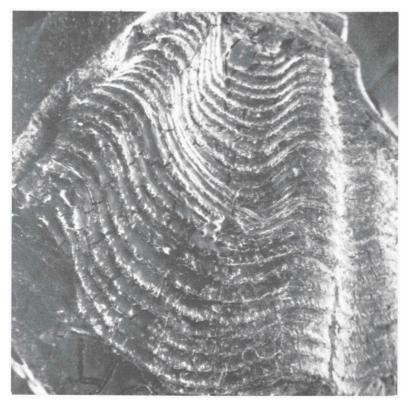


Fig. 5. Plicotorynifer lamellosus sp. nov., same locality and horizon as Fig. 4. Latex cast of a fragmentary external mould of a pedicle valve, RGM 130 031, S.E.M. radiograph, x 21; cracks caused by the vacuum for gilding.

| Specimen    | L p.v. | L b.v. | W   | W hinge |
|-------------|--------|--------|-----|---------|
| RGM 143 669 | 1.8    |        | 1.0 |         |
| DPO 5082    | 2.5    |        | 2.3 | 2.1     |
| DPO 5136    | 3.0    |        | 2.9 | 2.4     |
| DPO 5079    | 3.3    |        | 4.0 | 3.3     |
| DPO 5123    | 4.0    |        | 4.2 | 2.7     |
| DPO 5139    | 4.1    |        | 5.2 | 4.0     |
| DPO 5112    | 5.6    |        | 7.0 | 5.5     |
| DPO 5078    | 6.8    |        | 7.0 | 5.5     |
| DPO 5120    |        | 1.2    | 1.1 | 0.7     |
| DPO 11 186  |        | 1.7    | 2.1 | 1.4     |
| DPO 5114    |        | 2.1    | 2.4 | 1.4     |
| RGM 143 694 |        | 2.4    | 2.8 | 1.6     |
| RGM 143 666 |        | 3.2    | 3.2 | 2.0     |
| RGM 130 033 |        | 3.9    | 4.8 | 3.0     |
| DPO 5127    |        | 6.0    | 7.2 | 4.0     |
| DPO 5116    |        | 7.8    | 9.0 | 6.5     |

Table 8. Measurements (in mm) of Plicotorynifer lamellosus sp. nov.

posteriorly curved inner socket ridges and weaker, straight outer ones. The crural plates are high, rather short, concave, ventro-laterally directed, and subparallel at the valve floor; they border the adductor scars. The median septum is rather long but very low, so that in some specimens it is hardly perceivable.

Discussion — P. lamellosus agrees both in external ornamentation and in internal characteristics with the original descriptions of Plicotorynifer, only its dental plates are much shorter than those of the Russian species, so the diagnosis of the genus had only to be emended so as to read dental plates of variable length instead of long dental plates. Our species resembles P. minor Abramov, 1970, most, but is distinguished by its ventri-biconvex shape, smaller size, greater number of lamellae, and — as discussed above — shorter dental plates.

Occurrence — Plicotorynifer lamellosus is only known from its type locality and type horizon.

Order Terebratulida Waagen, 1883 Suborder Terebratulidina Waagen, 1883 Superfamily Dielasmatacea Schuchert, 1913 Family Cranaenidae Cloud, 1942

Cranaenidarum gen. & sp. indet. Pl. 14, figs. 1-5.

Material — Ten external and internal moulds of both valves.

Description — The shells are minute, ventri-biconvex, both valves being moderately convex, subelliptical, elongate, smooth, and without fold nor sulcus.

The interior of the brachial valve has an imperforate, concave, short cardinal plate supported by a short, shallow median ridge. The sockets have stout, curved inner socket ridges and shallow outer ones. The adductor scars are elongate, slightly impressed in the valve floor, separated by the shallow myophragm, and originate in front of the cardinal plate.

The length of the pedicle valve varies from 1.5 to 3.5 mm, its width from 1.6 to 3.6 mm, and the hinge width from c. 0.5 to 1.2 mm. The length of the brachial valve varies from 1.5 to 3.0 mm, its width from 1.4 to 2.8 mm, and the hinge width approximately from 0.6 to 1.2 mm.

Discussion — The material could belong to *Hamburgia*, but it is too scarce and too poorly preserved to be identified specifically or generically.

Occurrence — The material was collected from the Namurian (Marsdenian?) Meré beds north of Meré.

## Conclusions

## **COMPARISONS**

The Meré brachiopod fauna has some genera in common with Viséan Culm faunas from Germany, especially the one from Aprath, notably *Drahanorhynchus*, *Tornquistia*, *Leiorhynchus*, *Crurithyris*, *Martinia*, and possibly also *Anopliopsis* and *Caenanoplia* (compare Nicolaus, 1963). It has *Drahanorhynchus* and *Tornquistia* in common with the (incomplete?) list of brachiopods from the Březina Shales by Havliček (in Holub, 1973, p. 77). The Meré fauna can, as far as the brachiopods are concerned, best be considered a specialised Culm fauna.

The only brachiopod fauna that is closely comparable in general composition is the one described by Girty (1926) from the Boone Limestone of San Saba County, nowadays called Chappel Limestone (see Carter, 1967). Table 9 shows clearly that both faunas are only comparable at the generic level, which is not surprising since the Chappel Limestone is considered to be of late Kinderhookian (late Tournaisian) age (Carter, 1967, p. 259) in contrast to the middle Namurian (Marsdenian?) age considered likely for the Meré beds (see below). Ecologically, however, the two deposits must have been quite similar since not only the general aspect of both brachiopod faunas is similar (predominance of small forms) but nearly all species of the fauna have a corresponding (not identical!) species in the Chappel Limestone of San Saba County.

The generally small size of the species may indicate a soft bottom unsuitable for most brachiopods; part of the brachiopods may have lived attached to seaweed. It is interesting to note that the new productid, *Aseptella asturica*, is characterized by large spines and a flange which may have helped to prevent it from sinking away in the mud.

## AGE OF THE MERÉ BEDS

The species composition gives little information on the age of the Meré beds since most species are new. Crania? quadrata (M'Coy) was sofar only known from the European Lower Carboniferous, but it is closely related to the Permian species C.? kirkbyi Davidson, 1858, so it would not be surprising if C.? quadrata was also found in the Middle (and Upper) Carboniferous. Tornquistia polita (M'Coy) is known from the Lower Carboniferous and Namurian of Europe and

Table 9. Comparison between the brachiopod faunas from the Meré beds (described herein) and from the Boone Limestone of Girty, 1926 (= Chappel Limestone) The latter fauna was described by Girty (1926) and revised by Carter (1967, p. 267-269).

| Limestone). The latter fauna was described by Girty (1926) and revised by Carter (1967, p. 267-269).  | / Carter (1967, p. 267-269).   |
|---|--|
| Meré beds   | Boone Limestone (= Chappel Limestone)  |
| Species most probably belonging to the same genus   |  |
| Crania? quadrata (M'Coy, 1844) sensu Brunton, 1968 Schizophoria sp. Anopliopsis? parva sp. nov. Crurithyris cf. C. urii (Fleming, 1828) Cranaenidarum gen. & sp. indet. | Crania? pertenuis Girty, 1926 Schizophoria sp. (= Rhipidomella perminuta Girty, 1926, var.) Anopliopsis subcarinata (Girty, 1926) Crurithyris parva (Weller, 1899) Cranaenidarum gen. & sp. indet. |
| Species that might belong to the same genus   |  |
| Drahanorhynchus cantabricus sp. nov.<br>Aseptella asturica gen. & sp. nov.  | Schuchertella cf. morsei Foerste, sensu Girty, 1926<br>Pustula inconspicua Girty, 1926   |
| Unrelated species of similar shape possibly occupying a similar ecological niche  | niche  |
| Leiorhynchus? sp.<br>Camerisma sp.<br>Kitakamithyris merensis sp. nov.<br>Plicotorynifer lamellosus sp. nov.  | Hustedia? texana Girty, 1926<br>Coledium sp.<br>Reticularia? cooperensis (Swallow, 1860)<br>Plectospira problematica (Girty, 1926)   |
| Species most probably belonging to the same genus but not found at the  | Species most probably belonging to the same genus but not found at the original Boone Limestone locality but at other Chappel Limestone localities   |
| Caenanoplia martinezi sp. nov.<br>Tornquistia cf. T. polita (M'Coy, 1844)   | Caenanoplia gibberula (Carter, 1967)<br>Tornquistia? transversalis Carter, 1967  |

so are Crurithyris urii (Fleming) and Martinia (aff.) glabra (Sowerby).

Some additional information on the age is given by the genera, although some — Schizophoria, Leiorhynchus, Camerisma, and Kitakamithyris — are too wide ranging to be of any value. Drahanorhynchus and Anopliopsis have sofar only been described from the Lower Carboniferous, but they are seldomly mentioned in the literature and their range could actually prove to be more extended. Similarly, Caenanoplia is only known from the Lower Mississippian (Carter, 1968) and Tournaisian (Afanasjeva, 1975). The new genus Aseptella does not give any clue about the age of the Meré beds. Plicotorynifer was originally described from Serpukhovian to Kasimovian strata of the U.S.S.R. Finally, the subfamily Productellinae occurs only in the Lower Carboniferous and the family Cranaenidae in the Lower Carboniferous and Namurian.

Apart from *Plicotorynifer*, all evidence points to an Early Carboniferous, or at the most early Namurian, age. The specialised fauna appears to be more indicative for the ecological conditions, however, than for the age — the most closely related fauna being the late Kinderhookian Chappel fauna —, like the *Chonetipustula-Plicochonetes* fauna adapted to a similar environment (Winkler Prins, 1968, p. 56, 61). This gives all the more weight to the occurrence of *Plicotorynifer*. It may therefore be concluded that the Meré beds are earliest Middle or latest Early Carboniferous (in the Russian sense), i.e. Namurian (probably Namurian B-C), in age.

The only other faunal group that sofar has given an exact age for the Meré beds are the goniatites who indicate an Early Morrowan, or late Namurian B (Marsdenian) age according to Mrs C. H. T. Wagner-Gentis (in Moore et al., 1971, p. 341, 346, 347; in Martínez García, 1971, p. 271).

The stratigraphic position of the Meré beds, above the Barcaliente Formation (dated as Marsdenian, see the chapter Geological setting) and a thin layer of limestone presumably belonging to the basal part of the Valdeteja Formation, makes it likely that the Meré beds are the lateral equivalent of a large part of the Valdeteja Formation. A late Namurian B (Marsdenian) or Namurian C (Yeadonian) age seems therefore quite likely and this is in good agreement with the faunal evidence.

## Resumen

Se describe una interesante fauna de braquiópodos procedente de unos materiales, denominados aquí provisionalmente Capas de Meré.

La fauna de braquiópodos está constituida por 17 especies, 7 de las cuales: Drahanorhynchus cantabricus, Anopliopsis? parva, Caenanoplia martinezi, Tornquistia scutiformis, Aseptella asturica, Kitakamithyris merensis y Plicotorynifer lamellosus son nuevas. El género Aseptella es tambien nuevo. Asimismo, es probable que otros dos géneros sean nuevos, uno incluido en la subfamilia Productellinae y otro en la familia Ambocoeliidae, pero el material recogido de ambos es demasiado pobre para permitir nombrarlos formalmente.

Drahanorhynchus cantabricus difiere de la especie tipo del género por su forma menos transversa, valva peduncular menos cónica, costillas primarias más numerosas y dentiferos marcadamente divergentes con la charnela.

Anopliopsis? parva se asigna solo tentativamente al género Anopliopsis porque presenta un estrecho seno en la valva peduncular y porque las crestas radiales adicionales no están tan bien desarrolladas como en la especie tipo, faltando por completo en la valva peduncular.

Caenanoplia martinezi se distingue de las restantes especies del género por su concha debilmente concavoconvexa, de contorno subrectangular, no lamelosa, con un corto septo medio en el interior peduncular y sin crestas braquiales en el interior braquial.

Tornquistia scutiformis se distingue de la mayoría de las restantes especies del género por su pequeño tamaño, siendo además su forma mucho menos concavoconvexa.

El género Aseptella, con A. asturica como especie tipo, es un productido con ornamentación rugosa; la valva peduncular presenta unas pocas y gruesas espinas en la charnela y en fila sobre los flancos; la valva braquial no tiene espinas. En los ejemplares efébicos un reborde plano y liso rodea ambas valvas, formando con el resto de la concha un ángulo casi recto. La valva braquial de algunos ejemplares juveniles presenta un debil septo medio, del cual carecen los adultos, en los que queda probablemente embebido por material calloso.

Kitakamithyris merensis se caracteriza por su septo medio ventral ancho, alto y relativamente corto, presentando una hendidura media.

Plicotorynifer lamellosus se distingue de las especies rusas por su menor talla, mayor número de lamelas concéntricas y, sobre todo, por sus lamelas dentales mucho más cortas.

El pequeño tamaño de la mayoría de los ejemplares de braquiópodos de esta asociación indica un medio con unas condiciones especiales, como podría ser un fondo blando, poco favorable para la mayoría de los braquiópodos. Es interesante destacar que el nuevo productido *Aseptella asturica* presenta grandes espinas y un reborde, cuya misión podría ser impedir que el organismo quedara enterrado en el barro.

La edad de las Capas de Meré, de acuerdo con los datos proporcionados por goniatítidos, es Namuriense B superior (Marsdeniense). La fauna de braquiópodos parece ser más indicativa de unas determinadas condiciones ecológicas que de la edad de estas capas. De todas formas, los datos de los braquiópodos parecen apuntar hacia una edad Namuriense, probablemente Namuriense B-C, que se ajusta bien a la indicada por los goniatítidos y a la posición estratigráfica de estas capas.

## References

- Abramov. B. S., 1970. Biostratigrafiya kamennougol'nykh otlozhenii Sette-Dabana (Yuzhnoe Verkhoyan'e) (Biostratigraphy of the Carboniferous deposits from Sette Daban, South Verkhoyan). Izdat. Nauka, Moscow: 1-178, pls. 1-38 (in Russian).
- Afanasjeva, G. A., 1975. Kamennougol'nyj etap razvitiya nadsemeistva Chonetacea (Brachiopoda) (The Carboniferous Stage in the development of the superfamily Chonetacea, Brachiopoda). Paleont. Zh., 1975, 1: 3-9 (in Russian; English translation: Paleont. Jour., 1975, 1: 1-6).
- Boucot, A. J. & C. W. Harper, 1968. Silurian to lower Middle Devonian Chonetacea. Jour. Paleont., 42: 143-176, pls. 27-30.
- Brand, P. J., 1970. Scottish Carboniferous chonetoids. Bull. Geol. Survey Great Britain, 31: 89-137, pls. 8-13.

- Brunton, C. H. C., 1968. Silicified brachiopods from the Viséan of County Fermanagh (II). Bull. Br. Mus. nat. Hist. (Geol.), 16, 1: 1-70, pls. 1-9.
- Campbell, K. S. W., 1955. Phricodothyris in New South Wales. Geol. Mag., 92: 374-383, pl. 18.
- —, 1961. Carboniferous fossils from the Kuttung rocks of New South Wales. Palaeontology, 4: 428-474, pls. 53-63.
- Carter, J. L., 1967. Mississippian brachiopods from the Chappel Limestone of Central Texas. Bull. Amer. Paleont., 53, 238: 248-488, pls. 13-45.
- —, 1968. New genera and species of Early Mississippian brachiopods from the Burlington Limestone. Jour. Paleont., 42: 1140-1152, pls. 145-148.
- Cooper, G. A. & R. E. Grant, 1974. Permian brachiopods of West Texas II. Smithsonian Contr. Paleobiology, 15: 233-793, pls. 24-191.
- Davidson, T., 1858-1863. A monograph of the British fossil Brachiopoda. Vol. II. Part. 5. The Carboniferous Brachiopoda. Palaeontogr. Soc. Mem., 2, 5: 1-280, pls. 1-55.
- Demanet, F., 1938. La faune des couches de passage du Dinantien au Namurien dans le synclinorium de Dinant. Mém. Mus. Roy. Hist. Nat. Belg., 84: 1-201, pls. 1-14.
- —, 1941. Faune et stratigraphie de l'Étage Namurien de la Belgique. Ibidem, 97: 1-327, pls. 1-18.
- Ferguson, L., 1962. Distortion of *Crurithyris urei* (Fleming) from the Visean rocks of Fife, Scotland, by compaction of the containing sediment. Jour. Paleont., 36: 115-119, pl. 22.
- Gallwitz, H., 1932. Die Fauna des deutschen Unterkarbons. 3. Teil: 2. Die Brachiopoden, 3. Teil. Die Orthiden, Strophomeniden und Choneten des unteren Unterkarbons (Etroeungt). Abh. Preuss. Geol. Landesanst., N.F., 141: 75-131, pls. 6-8.
- George, T. N., 1927. Studies in Avonian Brachiopoda: 1. The genera *Brachythyris* and *Martinia*. Geol. Mag., 64: 106-119.
- —, 1931. Ambocoelia Hall and certain similar British Spiriferidae. Quart. Journ. Geol. Soc., 87: 30-61, pls. 3-5.
- Ginkel, A. C. van, 1965. Spanish Carboniferous fusulinids and their significance for correlation purposes. Leidse Geol. Meded., 34: 171-225 (with enclosures).
- Girty, G. H., 1926. Pt. 3. The macrofauna of the limestone of Boone age. In: Roundy, P. V., G. H. Girty & M. I. Goldman: Mississippian formations of San Saba County, Texas. U.S. Geol. Survey Prof. Paper, 146: 24-43, pls. 5-6.
- —, 1938. Descriptions of a new genus and a new species of Carboniferous brachiopods. Jour. Washington Acad. Sci., 28: 278-284, 1 pl.
- Graham, D. K., 1970. A review of the brachiopod genus *Crania* in the Scottish Carboniferous.

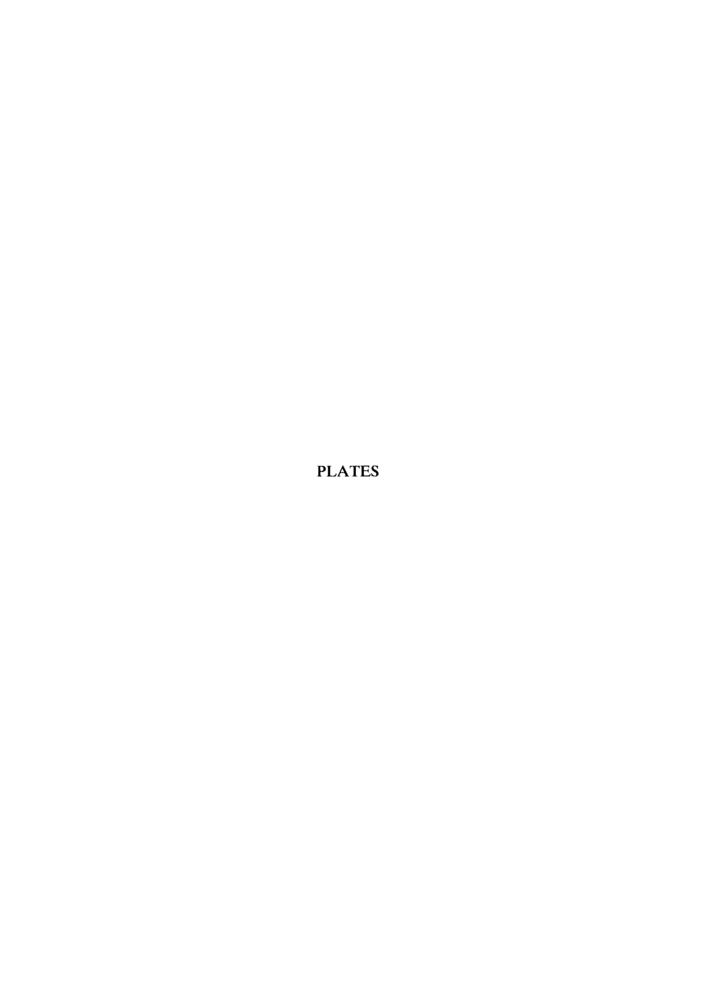
   Bull. Geol. Survey Great Britain, 33: 57-65, pls. 3-4.
- Grant, R. E., 1972. The lophophore and feeding mechanism of the Productidina (Brachiopoda).

   Jour. Paleont., 46: 213-248, 9 pls.
- —, 1976. Permian brachiopods from Southern Thailand. Paleont. Soc. Mem. 9 (Jour. Paleont., 50, 3, supp.): 1-269, pls. 1-71.
- Havlíček, V., 1967. Brachiopoda of the Suborder Strophomenidina in Czechoslovakia. Rozpr. Ústř. Úst. Geol., 33: 1-236, pls. 1-52.
- Holub, V. (ed.), 1973. Carboniferous and Permian of the Bohemian Massif. Excursion Guide
   S.C.C.S. Field Meeting in Czechoslovakia, Ostrava-Brno-Praha September 17-27, 1973.
   Geol. Survey, Prague: 1-155.
- Ivanova, E. A., 1972. Osnovnye zakonomernosti evolyutsii spiriferid (Brachiopoda) (The main features of spiriferid evolution (Brachiopoda)). Paleont. Zh., 1972, 3: 28-42 (in Russian; English translation: Paleont. Jour., 1972, 3: 309-320).
- Julivert, M., 1960. Estudio geológico de la Cuenca de Beleño, valles altos del Sella, Ponga, Nalón y Esla de la Cordillera Cantábrica. — Bol. Inst. Geol. Minero España, 71: 3-346, pls. 1-17 (with map).
- —, 1967a. La ventana tectonica del Rio Color y la prolongación septentrional del manto del Ponga (Cordillera Cantábrica, España). — Trabajos Geol., Oviedo, 1: 1-26 (with map).
- —, 1967b. La ventana del Rio Monasterio y la terminación meridional del manto del Ponga. Ibidem, 1: 59-76 (with map).
- Kalashnikov, N. V., 1970. O bessamkovykh brakhiopodakh karbona Severnogo Urala i ikh ekologii (On the inarticulate brachiopods from the Carboniferous of the northern Urals and their ecology). In: Plotnikov, M. A. (ed.): Fauna i flora paleozoya severovostoka evropejskoj chasti SSSR (Palaeozoic fauna and flora from the north-east European part of the U.S.S.R.). Inst. Geol. Komi Filial Akad. Nauk SSSR, Leningrad: 5-15.

- 2 pls. (in Russian).
- Kotljar, G. V. & L. I. Popeko, 1967. Biostratigrafiya mshanki i brakhiopody verkhnego paleozoya zabajkal'ya (Biostratigraphy of the bryozoans and brachiopods from the Upper Palaeozoic of the Baical region). Zapiski Zabajkal. Filiala Geograf. Obshchestva SSSR, 28, Trudy Otdel. Geol. im. V. A. Obrucheva, 5: 1-323, pls. 1-57 (in Russian).
- Kruytzer, E. M., 1969. Le genre Crania du Crétacé Supérieur et du post-Maastrichtien de la Province de Limbourg Néerlandais (Brachiopoda, Inarticulata). Publ. Natuurhist. Genootsch. Limburg, 19, 3: 1-42.
- Marcos, A., 1967. Estudio geológico del reborde NW de los Picos de Europa (Región de Onís-Cabrales, Cordillera Cantábrica). Trabajos Geol., Oviedo, 1: 39-46 (with map).
- Martínez García, E., 1971. The age of the Caliza de Montaña in the eastern Cantabrian Mountains. In: Wagner, R. H. (ed.): The Carboniferous of Northwest Spain. Part 1. Trabajos Geol., Oviedo, 3: 267-276.
- Maxwell, W. G. H., 1961. Lower Carboniferous brachiopod faunas from Old Cannindale, Queensland. Jour. Paleont., 35: 82-103, pls. 19-20.
- Minato, M., 1951. On the Lower Carboniferous fossils of the Kitakami Massif, northeast Honshu, Japan. Jour. Fac. Sci. Hokkaido Univ., 4 (Geol., Miner.), 7, 4: 355-382, pls. 1-5.
- Moore, L. R., R. Neves, R. H. Wagner & C. H. T. Wagner-Gentis, 1971. The stratigraphy of Namurian and Westphalian rocks in the Villamanín area of northern León, N.W. Spain. In: Wagner, R. H. (ed.): The Carboniferous of Northwest Spain. Part. 1. Trabajos Geol., Oviedo, 3: 307-363, 8 pls.
- Moore, R. C. (ed.), 1965. Part H. Brachiopoda. Vols 1 & 2. Treatise on Invertebrate Paleontology, H: 1-927.
- Muir-Wood, H. M., 1951. The Brachiopoda of Martin's 'Petrificata Derbiensia'. Ann. Mag. Nat. Hist., 12, 4: 97-118, pls. 3-6.
- —, 1962. On the morphology and classification of the brachiopod Suborder Chonetoidea. British Mus. (Nat. Hist.), London: 1-132, pls. 1-16.
- Nicolaus, H. J., 1963. Zur Stratigraphie und Fauna der *crenistria-*Zone im Kulm des Rheinischen Schiefergebirges. Beih. Geol. Jahrb., 53: 1-246, pls. 1-15.
- Paeckelmann, W., 1930. Die Fauna des deutschen Unterkarbons. 3 Die Brachiopoden des deutschen Unterkarbons. 1. Teil: Die Orthiden, Strophomeniden und Choneten des Mittleren und Oberen Unterkarbons. Abh. Preuss. Geol. Landesanst., N.F., 122: 143-326, pls. 9-24.
- Pavlova, E. E., 1969. Razvitie brakhiopod semeistva Reticulariidae (Evolution of the brachiopod family Reticulariidae). Trudy Paleont. Inst. Akad. Nauk SSSR, 120: 1-130, pls. 1-13 (in Russian).
- Řehoř, F. & M. Řehořova, 1972. Makrofauna uhlonosného karbonu Československé části hornoslezské pánve (Die Makrofauna des kohlenführenden Karbons im tsechoslowakischen Teil des oberschlesischen Beckens). Ostravké Muz. šustova Paleont. Sbírka, Ostrava: 1-137, pls. 1-64 (in Czech with an extensive German summary).
- Roberts, J., 1965. A Lower Carboniferous fauna from Trevallyn, New South Wales. Palaeontology, 8: 54-81, pls. 10-13.
- —, 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, Northwestern Australia Bull. Bureau Mineral Res. Geol. Geophys., 122, 1: 1-319; 2: pls. 1-59.
- Rowell, A. J., 1967. A numerical taxonomic study of the chonetacean brachiopods. In: Teichert, C. & E. L. Yochelson (eds.): Essay in paleontology and stratigraphy, Raymond C. Moore Commemorative Volume. Univ. Kansas Press, Lawrence: 113-140.
- Sarytcheva, T. G., A. N. Sokolskaja, G. A. Besnossova & S. V. Maksimova, 1963. Brakhiopody i paleogeografiya karbona Kuznetskoj kotloviny (Brachiopods and palaeogeography of the Carboniferous of the Kuznetsk Basin). Trudy Paleont. Inst. Akad. Nauk SSSR, 95: 1-547, pls. 1-64 (in Russian).
- Shiells, K. A. G., 1968. Kochiproductus coronus sp. nov. from the Scottish Viséan and a possible mechanical advantage of its flange structure. Trans. Roy. Soc. Edinb., 67 (1967-1968), 10: 477-507, pl. 1.
- Sjerp, N., 1967. The geology of the San Isidro-Porma area (Cantabrian Mountains, Spain). Leidse Geol. Meded., 39: 55-128, 2 pls. (with map).
- Sokolskaja, A. N., 1941. Brakhiopody osnovaniya podmoskovnogo karbona i perekhodnykh devonskogo-kamennougol'nykh otlozhenij (chernyshinskie, upinskie i malevko-muraevninskie sloi). Chast Spiriferidae (Brachiopodes du Carbonifère inférieur et des couches

- de passage du Dévonien-Carbonifère du Bassin de Moscou (Tchernyshine, Upa et Malevka-Muraievnia). 1e Partie: Spririferidae). Trudy Paleont. Inst. Akad. Nauk SSSR, 12, 2: 1-139, pls. 1-12 (in Russian; French translation: B.R.G.M. 54).
- Solomina, R. V., 1970. Brakhiopody (Brachiopods). In: Menner, V. V., T. G. Sarytcheva & G. E. Tschernjak (eds.): Stratigrafiya kamennougol'nykh i permskikh otlozhenii severnogo Verkhoyana (Stratigraphy of the Carboniferous and Permian deposits of northern Verkhoyan). Trudy Nauchno-Issled. Inst. Geol. Arktiki, Vses. Aérogeol. Trest, 154: 70-113, pls. 3-12 (in Russian).
- Stoll, N. R. et al. (eds.), 1964. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology. Second edition. — Internat. Trust Zool. Nomenclature, London: 1-176.
- Thomas, G., 1970. Carboniferous and Early Permian brachiopods from western and northern Australia. Bull. Bureau Mineral Res. Geol. Geophys., 56: 1-276, pls. 1-31.
- Wagner, R. H., C. F. Winkler Prins & R. E. Riding, 1972. Lithostratigraphic units of the lower part of the Carboniferous in northern León, Spain (with a Note on some goniatite faunas by C. H. T. Wagner-Gentis). In: Wagner, R. H. (ed.): The Carboniferous of Northwest Spain. Part. 2. Trabajos Geol., Oviedo, 4 (1971): 603-663, 3 pls.
- Weyer, D., 1967. Kitakamithyris Minato, 1951 (Brachiopoda, Spririferida) aus dem Etroeungt (Oberdevon) und Tournai (Unterkarbon) des Rheinischen Schiefergebirges. Geologie, 16: 433-447, 2 pls.
- Winkler Prins, C. F., 1968. Carboniferous Productidina and Chonetidina of the Cantabrian Mountains (NW Spain): systematics, stratigraphy and palaeoecology. — Leidse Geol. Meded., 43: 41-126. 9 pls.
- Yochelson, E. L. (ed.), 1973. Announcement by International Commission on Zoological Nomenclature. Jour. Paleont., 47: 1009-1011.
- Zakowa, H., 1966. Poziom Goniatites crenistria Phill. w okolicy Sokolca i Jugowa u podnóży
   Gór Sowich (Sudety Środkowe) (Zone Goniatites crenistria Phill. in the vicinity of
   Sokolec and Jugów, at the foot of the Sowie Góry (Mountains) (Central Sudetes)).
   Prace Inst. Geol., 43: 1-197, pls. 1-23 (in Polish with Russian and English summaries).

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- Fig. 1. Crania? quadrata (M'Coy, 1844) sensu Brunton, 1968. Internal mould of a brachial valve, RGM 130 077, x 2.5.
- Fig. 2. Schizophoria sp. Incomplete internal mould of a pedicle valve. RGM 143 556, x 4.3.
- Figs. 3-10. Drahanorhynchus cantabricus sp. nov.
- Fig. 3. Juvenile brachial valve, RGM 143 583, x 11; a: internal mould; b: external mould.
- Fig. 4. Pedicle valve, RGM 143 568; a: internal mould, x 11; b: external mould, x 10.
- Fig. 5. Internal mould of a pedicle valve, RGM 143 587, x 4.4; in the lower right hand corner the external mould of a brachial valve of Aseptella asturica sp. nov. can be seen.
- Fig. 6. Internal mould of a gerontic brachial valve, RGM 143 581, x 6.6.
- Fig. 7. Internal mould of a pedicle valve, RGM 143 578, x 10; a: ventral view; b: posterior view.
- Fig. 8. Internal mould of a brachial valve, holotype, RGM 143 559, x 8.3.
- Fig. 9. Internal mould of a juvenile brachial valve, RGM 143 582, x 11.
- Fig. 10. External mould of a pedicle valve, RGM 143 582, x 6.4.

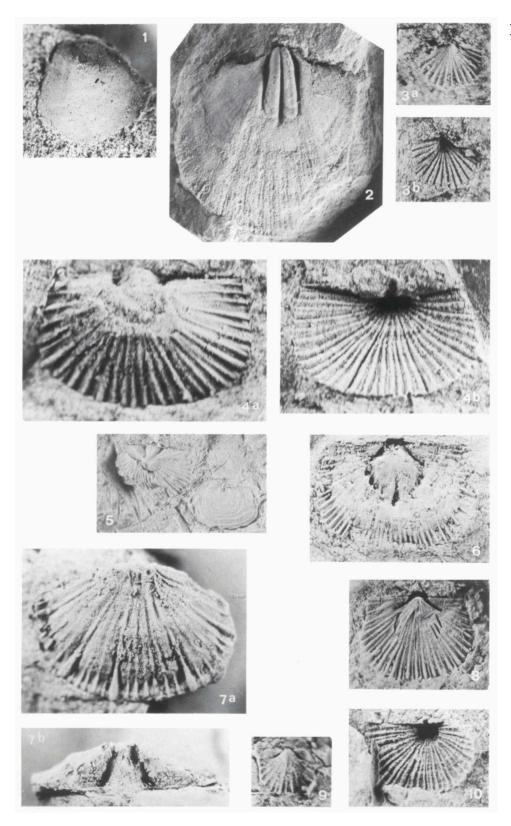


Plate 1

All specimens are from the same locality north of Meré, from the Namurian Meré beds. S.E.M. radiographs, all specimens were gilded.

- Fig. 1. Crania? quadrata (M'Coy, 1844) sensu Brunton, 1968. Latex cast of an external mould of a brachial valve, RGM 130 045; a: dorsal view, x 28; b: lateral view, x 37. For a better view of the spinules see text-fig. 1.
- Fig. 2. Drahanorhynchus cantabricus sp. nov. Internal mould of a juvenile pedicle valve, RGM 143 560, x 55.
- Fig. 3. Anopliopsis? parva sp. nov. Internal mould of a brachial valve, RGM 143 608, x 50.

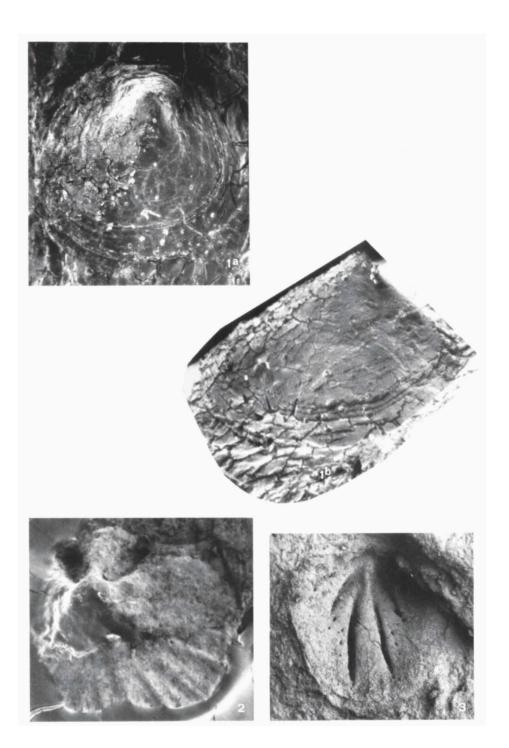


Plate 2

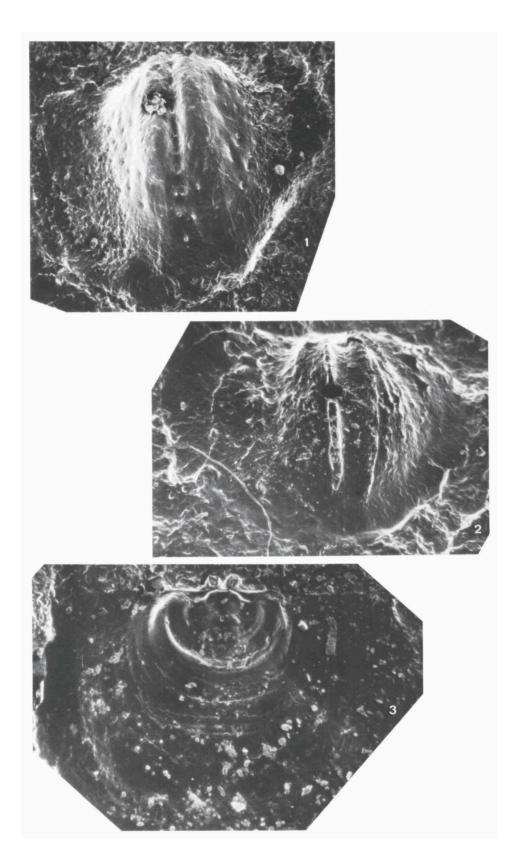
- Fig. 1. Drahanorhynchus cantabricus sp. nov. Brachial valve, RGM 143 576; a: latex cast of internal mould, x 7; b: internal mould, x 5.6.
- Figs. 2-11 Anopliopsis? parva sp. nov.
- Fig. 2. External mould of a brachial valve, RGM 143 666, x 20.
- Fig. 3. Internal mould of a pedicle valve, RGM 143 597, x 25.
- Fig. 4. Internal mould of a pedicle valve, RGM 143 686, x 21.
- Fig. 5. Pedicle valve, RGM 143 687, x 25; a: external mould; b: internal mould.
- Fig. 6. Brachial valve, holotype, RGM 143 684, x 25; a: internal mould; b: external mould.
- Fig. 7. External mould of a pedicle valve, RGM 143 666, x 20.
- Fig. 8. Internal mould of a brachial valve, RGM 143 687, x 10.5.
- Fig. 9. Internal mould of a brachial valve, RGM 143 595, x 18.
- Fig. 10. Brachial valve, RGM 143 658, x 25; a: internal mould; b: external mould.
- Fig. 11. Internal mould of a large pedicle valve showing well developed, radially aligned pits representing the pustules of the internal surface; RGM 143 670, x 18.

Plate 3

All specimens are from the same locality north of Meré, from the Namurian Meré beds. S.E.M. radiographs, all specimens were gilded.

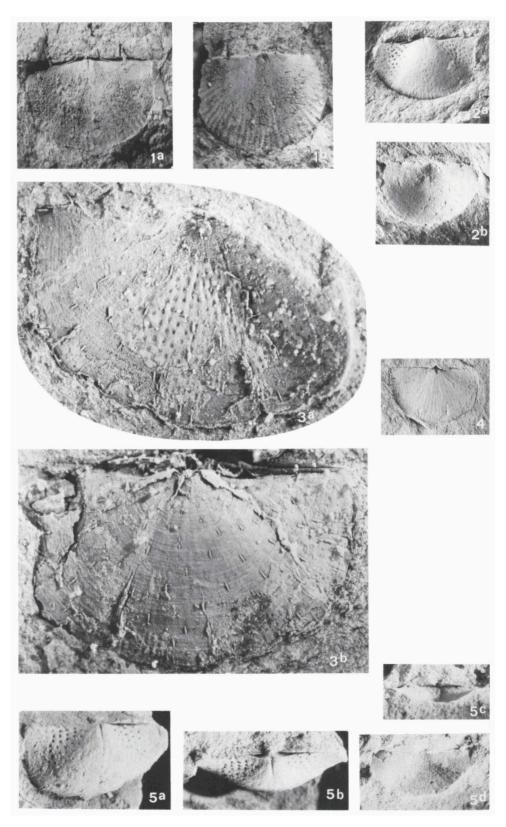
- Figs. 1-2. Anopliopsis? parva sp. nov.
- Fig. 1. Internal mould of a pedicle valve, RGM 143 599, x 53.
- Fig. 2. Latex cast of an internal mould of a brachial valve, RGM 143 609, x 58.
- Fig. 3. Aseptella asturica gen. & sp. nov. Latex cast of an external mould of a brachial valve, RGM 143 560, x 60.

Plate 4



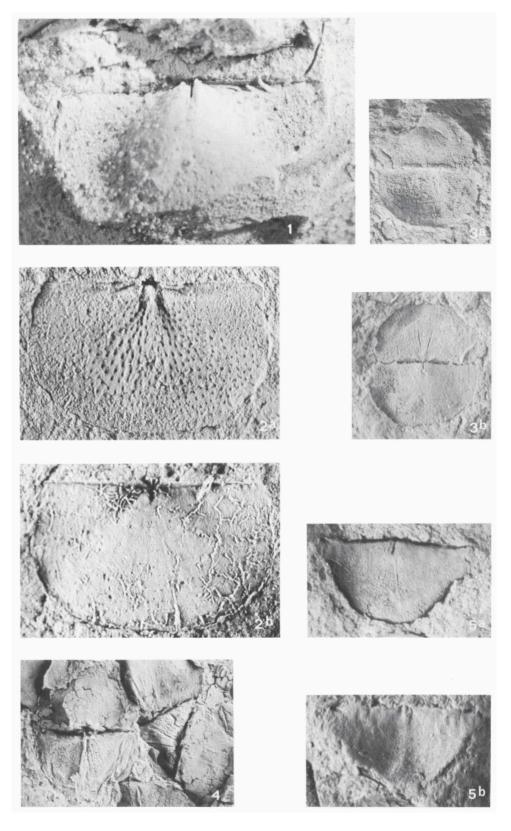
- Figs. 1-5. Caenanoplia martinezi sp. nov.
- Fig. 1. Pedicle valve of a rather strongly costate specimen showing the spine arrangement, RGM 143 658, x 8; a: internal mould; b: external mould.
- Fig. 2. Pedicle valve of a typical, rather weakly costate specimen, RGM 143 656, x 4.3; a: internal mould; b: external mould.
- Fig. 3. a: Fragmentary external mould of a pedicle valve with remains of the internal mould of the brachial valve; b: external mould of the brachial valve of the same individual. RGM 143 693, x 10.
- Fig. 4. External mould of a brachial valve, RGM 143 752, x 4.
- Fig. 5. Pedicle valve, RGM 143 623; a: internal mould, x 6.5; b: internal mould, posterior view, x 6.5; c: external mould, posterior view, x 5; d: external mould, x 5.

Plate 5



- Figs. 1-2. Caenanoplia martinezi sp. nov.
- Fig. 1. Fragmentary internal mould of a pedicle valve, RGM 143 694, x 10.
- Fig. 2. Brachial valve, holotype, RGM 143 655, x 10.5; a: internal mould; b: external mould.
- Figs. 3-5. Tornquistia cf. T. polita (M'Coy, 1844)
- Fig. 3. Both valves spread open, RGM 143 648; a: external moulds, x 4.6; b: internal moulds, x 5.3
- Fig. 4. Internal moulds of two sets of valves spread open, RGM 143 653, x 5.
- Fig. 5. Juvenile pedicle valve, RGM 143 646, x 10; a: internal mould, one of the lateral septa of the brachial valve interior peeps through as a thin groove; b: external mould.

Plate 6



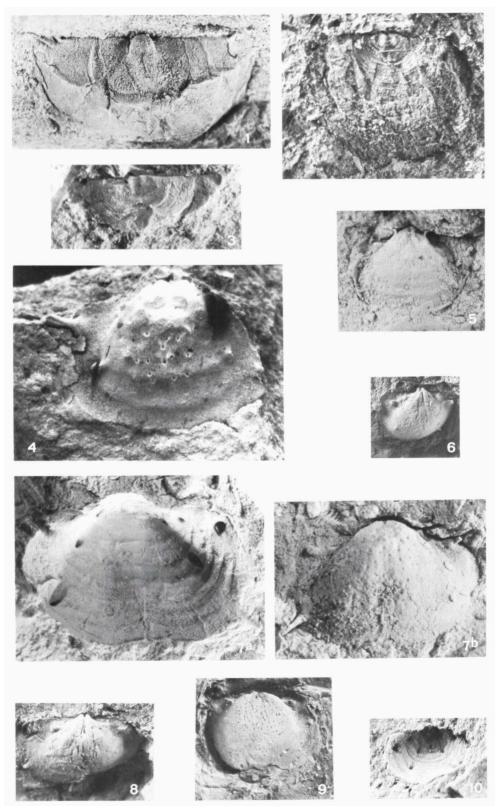
All specimens are from the same locality north of Meré, from the Namurian Meré beds; they were coated with ammonium chloride, unless otherwise stated.

- Figs. 1-10. Tornquistia scutiformis sp. nov.
- Fig. 1. External mould of a pedicle valve, RGM 143 696, x 20, uncoated.
- Fig. 2. Internal mould of both valves spread open, RGM 143 653, x 15, uncoated.
- Fig. 3. External mould of a pedicle valve, RGM 143 701, x 20, uncoated.
- Fig. 4. External mould of a brachial valve, RGM 143 704, x 9.5.
- Fig. 5. External mould of a brachial valve, RGM 143 697, x 10.
- Fig. 6. Internal mould of a pedicle valve, RGM 143 734, x 25.
- Fig. 7. Internal mould of a pedicle valve, RGM 143 708, x 13.
- Fig. 8. Internal mould of a juvenile brachial valve, RGM 130 053, x 25.
- Fig. 9. External mould of a juvenile brachial valve, RGM 143 698, x 25.
- Fig. 10. Internal mould of a brachial valve, holotype, RGM 143 706, x 25, uncoated.

All specimens are from the same locality north of Meré, from the Namurian Meré beds; they were all coated with ammonium chloride, except the one of fig. 4 which was gilded.

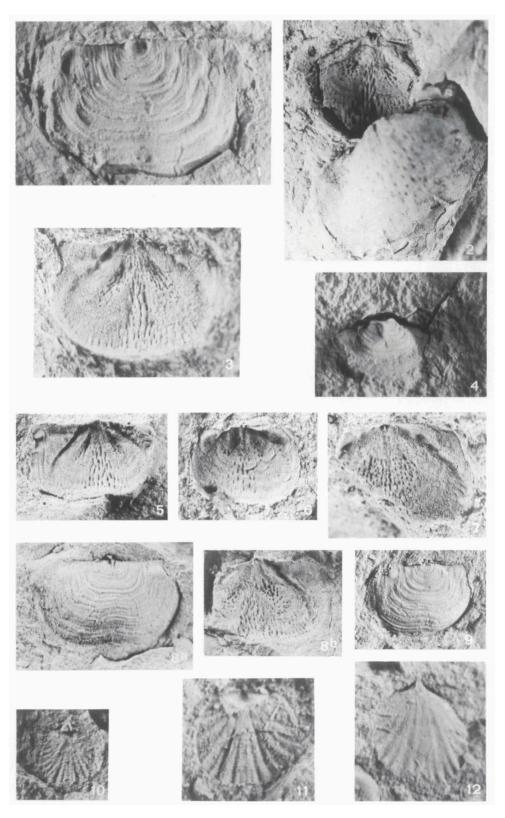
- Figs. 1-3. Productellinarum gen. & sp. nov.
- Fig. 1. Internal mould of a pedicle valve, RGM 143 756, x 3.2.
- Fig. 2. External mould of a brachial valve, RGM 143 759, x 10.
- Fig. 3. External mould of a brachial valve, RGM 143 735, x 11.5.
- Figs. 4-10. Aseptella asturica gen. & sp. nov.
- Fig. 4. Internal mould of a juvenile pedicle valve, RGM 143 723, x 20, S.E.M. radiograph.
- Fig. 5. Internal mould of a juvenile pedicle valve, RGM 143 671, x 12.
- Fig. 6. Internal mould of a pedicle valve, RGM 143 659, x 4.3.
- Fig. 7. Pedicle valve, RGM 143 741; a: external mould, x 8; b: internal mould, x 7.3.
- Fig. 8. Internal mould of a pedicle valve, RGM 143 728, x 5.6.
- Fig. 9. Internal mould of a pedicle valve showing the flange, RGM 143 662, x 4.
- Fig. 10. External mould of a pedicle valve, RGM 143 737, x 8.5.

Plate 8



- Figs. 1-9. Aseptella asturica gen. & sp. nov.
- Fig. 1. External mould of a brachial valve, RGM 143 732, x 11.
- Fig. 2. Fragmentary internal mould of the brachial valve and part of the external mould of the pedicle valve of a complete specimen, holotype, RGM 143736, x 6.3; in foreground part of the internal mould of another pedicle valve.
- Fig. 3. Internal mould of a brachial valve, RGM 143 742, x 6.9.
- Fig. 4. External mould of a juvenile brachial valve showing also some spines of the pedicle valve, RGM 143 744, x 10.
- Fig. 5. Internal mould of a brachial valve, RGM 143 738, x 5.
- Fig. 6. Internal mould of a juvenile brachial valve showing a short median ridge (exaggerated in the figure), RGM 143 663, x 6.6.
- Fig. 7. Internal mould of a brachial valve, RGM 143 756, x 5.6.
- Fig. 8. Brachial valve, RGM 143 720, x 5.1; a: external mould; b: internal mould.
- Fig. 9. External mould of a brachial valve, RGM 143 661, x 3.8.
- Figs. 10-12. Leiorhynchus? sp.
- Fig. 10. External mould of a brachial valve with the internal mould of the umbonal region of the pedicle valve, DPO 5045, x 7.5.
- Fig. 11. External mould of a brachial valve, DPO 5047, x 16.
- Fig. 12. Internal mould of a pedicle valve, DPO 5046, x 17.

Plate 9



All specimens are from the same locality north of Meré, from the Namurian Meré beds; they were coated with ammonium chloride, unless otherwise stated.

- Figs. 1-3. Camerisma sp.
- Fig. 1. Interior of the umbonal part of both valves, DPO 5054, x 3.6; a: internal mould; b: plasticine cast of the mould.
- Fig. 2. Internal mould of a brachial valve, RGM 143 661, x 4.7.
- Fig. 3. Pedicle valve, RGM 143 661; a: internal mould, x 4.3; b: external mould, x 4.
- Fig. 4. Ambocoeliidarum gen. & sp. nov. Brachial valve, DPO 5073, x 3.6; a: external mould; b: internal mould.
- Figs.5-8. Crurithyris cf. C. urii (Fleming, 1828)
- Fig. 5. Pedicle valve, DPO 5068, x 18; a: internal mould; b: external mould.
- Fig. 6. Internal mould of a brachial valve, DPO 5063, x 18.
- Fig. 7. External mould of a brachial valve, DPO 5071, x 7.5.
- Fig. 8. Internal mould of a brachial valve, DPO 11 182, x 11, uncoated.

Plate 10

- Figs. 1-6. Martinia aff. M. glabra (Sowerby, 1820)
- Fig. 1. Brachial valve, RGM 143 660, x 5; a: external mould; b: internal mould.
- Fig. 2. Internal mould of a brachial valve, DPO 5181, x 3.5.
- Fig. 3. Internal mould of a juvenile (?) brachial valve, DPO 11 187, x 5.6.
- Fig. 4. Internal mould of a pedicle valve, RGM 143 659, x 3.
- Fig. 5. Internal mould of a pedicle valve, DPO 5142, x 3.4.
- Fig. 6. Internal mould of an immature pedicle valve, DPO 11 188, x 5.

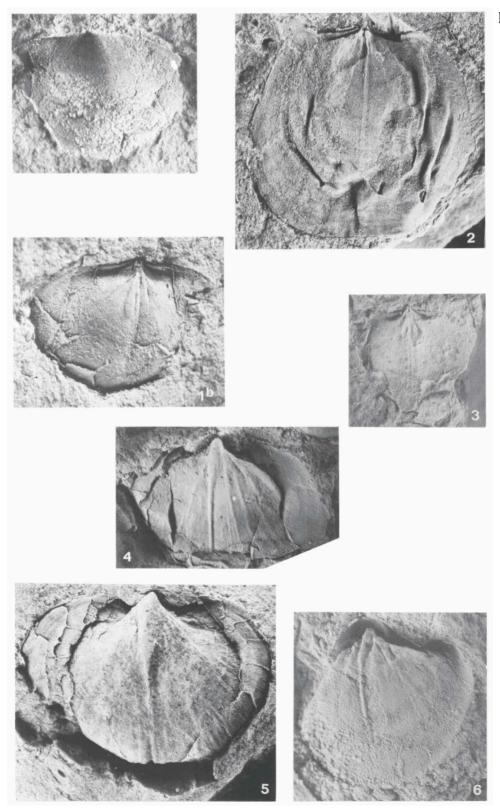
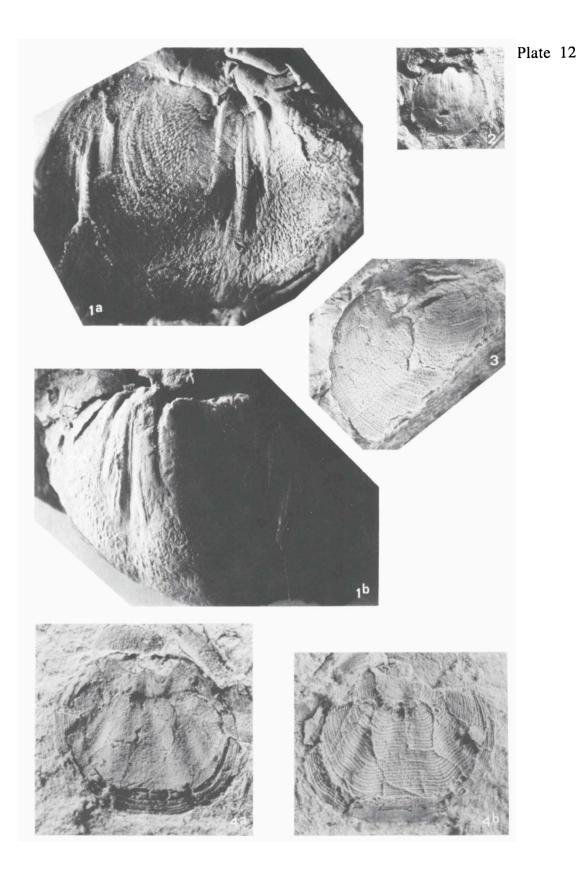


Plate 11

- Figs. 1-3. Kitakamithyris merensis sp. nov.
- Fig. 1. Interior of a pedicle valve, holotype, DPO 5075; a: plasticine cast of mould, x 3.8; b: mould, x 3.6.
- Fig. 2. Internal mould of a brachial valve, DPO 5076, x 3.5.
- Fig. 3. External mould of a pedicle valve, DPO 5077, x 3.
- Fig. 4. Plicotorynifer lamellosus sp. nov. Fragmentary brachial valve, DPO 11 342, x 9.5; a: internal mould; b: external mould.



- Figs. 1-10. Plicotorynifer lamellosus sp. nov.
- Fig. 1. External mould of a pedicle valve, holotype, DPO 5078, x 7.
- Fig. 2. Internal mould of a pedicle valve, DPO 11 183, x 7.
- Fig. 3. Internal mould of umbonal part of both valves, DPO 11 184, x 8.
- Fig. 4. Internal mould of an ephebic brachial valve, DPO 5116, x 6.5.
- Fig. 5. Internal mould of a juvenile brachial valve, RGM 143 694, x 10.
- Fig. 6. Internal mould of a juvenile brachial valve, DPO 11 185, x 8.5.
- Fig. 7. Internal mould of a juvenile brachial valve, DPO 11 343, x 10.
- Fig. 8. External mould of a juvenile brachial valve, DPO 11 186, x 8.5.
- Fig. 9. Internal mould of an immature brachial valve, RGM 143 666, x 15.
- Fig. 10. Neanic brachial valve; a: external mould, x 8.5; b: internal mould, x 9.

Plate 13

All specimens are from the same locality north of Meré, from the Namurian Meré beds; they were coated with ammonium chloride, unless otherwise stated.

- Figs. 1-5. Cranaenidarum gen. & sp. indet.
- Fig. 1. Pedicle valve, DPO 11 190, x 20, not whitened; a: internal mould; b: external mould.
- Fig. 2. Internal mould of a brachial valve, DPO 11 191, x 20.
- Fig. 3. Same specimen as fig. 1; a: internal mould, x 14; b: external mould, x 13.
- Fig. 4. Brachial valve, DPO 11 192, x 9.5; a: internal mould; b: external mould.
- Fig. 5. Internal mould of a pedicle valve, DPO 11 193, x 10.5.
- Fig. 6. Caenanoplia martinezi sp. nov. Internal mould of a brachial valve with productid spat attached (internal mould of a brachial valve and spines of the pedicle valve: Aseptella asturica gen. & sp. nov.); RGM 143 624, x 10.

Plate 14

